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Research Article

Whole-seedling trait adjustments of mountain birch under contrasting environmental conditions

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Warming temperatures can promote arctic tree seedling establishment and growth, but these effects depend on the environmental context and the seedlings' capacity to acquire limiting resources. Here, we tested how temperature, soil properties, and the presence of a neighbouring shrub influence seedling growth rates. We further explored how the environment-induced shifts in growth rates are related to traits associated with resource acquisition strategy. Seedlings of mountain birch *Betula pubescens* subsp. *czerepanovii* were grown in a growth chamber experiment with a fully factorial design manipulating temperature (ambient, warm), soil origin (low elevation, high elevation), and the presence or absence of a common neighbour, crowberry *Empetrum nigrum* subsp. *hermaphroditum*. Growth rate, carbon dioxide (CO_2) assimilation rates, ectomycorrhizal fungal colonisation, and above- and belowground functional traits that are linked to resource acquisition strategies, were measured for the mountain birch seedlings. Warming significantly increased seedling growth, and growth rates were positively associated with several above- and belowground traits associated with resource acquisition. Surprisingly, growth rates were not correlated with leaf traits such as specific leaf area and leaf dry matter content. Soil origin and the presence of *Empetrum* did not affect the growth rate responses to warming, although seedlings grown in high-elevation soils generally grew faster and had higher CO_2 assimilation rates. These seedlings also expressed traits, commonly associated with conservative growth strategy. Our results highlight that both above- and belowground plant traits adjust differently to warming as part of their growth response. While seedling functional traits can be highly plastic in response to changes in temperature and soil conditions, they are not always coupled with changes in seedling growth rates. This is likely because birch seedlings adopt different growth-promoting strategies under different environmental conditions.

Key words: Betula pubescens subsp. czerepanovii, CO_2 assimilation rate, Empetrum nigrum subsp. hermaphroditum, functional traits, growth rate, warming

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Introduction

At higher latitudes and altitudes, tree seedling establishment and growth is generally facilitated by warmer temperatures (Kullman 1979, Danby and Hik 2007, Truong et al. 2007, Sundqvist et al. 2008, Cannone and Malfasi 2024). In these temperature-limited regions, forests have been undergoing changes for decades, including large increases of tree biomass (Tømmervik et al. 2009), or expanding forest area (Kullman 2002, Tømmervik et al. 2004, Hagedorn et al. 2014), causing substantial changes in northern ecosystem structure and functions (Holtmeier 2009, Lavorel and Garnier 2002, Pearson et al. 2013). Successful tree seedling establishment and early seedling survival (reviewed by Holtmeier and Broll 2007) are related to seedling growth rates (Walters and Reich 1996, Limpens et al. 2014), with clear advantages for seedlings that reach a larger size at the end of the first growing season (Kullman 1984, 1986). While warming temperatures can promote seedling growth, favourable environmental conditions are also required for seedlings to persist and thrive (Callaway et al. 2003). At local scales, early tree seedling performance depends on synergies among multiple factors (Kullman 2003, Moen et al. 2008, Lett and Dorrepaal 2018), including the availability of belowground resources (Weih and Karlsson 1999a, Myers-Smith et al. 2015) and a variety of biotic interactions (Van Bogaert et al. 2011), such as herbivory (Lehtonen and Heikkinen 1995, Wielgolaski et al. 2005, Munier et al. 2010) or presence of neighbours (Dullinger et al. 2003, Kambo and Danby 2018, Marsman et al. 2020).

Due to variation in local-scale topography and elevation, soil properties including nutrient availability and cycling, and microbial community composition can vary over small spatial scales (Frangi et al. 2005, Björk et al. 2007, Bahram et al. 2012). Since high latitude and mountain ecosystems are strongly nutrient limited, this variation in environmental conditions has important implications for tree seedling establishment and growth (Hobbie and Chapin III 1998a). For example, pockets of increased nutrient availability tends to support more fertile vegetation types (Hobbie and Chapin III 1998a) and strongly stimulates tree growth (Sveinbjornsson et al. 1992, Weih and Karlsson 1999b). Furthermore, seedling interactions with soil microbes, such as mycorrhizal fungi which are known to be important for facilitating seedling growth and survival in infertile soils (Nara and Hogetsu 2004, Hewitt et al. 2017), have been found to change from negative to positive with increasing elevation (Wagg et al. 2011). As environmental conditions become more favourable, interactions among neighbouring plants often change from more positive towards more negative (Callaway 1998, Callaway et al. 2002, Klanderud and Totland 2005). Hence, while plant seedling survival in subarctic systems is generally promoted by warmer temperatures, the presence of neighbours can significantly lower this positive effect (Hobbie and Chapin III 1998a, Dormann et al. 2004, Okano and Bret-Harte 2015, Tingstad et al. 2015, Klanderud et al. 2021), especially for fast-growing species (Dahle et al. 2024). Furthermore, warming can amplify competitive dynamics when coupled with increased nutrient availability (Dormann et al. 2004, Klanderud and Totland 2005). Accounting for the role of soil properties and neighbouring plants is therefore important when studying early tree seedling growth and survival in warming high altitude and latitude ecosystems.

During early establishment, there is a trade-off between survival and rapid resource acquisition for fast growth in tree seedlings (Weih and Karlsson 1999a). Within the 'whole-plant economics spectrum' framework, rapid acquisition and processing of resources could be an advantage only when coordinated across leaves, stems, and roots (Reich 2014). While the whole-plant economic spectrum generally describes how traits reflect tradeoffs in life-history strategies among species and across scales (Freschet et al. 2010, Reich 2014), this spectrum can also occur within a species (i.e. intraspecific variation). Such intraspecific trait variation can significantly contribute to community trait variation (Siefert et al. 2015). Tree seedlings, even within the first growing season, can have functional traits that are associated with a more rapid acquisition of essential resources both above- and belowground, and these early traits can increase seedling chances for survival to the next growing season (Weih and Karlsson 1999a, 1999b, Jiang et al. 2022, Xu et al. 2023). For example, in temperate forests, higher tree seedling survival is associated with higher specific leaf area and root length (Xu et al. 2023), or higher total leaf area, even within the same species (Jiang et al. 2022). Similarly, alpine meadow species with more acquisitive traits have been found to benefit from increased temperatures if released from plant competition (Dahle et al. 2024). Further, an increase in carbon uptake, by investing in aboveground photosynthetic organs, can increase plant performance under some conditions (Jiang et al. 2022). However, these trait investments can be accompanied by whole-plant phenotype responses, such as increased root to shoot ratios, in nutrient-limited subarctic ecosystems (Ingestad and Lund 1979, Zurbriggen et al. 2013). There have been numerous studies exploring how plant traits that are linked to resource acquisition strategies respond to warmer temperatures (Hudson et al. 2011, Sundqvist et al. 2011a, Bjorkman et al. 2018, Spitzer et al. 2023), soil properties (Baddeley et al. 1994, Prager et al. 2020), and the presence of neighbours (Nilsson et al. 1993, Shevtsova et al. 1997, Britton et al. 2021). However, the interactive effects of these factors on tree seedling traits are less explored.

Tree growth rates in cold environments are not necessarily limited by carbon uptake via photosynthesis (Hoch and Körner 2009, Körner 2013, 2015). Rather than being limited by carbon uptake, plant productivity responses to temperature are commonly constrained by the availability of other resources such as soil nutrient or water availability (Hobbie and Chapin III 1998b, Dormann and Woodin 2002). On the other hand, increased photosynthetic rates can be directly linked to increasing temperatures (Reich et al. 2018). As a result, plants may produce a carbon surplus that cannot be used for growth. The surplus carbon produced under warmer

temperatures can either be stored as carbon reserves in the form of non-structural carbohydrates and used under less favourable conditions, or exuded by roots to support mycorrhizal fungi or other soil organisms, potentially increasing plant nitrogen supply (Körner 2003, Prescott 2022). Plants forming ectomycorrhizal symbioses are often characterized by more conservative traits, for example they tend to conserve nitrogen use (Averill et al. 2019). In high latitude ecosystems, where nitrogen uptake and seedling establishment is commonly linked to the functioning of ectomycorrhizal symbiosis (Hewitt et al. 2017), mountain birch *Betula pubescens* subsp. *czerepanovii*, may invest more carbon in ectomycorrhiza at higher elevations, where nitrogen is typically more limited (Ruotsalainen et al. 2009). However, the effects of temperature and other environmental factors on early seedling investments into fine roots versus mycorrhizal symbionts is less known.

We studied seedling growth and functional traits of mountain birch, a species that forms treeline in north-western Scandes. While the mountain birch forest has been observed to advance uphill in many locations (Rundqvist et al. 2011, Callaghan et al. 2013, Kullman 2021) and its seedlings can establish above the treeline (Truong et al. 2007), the seedlings' performance and survival is largely dependent on microclimatic conditions (Weih and Karlsson 1999a, Truong et al. 2007, Sundqvist et al. 2008). To shed more light on increasing success of this species in the Scandes, we explored how the growth rate of mountain birch seedlings responds to increased temperature, different soil conditions and the presence of its common neighbour, *Empetrum nigrum* subsp. *hermaphroditum* (hereafter, *Empetrum*). We also explored how the response of seedlings is associated with above- and belowground plant functional traits linked to resource-use strategy (shoot height, root/shoot ratio, total leaf area, specific leaf area, leaf dry matter content, N content per leaf area, C/N ratio in leaves, stems and roots, root/shoot ratio, fine root proportion in the root system, main root length), including CO_2 assimilation rate and investment in mycorrhiza. We grew mountain birch seedlings in a controlled environment where the effect of temperature, soil properties in birch stands from two different elevations, and the presence of *Empetrum,* were assessed in a fully factorial design. We hypothesized that 1) seedling growth rates would be highest under warmer temperatures and that soil originating from lower elevation (i.e. from warmer climate) would be more fertile and therefore stimulate higher seedling growth, but that the positive effects of warming and soil fertility would be negatively influenced by competition of an *Empetrum* individual. Furthermore, we hypothesised that 2) high growth rates of mountain birch seedlings would be strongly related to above- and belowground plant functional traits commonly related to a more resource acquisitive plant growth strategy. By testing these hypotheses we aim to advance understanding of how warming interacts with other environmental conditions in high latitude ecosystems to influence early tree seedling growth and functional traits.

Methods

Soil and plant material sampling

The plant and soil material used in this study was collected in Abisko, northern Sweden (68°21'15.97"N, 18°48'54.94"E). The climate in the area is subarctic with average annual temperature of 0.6°C and average temperature in July of 12°C (data from Abisko Scientific Research Station, 392 m a.s.l., for years 2019–2021), with a minimum annual precipitation of about 300–400 mm in the sheltered Abisko valley.

Over 14–16 September 2021 we collected mountain birch seeds and live *Empetrum* plants in the mountain birch forest immediately surrounding the Abisko Scientific Research Station (385 m) within an area of approx. 2 ha. Mountain birch seeds were collected from a random selection of 12 trees, by harvesting from branches that could be reached from the ground, and thereafter seeds were dried at room temperature. We collected intact *Empetrum* clones (including belowground stems, coarse and fine roots, soil and other species surrounding them) by excavating monoliths from six randomly selected *Empetrum*-dominated patches (size 0.5 × 0.7 m, including the humus layer down to a soil depth of 15–18 cm) that were at least 30 m apart within the forest. This random selection was based on first hiking through the forest to identify areas where *Empetrum* was dominant, and then randomly harvesting from six of those locations. Each sampled patch was placed in a plastic box of the same size, transported to Umeå, Sweden (63°49′13.638″N, 20°18′52.47684″E) and stored outside under ambient conditions in a common garden until further processing.

During the same time as seed and *Empetrum* clone sampling (over 14–16 September 2021), we sampled Mountain birch forest soil at a high (470 m) and a low (370 m) elevation along a north-facing slope in Abisko, with both elevations situated approximately 9 km north-west of Abisko Scientific Research station in order to avoid any home field advantage associated with proximity between soil and seed sources. Further, the populations of mountain birch are not genetically differentiated along elevational gradients in this region (Truong et al. 2007), but our results should be interpreted as phenotypic responses of mountain birch seedlings with a seed origin from low elevation trees in the region. At both elevations, sampling took place in closed mountain birch forest, within an area of approximately 3500 m^2, with phyllite as the underlying bedrock and understory heath vegetation dominated by *Empetrum*, with species such as *Linnaea borealis* and the ericaceous dwarf shrubs *Vaccinium myrtillus* and *Vaccinium vitis-idaea* also present. The soil was immediately transported to the laboratory where it was stored at +5°C until further processing.

Plant and soil preparation

Mountain birch seeds were germinated on sterilized sand following two weeks of cold stratification (+5°C), after which the seedlings were left to grow for 60 days. Two weeks prior to experimental setup, *Empetrum* clones were allowed to

acclimate from the winter conditions in the outdoor common garden in a greenhouse at 10°C.

The soil sampled at each elevation was mixed and homogenized by hand and stones and coarse roots were removed. Three subsamples per soil type were stored at +5°C until further analysis of initial soil properties (pH, soil organic matter content, concentration of mineral N (NH_4^+, NO_3^-) and phosphorus (PO_4^{3-}), total C and N content). Soil pH was measured by SevenCompact S210 device (Mettler Toledo) in water solution (41 ml of deionized water were added to 5 g of fresh soil, shook overnight at 40 rpm, Sundqvist et al. 2011b). Soil organic matter content was determined by loss on ignition (LOI) using the soil dry weight (soil dried at 105°C to constant weight) and soil weight after burning at 550°C in a Muffle furnace for 4 h. The concentrations of mineral N and P were determined by spectrophotometer analysis on different wavelengths (Analyzer 3 Spectrophotometer, Omniprocess) at SLU laboratory in KCl extract (80 ml of 1M KCl solution was added to approximately 5 g of fresh soil, shaken at 150 rpm for 2 h, filtered through Munktel filter paper no. 3). For determination of total C and N, soil samples were air-dried, ground on a ball mill and analysed using elemental analyzer and isotope ratio mass spectrometer (EA-IRMS) (Werner et al. 1999).

Experimental setup

On 14–18 February 2022, we set up the growth chamber experiment. First, seedlings were individually removed from the sand bed and their roots were rinsed with deionized water, gently dried with a paper tissue and weighed to obtain fresh weight of each seedling. One individual birch seedling was thereafter planted in a pot (7 × 7 × 7 cm) filled with soil from either the high or the low elevation. In addition, for half of the pots of each soil type, one randomly selected *Empetrum* individual (with belowground stem and root length of approx. 18 cm) from each of the six clones, was planted together with the mountain birch seedling following the planting method in Hupperts et al. (2023) for *Empetrum*. In total, the experiment consisted of 216 pots comprising eight treatment combinations: 2 different temperatures (ambient versus warm, +4°C) × 2 soil origins (low versus high elevation) × 2 neighbour treatments (no neighbour versus *Empetrum* present). Each treatment combination had 9 replicates, each comprising 3 sub-replicates. The 'ambient' temperature treatment was based on field temperature measurements in Abisko (De Long et al. 2015) and the 'warm' treatment was based on predicted summer temperature increase over 2071–2100 for this region (SMHI 2024) (see more details on climate chamber settings below). The sub-replicates were used to ensure sufficient plant biomass was produced per replicate for plant tissue analysis, and thus were pooled into final replicates (n = 9) for statistical analyses. For each temperature treatment, one replicate (i.e. a group of three sub-replicates) per soil origin and neighbour treatment was assigned to each of nine blocks. We placed one block at a time into each of the two growth chambers, to ensure the same treatment time for all blocks over the course of the experiment.

Concurrent with experimental setup, we measured total mountain birch seedling fresh weight for all seedlings that were subsequently planted (potted) into the experiment. We also measured total fresh weight and percentage of mycorrhizal colonization on 28 additional mountain birch seedlings from the same batch as the potted seedlings. The proportion of roots colonized by mycorrhizal fungi was estimated by counting the total number of fine roots, and the total number of ectomycorrhizal (EM) colonized root tips on each of the 28 birch seedlings under a dissecting microscope (Wild M400 Photomacroscope; 32× magnification). A root tip was considered colonized if it appeared swollen, opaque, and free of root hairs (Karst et al. 2021). The average colonization rate was 6.6 % (SD = 6.1). Following fresh weight measurements, the 28 additional birch seedlings were dried at 105°C until constant mass, and weighed. We used these measurements to estimate the initial dry weight of the potted seedlings in the experiment. In the same way, we measured fresh weight of all planted individuals of *Empetrum*, and fresh and dry weight of 17 more individuals of the same batch as the potted ones, in order to estimate the initial dry weight of the potted *Empetrum*.

Immediately after potting, half of the pots for each treatment were placed in a climate chamber with the temperature set to 20°C/15°C (day/night) corresponding to the 'warm' chamber treatment and the other half in a chamber set to 16°C/11°C (day/night; the 'ambient' chamber treatments (e.g. nine blocks per growth chamber). The 'ambient' setting is based on field temperature measurements at the study site in Abisko (mean maximum temperature in July at 450 m a.s.l.) (De Long et al. 2015). The 'warm' treatment of 4°C above the 'ambient' temperature falls within the range of predicted summer temperature increase (years 2071–2100) in northern Sweden (1.5–5.5°C above current temperatures, depending on RCP model scenario) (SMHI 2024). All chambers were set to 75% relative air humidity, with a 18 h day (light: 450 µmol m^{-2} s^{-1}), and 6 h night (light: 50 µmol m^{-2} s^{-1}) cycle, with one hour of transition period between the two light periods. We used a shade cloth to cover all pots for the first week in their respective growth chamber, to allow plants to acclimatize to growth chamber light conditions. Pots were watered as needed throughout the experiment to ensure sufficient water supply. Every third week throughout the experiment, all pots in each growth chamber were rotated to a new chamber (with the same climate setting) out of a total of four existing chambers.

Traits and biomass measurements

On 27 April–2 May 2022 (10 weeks after the experiment setup), immediately prior the harvest, we assessed treatments effects on photosynthesis of the mountain birch seedlings by measuring CO_2 assimilation rate on seven randomly chosen seedlings (sub-replicates) per treatment (temperature-soil origin-competition) using LiCor 6800 gas-exchange system (Li-Cor Biosciences). Due to the small size of the seedlings, multiple leaves were inserted into the 3 × 3 cm leaf cuvette, arranged not to have leaves shading each other. The CO_2

concentration was set to 500 ppm, to match the CO_2 concentration in the growth chambers. Relative humidity was maintained around 50%, and flow rate was 600 μmol s^{-1}. All measurements were done at a light intensity matching the conditions in the growth chambers (450 μmol m^{-2} s^{-1}). Mountain birch seedlings were measured at their ambient growth temperatures (i.e. at 16°C or 20°C). The measured leaves were marked, and their area was measured in connection with the harvest of the experiment.

On 16 May 2022, 12 weeks after the experiment setup, we initiated harvest of all pots, and measured the following mountain birch traits: shoot height, total leaf area, specific leaf area (SLA), leaf dry matter content (LDMC), N content per leaf area, C/N ratio in leaves, stems and roots, root/shoot ratio, fine root proportion in the root system, main root length, and visually estimated percentage of mycorrhizal colonisation (for overview of traits measured see the Supporting information).

For each pot, we first recorded seedling shoot height by measuring the vertical distance between soil surface and the highest branch tip. Mountain birch seedlings were then carefully taken out from the pots and the roots were washed with deionized water to remove any soil particles. We measured the length of the main root on each individual seedling, after which the roots, stem and leaves were clipped and separated. All leaves were immediately scanned (300 dpi resolution) and weighed (fresh weight). For two randomly chosen sub-replicate root samples per pot, the roots were separated by coarse (> 0.5 mm) and fine roots (≤ 0.5 mm), after which they were dried at 40°C to a constant weight and weighed. The remaining root system from each of three sub-replicate pots per replicate was stored in 50% ethanol for further estimation of percentage of mycorrhizal colonisation.

We obtained total leaf area from the leaf scans, using the ImageJ software (Schneider et al. 2012), and calculated SLA by dividing the leaf area (cm^2) by leaf dry weight (g) for each seedling. LDMC was calculated by dividing the leaf dry weight (g) by the leaf fresh weight (g). To obtain C/N ratios in leaves, stems and roots, the dried samples for these tissues were ground on a ball mill and analysed for C and N content using elemental analyzer and isotope ratio mass spectrometer (EA-IRMS) (Werner et al. 1999). To obtain belowground traits, we calculated fine root proportion (≤ 0.5 mm) as the percentage of fine root biomass of the total root biomass. Proportion of root tips that were colonized by mycorrhizal fungi were visually estimated under a macroscope at 50 grid-root intersects following Karst et al. (2021). The percent of colonised seedling root tips was very low prior to the start of the experiment; we therefore considered the percentage of root tips at the end of the experiment as the mycorrhizal colonisation rate.

We calculated the seedling growth rates as percentage dry weight gain over the course of the experiment. To calculate initial dry mass for each seedling at the start of the experiment, we used the initial fresh weight for each seedling at the time of potting, and the allometric equation based on fresh and dry weight for the additional 28 seedlings measured at the time of experimental setup (Supporting information).

Statistical analyses

For all measured variables in our dataset, each replicate represents the mean of respective sub-replicates (when available, see the Supporting information). Therefore, the final dataset consisted of 72 experimental units (9 replicates in each of the 8 treatment levels). Prior to analyses, the dataset including all sub-replicates was checked to meet the assumptions of normality and homoscedasticity across treatments for each of the variables (Zuur et al. 2010), and three data points (out of 216 in total) of growth rate were excluded as statistical outliers based on the interquartile range criterion (i.e. three out of 72 growth rate values in our dataset are calculated as a mean of two rather than three sub-replicates). Further, we tested if the variation in *Empetrum* size co-varied with final birch seedling trait values: on a subset of replicates under the 'neighbour presence' treatment, we performed redundancy analysis (RDA) with *Empetrum* initial dry weight as explanatory and the growth-related and photosynthetic birch seedling traits as dependent variables. Since there was no significant relationship ($p \geq 0.42$), we use the neighbour treatment as a binary (presence/absence) explanatory variable in all further analyses.

To test how the mountain birch functional traits (stem height, total leaf area, SLA, LDMC, N per leaf area, leaf C/N, stem C/N, root C/N, root/shoot ratio, root length, fine root proportion) are affected by the experimental treatments, we performed permutational analysis of variance (PERMANOVA) with 9999 permutations using Euclidean distances based on scaled functional trait matrices, with an interaction of the experimental treatments (temperature × soil origin × neighbour) as explanatory variables (*adonis* function in R package 'vegan', Oksanen et al. 2020). The similarities between birch seedlings in their traits were visualized using nonmetric multidimensional scaling (NMDS) in R package 'vegan'.

Using ANOVA, we tested how seedling CO_2 assimilation rate, mycorrhizal colonisation, growth rate and individual traits were influenced by the main and interactive effects of the experimental treatments. To assess the relationship between seedling growth rate and carbon and nutrient acquisition, as well as functional traits, we correlated the growth rate to 1) CO_2 assimilation rate and 2) mycorrhizal colonisation.

Results

Compared to soil from the high elevation, the soil from the low elevation was characterized by lower pH, higher organic matter content, higher total N, C, plant-available phosphorus concentrations, and higher C/N ratio, while it had lower levels of mineral N than soil from the high elevation (Supporting information).

The growth rates of mountain birch seedlings were 162% higher in the warm compared to the ambient temperature treatment (Fig. 1, Supporting information). Growth rates and CO_2 assimilation rates were both 39% higher in soil from the high compared to the low elevation. While there was a tendency for mycorrhizal colonisation to be higher in the warm

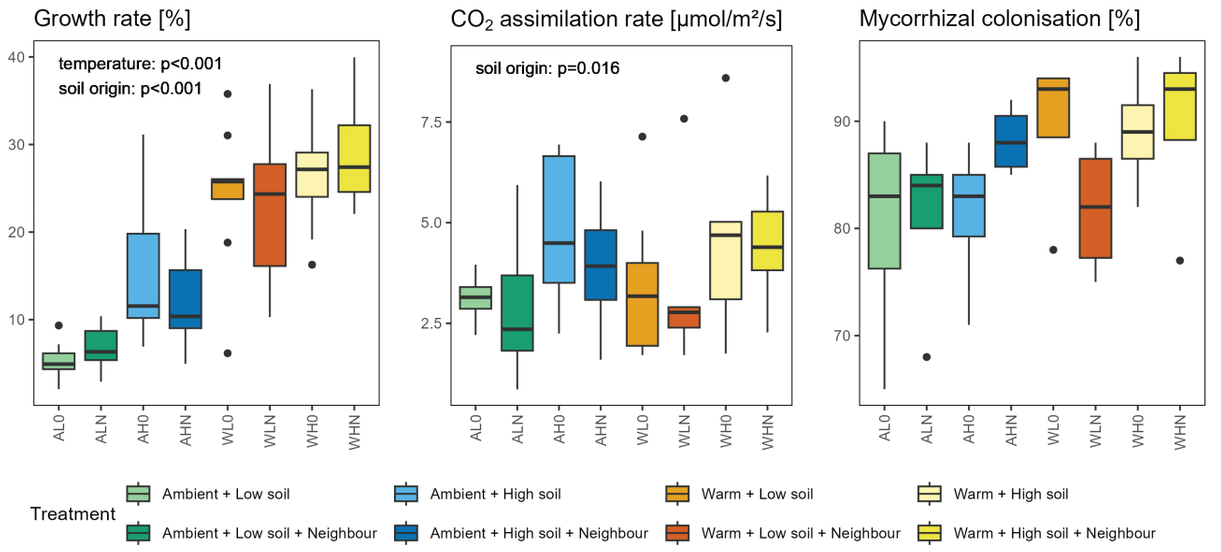


Figure 1. Mountain birch seedling growth rate, CO_2 assimilation rate and mycorrhizal colonisation rate (%) in a growth chamber experiment including three treatments: temperature (ambient versus warm), soil origin (high versus low elevation soil) and presence or absence of *Empetrum* as a neighbour. The data is displayed as boxplots; the colour coding of the individual treatments is shown in the legend. The main and interactive effects of the treatments were analysed by ANOVA (see the Supporting information), and whenever significant effects of the treatments occurred the p-values are included in the figure.

compared to the ambient temperature treatment this was not statistically significant ($p = 0.088$; Fig. 1, Supporting information) and soil origin had no significant effect on mycorrhizal colonisation ($p = 0.16$; Supporting information). The presence of *Empetrum* as a neighbour, and the interactions among treatments, did not affect seedling growth rates, nor did they affect CO_2 assimilation rates or the % root tips colonized by mycorrhizal fungi (Fig. 1, Supporting information).

Mountain birch seedlings grown in the warmer temperature treatment had overall taller shoots, longer roots, larger total leaf area, less N per leaf area, higher C/N ratio in stems and roots ($p \leq 0.031$; Fig. 2, Supporting information), and they had a tendency for higher SLA compared to seedlings grown in the ambient temperature ($p = 0.056$). Seedlings grown in soil from the high elevation had longer roots, higher LDMC, and a higher root C/N ratio ($p \leq 0.024$; Fig. 2, Supporting information). They also tended to have higher root/shoot ratios, and higher leaf and stem C/N ratios, but these trends were not statistically significant (Fig. 2, Supporting information). There was a significant interactive effect of temperature and soil origin on total leaf area, which was higher in the warm than in the ambient temperature treatment, and higher in low- than in high-elevation soils in the warm treatment, but unaffected by soil origin in the ambient treatment (Fig. 2, Supporting information). There was a tendency for temperature, soil origin and presence of *Empetrum* as a neighbour to interact to affect fine root proportion but this effect was not statistically significant (Fig. 2, Supporting information).

Seedling above- and belowground functional traits were significantly affected by the interactive effect of temperature and soil origin (PERMANOVA, $p = 0.041$; $R^2 = 0.03$; Fig. 3, Supporting information), but not by the main or interactive effect of the neighbour treatment ($p > 0.39$; Supporting information). The first NMDS axis was mostly separated by fine root proportion, total leaf area, root length, and C/N ratios in leaves, stems and roots. Specifically, the proportion of fine roots was positively related to the axis scores and associated with the ambient temperature treatment. Total leaf area, root length, and C/N ratios in leaves, stems and roots were instead negatively related to the axis scores and associated with the warmer temperature treatment, and hence with seedling growth rates and percent root tips colonized by mycorrhizal fungi (Fig. 3, Supporting information). Axis 2 was largely linked to stem height and leaf traits: LDMC, C/N ratios in leaves, N content per unit leaf area, and was associated with CO_2 assimilation rates (Fig. 3, Supporting information). Pearson's correlations further show that mountain birch seedling growth rates were positively correlated to mycorrhizal colonisation ($r = 0.509$, $p = 0.003$, $df = 30$), and not correlated with the CO_2 assimilation rate ($r = -0.0001$, $p = 0.99$, $df = 50$).

Discussion

In line with our first hypothesis, and unsurpingly, the growth rates of mountain birch seedlings were positively influenced by warmer temperatures, but contrary to expectation, the seedlings grew faster in soils originating from higher elevation (i.e. treeline) than lower elevation forest. At the same time, the presence of a common neighbour (*Empetrum*) had no

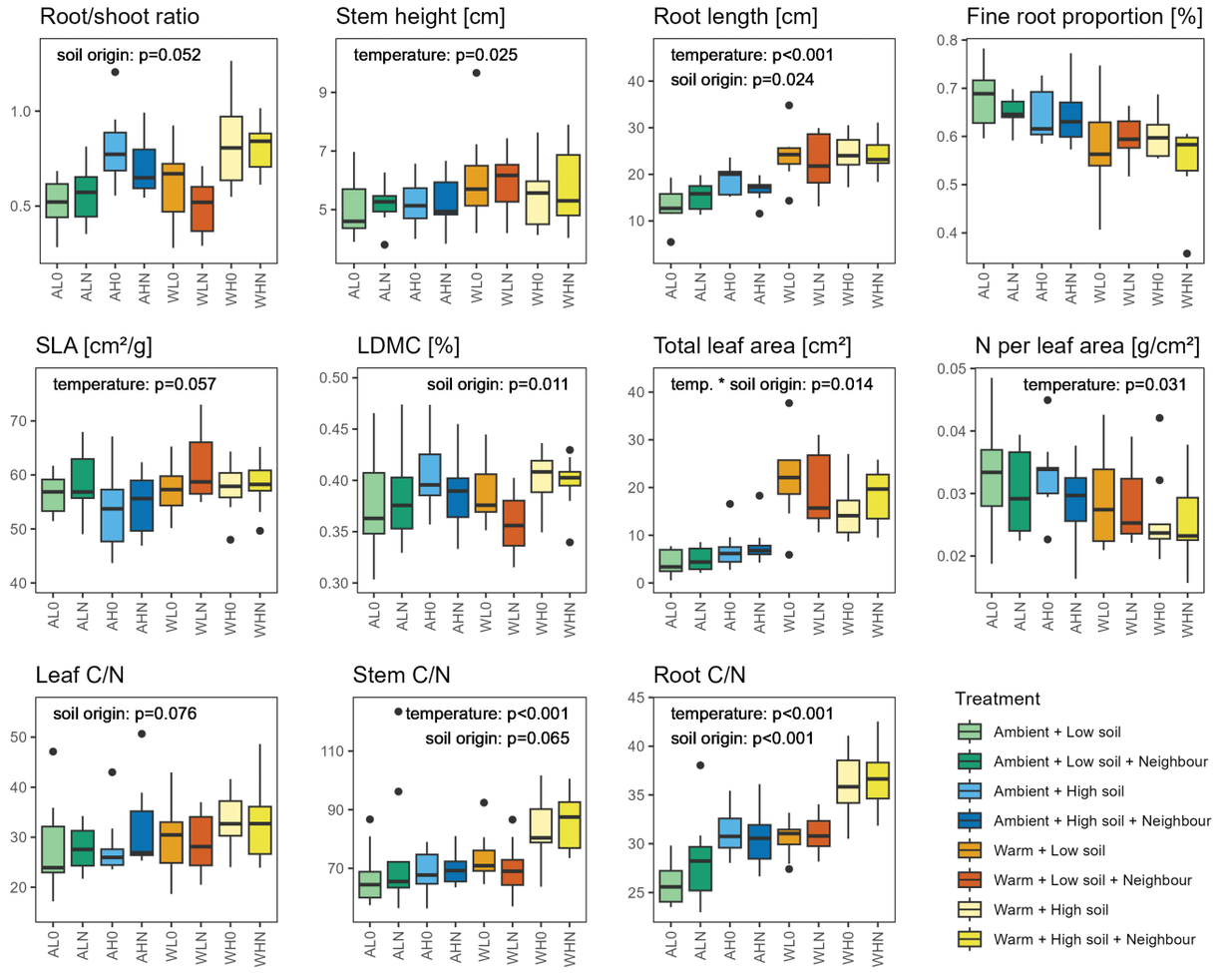


Figure 2. Mountain birch seedling functional traits in a growth chamber experiment including three treatments: temperature (ambient versus warm), soil origin (high- versus low-elevation soil) and presence or absence of *Empetrum* as a neighbour. The data is displayed as boxplots; the colour coding of the individual treatments is shown in the legend. The main and interactive effects of the treatments were analysed by ANOVA (Supporting information), and whenever significant effects of the treatments occurred the p-values are included in the figure.

effect on the seedling growth rates which is in contradiction to our first hypothesis. Further, we found mixed support for our second hypothesis that mountain birch seedling growth rates are positively related to traits associated with a resource acquisitive strategy, but our results also show that in certain environmental conditions, faster growth rates were associated with traits related to a more conservative strategy.

Tree seedling establishment and growth are often limited by temperature in sub-arctic regions (Körner 1998, Clemmensen and Michelsen 2006, Way and Oren 2010, Cannone and Malfasi 2024), with higher growth rate increasing seedling chances for survival (Walters and Reich 1996, Limpens et al. 2014) due to their larger size at the end of the growing season (Kullman 1984, 1986). Several natural gradient and experimental studies have shown that growth rates respond positively to warming (Haukioja et al. 1985, Hoch and Körner 2009, Hudson et al. 2011, Zurbriggen et al. 2013). Our results similarly indicate that mountain birch seedlings have a significantly higher growth rate with a 4°C temperature rise. We found that the birch seedlings grew better in high-elevation soil than in low-elevation soil. This is partially contradicting our first hypothesis that the seedlings would reach higher growth rates in the low-elevation soil which had higher nitrogen content. However, the soil analyses showed that the high-elevation soil, despite having lower total nitrogen content, had higher mineral N concentrations, which usually correlates with greater growth rates (Weih and Karlsson 1999a, Zurbriggen et al. 2013). High-elevation soils also had higher pH that is usually linked to higher availability of other nutrients such as calcium and magnesium cations, which may improve plant performance (Han et al. 2011, Maire et al. 2015, Wang et al. 2018). Furthermore, the two

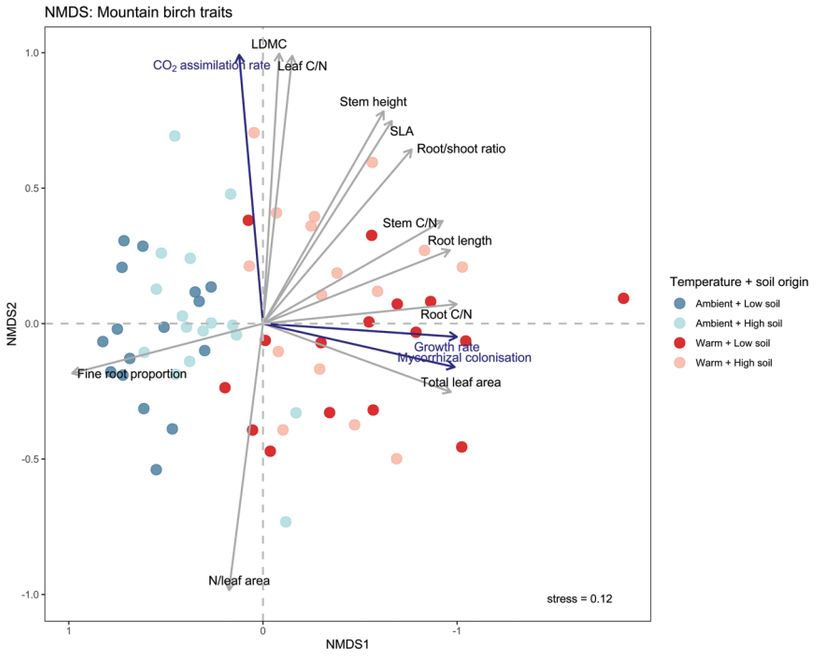


Figure 3. Mountain birch seedling traits as influenced by an interaction temperature × soil origin ($p = 0.041$, PERMANOVA, Supporting information). NMDS was calculated on Euclidean dissimilarities based on scaled mountain birch seedling trait values. The dots represent seedling individuals belonging to the temperature/soil origin treatments, neighbour treatment is not distinguished. Grey arrows represent traits used for NMDS construction, blue arrows are variables that were not used to construct the NMDS axes but were projected onto the ordination as environmental variables.

soils, developed under different environmental conditions, may have differed in microbial community composition, which can impact seedling performance both directly and indirectly (Deslippe et al. 2011, Wagg et al. 2011, Bennett and Classen 2020, Delgado-Baquerizo et al. 2020), although there we did not see a difference in the rate of mycorrhizal colonisation. Regardless of the underlying mechanisms, the effect of soil origin on the seedling growth rates was smaller than the effect of temperature, suggesting that climatic conditions are likely the main limiting factor of mountain birch seedling establishment.

We found no evidence that the presence of the neighbour *Empetrum* hampered seedling growth, which is in contrast with our hypothesis and with other literature reporting negative effects of competitors on tree seedling growth (Hobbie and Chapin III 1998a, Weih and Karlsson 1999a, Dormann et al. 2004, Okano and Bret-Harte 2015, Tingstad et al. 2015, Klanderud et al. 2021). Generally, there are three hypothetical pathways of potential neighbour effects of *Empetrum* on mountain birch seedlings: aboveground competition, belowground competition and indirect effects via allelopathic litter. While mountain birch seedlings have been shown to perform worse when experimentally shaded (Weih and Karlsson 1999a), they would need to grow within a large *Empetrum* individual to experience shading since this species is rather slow growing and not a typical strong aboveground competitor. However, we expected belowground competition to take place in our experiment as the pots were relatively small and mountain birch seedlings and *Empetrum* roots would therefore very likely interact. Nevertheless, our results did not confirm any such competition effects. Weih and Karlsson (1999a) have previously shown that mountain birch seedlings are negatively affected by allelopathy caused by *Empetrum*. The allelopathic compounds can be released from both *Empetrum* leaves and litter and as such can persist in soils as a legacy (González et al. 2015, Ryde et al. 2025). Therefore, as both our high and low elevation soils were sampled in birch forests where *Empetrum* is dominant in the understory, such persisting legacies may have overridden any direct competition effects of *Empetrum* as a neighbour (Nilsson et al. 1993, Weih and Karlsson 1999a, Pilsbacher et al. 2020). Indeed, our results showed that the close proximity of *Empetrum* alone did not result in any negative or positive plant interactions with mountain birch. A scenario including *Empetrum* soil legacies and mountain birch seedlings establishing in openings in the vegetation is not uncommon in natural settings as *Empetrum* generally dominates both forest understories and heath vegetation above the treeline, serving as an important 'niche constructor' affecting the vegetation structure and soil nutrient cycling (Nilsson and Wardle 2005, Bråthen et al. 2018).

Regarding our second hypothesis, we anticipated that growth responses to the experimental treatments would correlate with coordinated shifts in seedling traits. In support of this, we observed that higher mountain birch seedling growth rates under warming were negatively related to the amount of

fine roots and positively related to the percentage of mycorrhizal colonisation and some plant functional traits associated with increased resource acquisition, such as total leaf area and root C/N ratios and length (Graglia et al. 1997, Clemmensen and Michelsen 2006). As well as the growth rates, the shifts in the seedling functional traits were strongly driven by the warming treatment, with seedlings reaching larger height, root length, total leaf area and higher C/N ratios in the warmer temperatures, patterns consistent with previous findings for subarctic systems (Bjorkman et al. 2018, Spitzer et al. 2023), pointing to high importance of temperature for mountain birch seedling performance (Kullman 1979, Truong et al. 2007, Sundqvist et al. 2008). Further, these results reveal a coordinated above- and belowground shift in some traits related to carbon capture aboveground and nutrient and water capture belowground in the early seedling stage of this species. However, our results also show that faster growing mountain birch seedlings invest more carbon in ectomycorrhizal symbioses and total root length, but less in fine roots. These observations point to differences between seedling and tree investments in mycorrhizal symbionts. Adult mountain birches have been shown not to vary in mycorrhizal colonization rates with changing environmental conditions, but to invest relatively more in high-biomass mycorrhizal morphotype with increased environmental stress near the treeline (Ruotsalainen et al. 2009).

Certain traits that were unresponsive to temperature were instead strongly responsive to soil properties. Specifically, birch seedlings grown in high-elevation soil had higher C allocation to root than shoot biomass, higher leaf C/N ratios, higher LDMC, as well as higher CO_2 assimilation rates per unit leaf area, than birch seedlings in low-elevation soils. Higher root:shoot ratios often occur with increasing elevation (Zurbriggen et al. 2013) and usually point to increased N limitation (Ingestad and Lund 1979). Similarly, higher leaf C/N ratios and higher LDMC in high-elevation soil could illustrate nutrient limitation and seedling tendency to conserve resources in the high elevation soils. However, the seedlings had higher growth rates in high- relative to low-elevation soil. In other words, these seedlings grown in soils that promoted higher growth rates also invested more of assimilated CO_2 into leaf structural tissues, and to roots rather than shoots. It has been shown that tree seedlings can optimise their nutrient allocation to increase growth rate, which can allow them to progress out of the most vulnerable seedling phase more quickly (Karlsson and Weih 1996), and therefore increase chances for survival (Kullman 1984, 1986). In line with these findings, our results suggest that at higher soil fertility seedlings simultaneously invest into growth and growing more resilient tissues (usually associated with more conservative growth strategy) to support survival in the face of stressors (e.g. herbivory) and through to the next growing season.

Furthermore, CO_2 assimilation rate per unit leaf area was not directly correlated with the mountain birch seedling growth rate and did not differ between temperature treatments, consistent with growth rates not necessarily being related to C assimilation rates per unit leaf area, under warmer temperatures (Körner 2003, 2013, 2015, Hoch and Körner 2009, 2011). Instead, other traits were associated with increased seedling C acquisition at higher growth rates. For example, birch seedlings growing under warm temperatures had the largest total leaf area (an acquisitive trait), leading to more total C uptake at the same CO_2 assimilation rate per unit leaf area as seedlings in the ambient temperature treatment. Interestingly, two observed strategies leading to increased C acquisition in mountain birch seedlings, increased total leaf area with warming and high CO_2 assimilation rate per unit leaf area in high-elevation soils, revealed a clear separation between traits associated with growth rates versus traits associated with CO_2 assimilation rate (Fig. 3). Specifically, the NMDS showed that CO_2 assimilation rate per unit leaf area was positively associated to more conservative traits such as LDMC and leaf C/N ratio, and negatively associated with N per unit leaf area, which is not overall in line with leaf N content being typically coupled with plant photosynthesis (Evans 1989). However, we also found that N content per leaf area, but not N content per dry mass, was higher under the ambient than under the warm temperatures, while the CO_2 assimilation rate per leaf area was unaffected by temperature. Higher leaf N concentration per leaf area in plants grown in colder temperatures is common across plant life forms (Körner 1989). Our results thus suggests that at the colder (ambient) growth conditions, where photosynthesis is less efficient due to lower enzymatic activity (Liu et al. 2018), higher leaf N concentration is necessary for mountain birch seedling photosynthetic acclimation to achieve the same C assimilation rate per unit leaf area as under the warmer temperature (Sendall et al. 2015).

Conclusions

We found that increases in mountain birch seedling growth rates in response to warming were positively related to several seedling traits that are associated with increased resource acquisition, both above- and belowground. Additionally, the effect of warming on birch seedlings did not depend on whether they were grown in high-elevation or a low-elevation soils, nor did it depend on the presence of *Empetrum*. Instead, soil origin had a strong independent main effect on growth rates and influenced several other seedling traits, resulting in the highest growth rates for birch seedlings grown in high-elevation soil under warmer temperatures.

Our results also show that the high-elevation soil, originating from a site closer to the treeline, promoted higher growth rates but also seedling traits associated with a more conservative growth strategy such as higher leaf dry matter content (LDMC) and higher root:shoot ratio. Taken together, these results demonstrate that first year mountain birch seedlings, experiencing varying temperatures and soil conditions, adjust several aboveground traits that are important for C acquisition under varying temperatures and soil properties, as well as belowground traits associated with nutrient acquisition.

These findings build on previous research indicating that nitrogen availability and temperature influence nitrogen acquisition for mountain birch seedling (Weih and Karlsson 1999a). They indicate that in nutrient-poor subarctic ecosystems, variability in soil properties (such as between our high and low elevation soils) is an important mediator of mountain birch seedling growth. How the growth rate-enhancing functional trait adjustments contribute to seedling survival, however, remains to be explored by future studies. Nonetheless, our study clearly shows that intra-specific trait adjustments to the abiotic environment is an important factor that will allow species to respond to environmental change.

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Author contributions

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.0zpc8679x (Kuťáková et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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