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RESEARCH

Comparison of deacclimation and reacclimation of silver birch, Norway spruce and Scots pine seedlings during winter warm and cold spells in Nordic boreal conditions

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Abstract

Climate change means that in many areas in boreal region, the duration and thickness of the winter snow cover is decreasing. Young seedlings are exposed to fluctuating winter temperatures in the absence of protecting snow cover. Responses to winter warm and cold spells were studied with Scots pine (*Pinus sylvestris* L.), silver birch (*Betula pendula* Roth.), and Norway spruce (*Picea abies* (L.) Karts.) container seedlings in Finland. The frost hardiness of whole seedlings and buds was determined for seedlings sampled directly from outdoor overwintering conditions, after 7-day deacclimation (+5 °C; +7 °C in late March) and deacclimation combined with 7-day reacclimation (−7 °C) treatments between January and late March. The frost hardiness of buds and whole seedlings in Scots pine was between −40 and −30 °C from January to early March. Norway spruces tolerated at least −50 °C in midwinter, but their frost hardiness in outdoor conditions decreased more rapidly in March than that of Scots pines. Silver birch tolerated −30 °C in February. During simulated warm spells, the Scots pine and silver birch deacclimated without an ability to reacclimate during simulated cold spells. The buds and whole seedlings of Norway spruces also deacclimated, but they had some ability to reacclimate in February and early March, but not in late March. In Nordic boreal conditions, one-year-old Scots pines and silver birches respond strongly to fluctuating winter temperatures during snowless winters, whereas Norway spruces can tolerate typical winter temperatures in midwinter, but their frost hardiness may reduce during warm spells in March.

Keywords *Betula pendula* · *Picea abies* · *Pinus sylvestris* · Frost hardiness · Container seedlings · Tree seedling nursery

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Introduction

Winter weather conditions have been predicted to change in boreal conditions due to climate change (Venäläinen et al. 2022). Climate models predict that total snowfalls during the winter may decrease in most parts of Northern Europe (Räisänen 2016), although in eastern and northern parts it may even increase (Lehtonen et al. 2016). The duration of snow cover has already shortened, and it has become thinner during the winter in Finland (Luomaranta et al. 2019). Under snow cover, temperatures fluctuate less than in snowless conditions and under snow cover of more than 30 cm temperatures rarely fall below − 1.5 °C (Sutinen et al. 2008). Without snow cover, shoots and roots of overwintered seedlings in nurseries and planted seedlings in the forest are exposed to winter weather conditions.

It is also predicted that the intensity and number of warm winter periods will increase, but cold periods will still exist (Laapas et al. 2012). Warm periods during midwinter can cause a reduction of more than 10 °C in frost hardiness in trees, increasing the risk of frost damage (Strimbeck et al. 1995). Winter weather conditions have already been observed to cause frost damage to seedlings and saplings in regeneration sites at least in Finland (Luoranen et al. 2018, 2022) and Canada (Man et al. 2013; Lamhamedi et al. 2022). Norway spruce (*Picea abies* (L.) H. Karst.) and Scots pine (*Pinus sylvestris* L.) are the main tree species in Northern European forests. These tree species account for more than 95% of the seedlings used in forest regeneration in Finland, Norway, and Sweden (Solvin et al. 2021). In Finland, 3–4% of the seedlings delivered for planting has been silver birch (*Betula pendula* Roth.) seedlings (OSF). Nowadays silver birch seedlings for spring planting are produced in the Finnish nurseries by sowing in June, and growing the seedlings in containers similar to those used for conifers (i.e. with a cell volume of 85–90 cm^3) and then overwintering the 20–30 cm long seedlings either in outdoors or in freezer storage. The growing season for small-sized birch seedlings is shorter than normal, which may affect their survival in harsh winter weather conditions. To ensure the survival of seedlings in the nursery conditions and of newly planted seedlings in the regeneration sites, it is important to know how the young seedlings of these tree species respond to fluctuating winter temperatures in Nordic boreal conditions.

In the late fall and early winter, the meristemic activity of plants is in endodormancy, and it is regulated by the metabolism and physiology of meristem (Kalberer et al. 2006). The frost hardiness of seedlings develops toward its seasonal maximum during endodormancy. The fulfilment of species-specific chilling requirements releases meristems from endodormancy, and they turn to an ecodormant state, in which the ability of plants to respond to the environmental conditions increases (Kalberer et al. 2006). In the middle of winter, plants can tolerate much lower temperatures than normally occur in boreal forest conditions (Glerum 1973; Repo 1992). Warm winter spells can cause deacclimation, and a plant organ may lose its frost hardiness (Kalberer et al. 2006). Deacclimation may be very rapid, and even a short warm exposure (of hours) may reduce the frost hardiness of buds by several degrees (Räisänen et al. 2006). Root deacclimation is controlled by soil temperature and in Scots pine and Norway spruce seedlings it can be initiated even in freezer storage at − 3 °C (Lindström and Stattin 1994). Roots also start to deacclimating earlier than shoots in winter (Calmé et al. 1994) which may affect the overall survival of seedlings under fluctuating winter temperatures. In subsequent cold temperatures, plants can reacclimate when temperatures decrease, but this process takes much longer than deacclimation, and the ability to reacclimate also decreases toward the spring (Kalberer et al. 2006).

The frost hardiness of aboveground part of plant organs, like needles of evergreen conifers and vegetative buds, may differ, and the buds are usually the most sensitive aboveground plant tissue (Charrier et al 2015). However, the most sensitive parts of seedlings are the roots (Bigras et al. 2001). If the frost hardiness of shoots of Norway spruce and Scots pine can be as low as < −80 °C in mid-winter (Bigras et al. 2001), the maximum hardiness of their roots is < −25 °C (Lindström and Nyström 1987). Similarly, the maximum frost hardiness of shoots and buds of silver birch seedlings can be < −60 °C under Nordic boreal conditions (Riikonen et al. 2013; Repo et al. 2021), but the roots of, for example container-grown yellow birch (*Betula alleghaniensis* Britton) seedlings have been damaged already at − 33 °C in mid-winter (Calmé et al. 1994).

The frost hardiness of different tree species and their ability to respond to fluctuating winter temperatures differ during winter. Pine species have been observed to be less hardy than spruce species, but there can be differences even within a genus. In Ontario, Canada, seedlings of two pine species, lodgepole pine (*Pinus contorta* Dougl. ex. Loud) and jack pine (*Pinus banksiana* Lamb.) were less hardy than spruce species [white (*Picea glauca* (Moench) Voss), and black spruce (*Picea mariana* (Mill.) B.S.P.)] during the winter (Man et al. 2017). In Northern European conditions, an increased air temperature during the winter reduced the frost hardiness of lodgepole pine seedlings without any effects on the frost hardiness of Scots pine and Norway spruce seedlings (Ögren 2001). Fluctuating winter temperatures have deacclimated needles in 30-year-old Scots pine trees in Eastern Finland (Leinonen et al. 1997). Seedlings and saplings are normally more sensitive to frost than adult plants (Aronsson and Eliasson 1970; Charrier et al. 2015). There are some observations from operational scale reforestation sites that the field performance of Scots pine seedlings planted in the previous growing season was poorer than that of Norway spruce seedlings after a snowless winter (Luoranen et al. 2018). It is suspected that one reason for the difference is the lower frost hardiness of one-year-old Scots pine seedlings and the stronger response to fluctuating winter temperatures compared with Norway spruce seedlings. The ability of young silver birch seedlings to deacclimate- and reacclimate in Nordic conditions has not been studied, but the white birch (*Betula papyrifera* Marsh.) seedlings are quite resilient to fluctuating winter temperatures in Ontario, Canada (Man et al. 2014). As far as we know, the effect of age on the ability to de- and reacclimate in one- and two-year-old Norway spruce seedlings has not previously been studied. There are also no studies comparing the ability of Norway spruce, Scots pine and silver birch container seedlings to deacclimate and reacclimate in Nordic boreal conditions.

The study aimed to investigate the ability of one- and two-year-old Norway spruce, one-year-old Scots pine, and half-year-old silver birch container seedlings to de- and reacclimate in response to warm spells followed by a cold spell in different periods in the winter. The frost hardiness of terminal buds and survival of whole seedlings was measured before and after a 7-day warm spell and after a subsequent 7-day cold spell, four times between midwinter and late winter. Our hypothesis was that one-year-old Norway spruce seedlings were less hardy than two-year-old spruce seedlings, without differences in their responses to the acclimation treatments, and that Scots pine and silver birch seedlings were less hardy, and their ability to reacclimate after warm spells was weaker than in Norway spruce seedlings. The second hypothesis was that the responses of terminal buds and whole seedlings to varying winter weather conditions would vary between tree species and at different times of the winter.

Material and methods

Seedling material

The study consisted of two experiments undertaken in 2021 and 2022. For both experiments, seedlings were grown in the Suonenjoki Research Nursery of Natural Resources Institute Finland (Luke) (62°39′N, 27°03′E, 142 m above sea level) in Central Finland. For the first experiment in the winter of 2021, seed orchard seeds of Scots pine (national seed orchard identification code SV434) were sown on May 26, 2020. In the second experiment in 2022, one- (SV117; sown on May 4, 2021) and two-year-old (SV175; June 8, 2020) Norway spruce, one-year-old (SV323; May 18, 2021) Scots pine, and a half-year-old silver birch (SV460; June 15, 2021) seedlings were used. All the seed orchard origins were targeted for use in Central Finland conditions. All the seeds were sown in hard-walled plastic containers (Plantek PL81F, 81 seedlings per tray, volume: 85 cm^3, surface area of a cell: 18.3 cm^2, growing density: 546 cells m^{-2}; BCC, Iso-Vimma, Finland), which were filled with base-fertilized (1.0 kg m^{-3} of 16N:4P:7K soluble fertilizer with micronutrients; 6.5% slow-release N) and limed (1.8 kg m^{-3}) light sphagnum peat (Kekkilä Professional Co., Vantaa, Finland). In their first year, all the conifer seedlings were grown on raised pallets in an unheated greenhouse, and they were irrigated and fertilized regularly. During the falls, the doors of the greenhouses were kept open to allow the air temperature to fluctuate as in outdoor conditions. The silver birch seedlings were in the same greenhouse as the conifers until mid-July in 2021, when they were moved to a greenhouse with raised side walls. All seedlings were fertilized using Taimi Superex NPK 19-4-20 and Metsä Superex NKP 22-5-16, produced by Kekkilä Professional Co., Vantaa, Finland and Ferticare 10-52-17, by Yara Suomi Oy, Finland. In 2020, the total amount of macronutrients that Scots pine seedlings received was 7.6 N, 1.6 P, and 8.0 K g m^{-2}. In 2021, the respective values for one- and two-year-old Norway spruce were 25.9 N, 9.1 P, 21.2 K, and 23.1 N, 9.0 P, and 17.9 K, and for the one-year-old Scots pine seedlings 12.9 N, 2.9 P, and 9.4 K and 3.3.N, 0.8 P, and 2.4 K g m^{-2},for the silver birch seedlings Two-year-old Norway spruce seedlings were moved outdoors in October 2020, and they overwintered under snow cover in seedling containers put down on a sand field. In May 2021, the seedling containers were transferred again to raised pallets to the outdoor growing area where the seedlings were grown until the sampling for the experiment in early November 2021. Two-year-old Norway spruce seedlings were short-day treated (12 h per day) between July 6 and August 3, 2021, using a blackout curtain. In 2020, the Scots pine seedlings were in the greenhouse until sampling. In 2021, both the one-year-old Scots pine and the Norway spruce seedlings were in the greenhouse until October 20. The heights of the one-year-old Scots pine (in both experiments), one-year-old Norway spruce, two-year-old spruce, and half-year-old silver birch seedlings used in the experiments were 12–15 cm, 15–20 cm, 25–30 cm, and 20–25 cm, respectively.

In Experiment 1, Scots pine seedlings were sampled on October 26, 2020, put into eight Plantek PL81F containers, each containing 36 seedlings, and moved to the outdoor growing area. The seedlings were outdoors until November 19, 2020, when they were transferred to an unheated greenhouse, with the doors left open to exclude snowfall. This was done to enable sampling during January 2021.

For the second experiment, 5760 seedlings from four seedling lots (one-year-old spruce, two-year-old spruce, one-year-old pine, and half-year-old birch) were randomized to 72 containers, 20 seedlings from each seedling lot per container (total of 80 seedlings per container), on November 8, 2021. Within a container, the seedling lots were mixed, placing seedlings from each lot one after another and forming three blocks within a container. The containers were kept in the outdoor growing area in raised pallets until the beginning of November 2021, when seedlings were transferred before snowing and soil freezing to an open-walled shelter on gravel-covered ground where the air temperature was the same as that of the open air.

Weather conditions

The long-term (1991-2020) weather data from the official weather station of the Finnish Meteorological Institute in Kuopio Maaninka (69°77′N, 19°90′E) describes the weather conditions also in Suonenjoki. The coldest month in the study region is February with the average temperature −8.4 °C and minimum temperature −37 °C. There are on average 169 days when daily mean temperature is <0 °C and 57 days per year when it is <−10 °C. The warmest month is July (17.1 °C). Annual rainfall is on average 617 mm. There is snow cover from November (median snow depth 4 cm on November 30) to April (median depth 15.4 cm on April 15) and the thickest snow depth is in March (47 cm).

During the winter, the seedlings were not watered, and there was no snow cover on the seedlings in the greenhouse (Exp. 1) or shelter (Exp. 2). During the experiments, the hourly temperatures at the seedling top level were measured with data loggers (HOBO Pendant UA-001-64; Onset Computer Corp., Bourne, MA, USA) placed on seedling containers. In the first experiment, the monthly mean air temperatures in the greenhouse with doors open were 0.4, −1.3, and −3.5 °C, the minimum temperatures were −5.8, −7.3, and −9.4 °C, and the maximum temperatures were 9.4, 1.6, and −0.2 °C in November, December, and January respectively (Fig. 1a).

In the second experiment, the monthly mean air temperatures were below zero in all months (−1.7, −8.8, −6.3, −4.2, and −0.7 °C in November, December, January, February, and March respectively (Fig. 1b). Correspondingly, the minimum temperatures were −14.3, −21.5, −24.0, −16.6, and –13.0 °C. The maximum temperatures varied from 0.8 in December to 5.2 °C in February. Between March 9 and March 25, the air temperatures were >0 °C during the daytime (maximum 16.2 °C) and a few degrees below zero during the nighttime (occasionally >0 °C). On March 26, the mean daily temperature dropped rapidly to −5 °C, and the minimum temperature even below −15 °C.

Acclimation treatments

Separate seedlings were used for each acclimation treatment and exposure temperature, and containers were randomly selected from overwintering sites for each treatment, exposure temperature and test occasion. During the acclimation treatments and freezing exposure, seedlings were in containers without root protection. The seedlings were exposed to three acclimation treatments (initial, deacclimation, and reacclimation), once in January 2021 (Experiment 1 with pine) and on three occasions in 2022 (Experiment 2 with birch, pine and spruce of two ages) (Table 1). In the initial treatment, the frost hardiness of seedlings sampled directly from overwintering conditions was determined. In the deacclimation treatment, seedlings were exposed to a 7-day warm spell in a dark climate room where

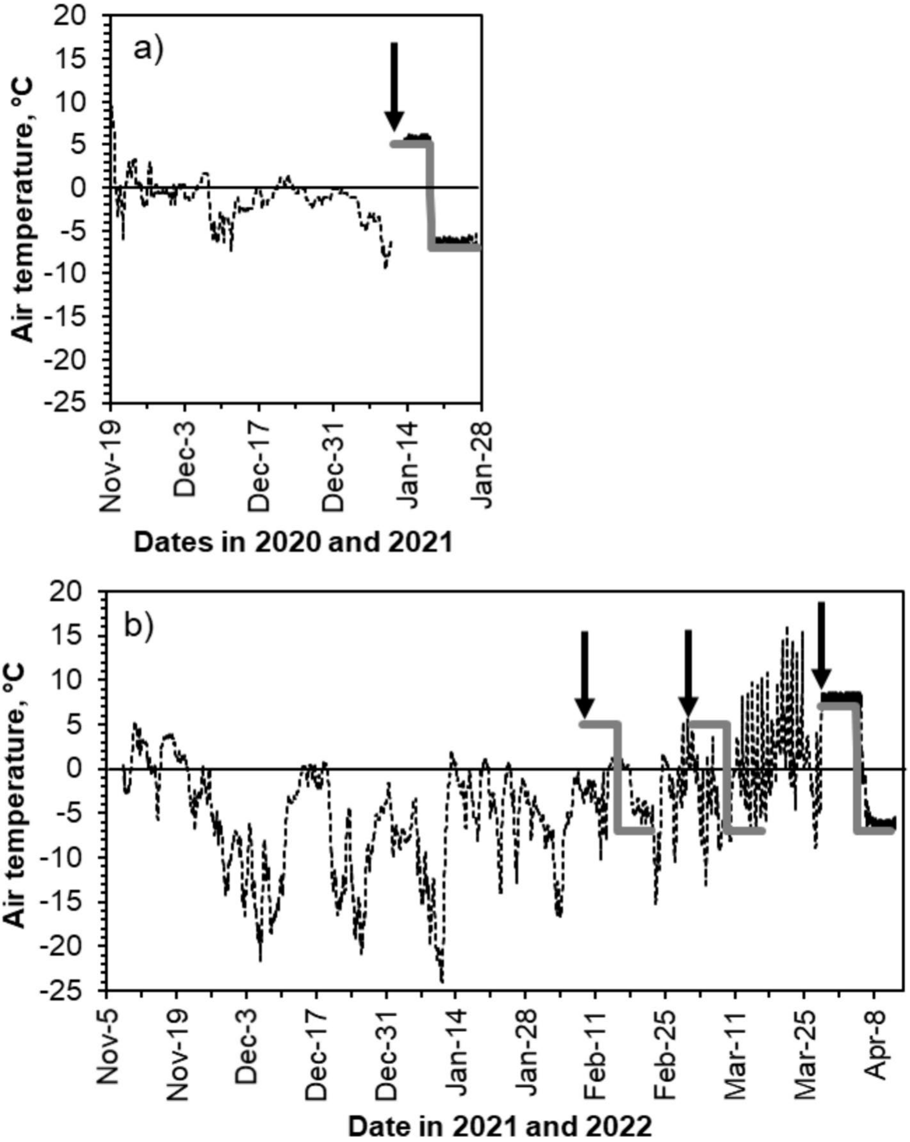

Fig. 1 Air temperatures (**a**) from November 19, 2020, to the end of January 2021 and (**b**) from November 8, 2021, to late March 2022 in overwintering conditions (**a**) in the unheated greenhouse with doors open and (**b**) in the open walled shelter in Luke's Suonenjoki Research Nursery, Finland. Temperatures were measured hourly with Hobo data logger placed on a seedling container. Between January 11–25, 2021 and March 28–April 11, 2021, the temperatures were measured during de- and reacclimation treatment in the climate room. The gray lines indicate the target temperatures during the de- and reacclimation periods, and the black arrows the dates of the initial freezing tests

the temperature was +7 °C (late March 2022) or +5 °C (all other occasions) (Fig. 1). The reacclimation treatment followed the deacclimation treatment, and the temperature in the climate room was lowered from + 3 °C h^{-1} to –7 °C for seven days.

Table 1 Dates of the initial frost hardiness tests conducted for one-year-old Scots pine (Experiments 1 and 2), half-year-old silver birch, and one- and two-year-old Norway spruce (Experiment 2) seedlings collected from overwintering conditions, timing of the de- and reacclimation treatments and target exposure temperatures in freezing tests on each occasion. Overwintering air temperatures (mean and minimum) at the time of the initial tests are also presented

Exp.	Initial test	Air temperature, °C	Deacclimation	Reacclimation	Test temperatures, °C
1	Jan 11, 2021	− 8.8(− 10.2)	Jan 11–18, 2021	Jan 18–25, 2021	+ 5, − 25, − 35, − 40, − 50, − 70
2	Feb 8, 2022	− 2.9(− 3.8)	Feb 8–15, 2022	Feb 15–22, 2022	+ 5/− 7, {− 20}, − 25, − 30, {− 35}, − 40, − 50, − 60, − 70
2	Mar 2, 2022	1.5(− 0.2)	Mar 2–9, 2022	Mar 9–16, 2022	+ 5/− 7, − 15, − 20, − 25, − 30, − 40, − 50, − 70
2	Mar 28, 2022	3.0(− 5.0)	Mar 28–Apr 4, 2022	Apr 4–11, 2022	+ 7, {− 5}, − 7, − 10, − 15, − 20, − 25, − 30, − 40, [− 60]

Test temperatures in brackets [] indicate that the temperature was used only in the initial test, and the value within {} that the temperature was used only in the freezing tests after the de- and reacclimation periods. In the reacclimation treatment, the highest test temperature was − 7 °C, and + 5 °C in the other treatments (+ 7 °C in late March)

Freezing tests

On each of the four test occasions, the seedlings were exposed to freezing tests three times: at the time when the seedlings were transferred to deacclimation treatment (initial); and at the end of the deacclimation and reacclimation treatments. On each exposure occasion, the seedlings were exposed to eight (six in 2021) test temperatures, from which one was the control temperature without freezing exposure (+7 °C in late March 2022, +5 °C for the others). Four air-cooled chambers (WT600/70, Weiss Umweltechnik GmbH, Reiskirchen-Lidenstruth, Germany) were used, each programmed to one target temperature. The starting temperature of each freezing test depended on the temperature at which the seedlings were growing at the time of the sampling. If the temperature in the sampling condition (either in overwintering shelter or in the climate room) was below 0 °C, the starting temperature was −5 °C (initial seedlings in January 2021), −3 °C (initial seedlings in February 2022), or −7 °C (reacclimated seedlings in 2022 tests). For the other occasions, the starting temperature was +5 °C. When the starting temperature was above 0 °C, the temperature was first cooled to −5 °C and kept at that temperature for 3 hours. After this, the rate of cooling and warming was 5 °C h^{-1}, and the duration of the target temperature was 4 h. The tests were performed during two successive nights. The test temperatures on each occasion are presented in Table 1. In 2021, 15 Scots pine seedlings at each test temperature were exposed. In 2022, one seedling container, containing 20 seedlings from each seedling lot, totally of 80 seedlings per container, was randomly selected for each freezing test temperature.

After the freezing exposures, the seedlings were moved to a greenhouse (20 °C, 18 h photoperiod). The seedlings were kept moist by watering them regularly with tap water. After about a month, when the buds had burst, the frost damage was assessed visually from the terminal buds and conifer needles. Damage (browning or drying) to the needles was scored visually at 10% intervals. For birch, seedlings were considered dead if no or only a few, small leaves had burst. The roots were not protected either during overwintering or during freezing exposure. Root damage may have been worsening the seedling damage. Therefore, needle damage in conifers was assessed as damage to the whole seedling, including roots but excluding buds. Later, we use needle damage to indicate damage to the whole seedling in conifers hardiness estimate as seedling frost hardiness. Similarly, in birch, if no buds were burst, a seedling was considered to be as dead, and it was used to estimate frost hardiness of whole birch seedlings. The burst and growing terminal buds were determined to be alive; unburst or browning after burst was classified as damaged.

Statistical analysis

The frost hardiness of the whole seedlings was analyzed for each treatment using a nonlinear mixed model (NLMIXED) in SAS for Windows 9.4 (Usage Note 56992; SAS Institute Inc., Cary, NC, USA). The proportion of the needle damage in each seedling was used in the analysis. For the buds and dead birches, the proportion of damaged buds or dead seedlings in each block (n=3) within a tested container was used. The model was

$$y_i = \mu + \varepsilon_i = d + \left[\frac{1 - d}{1 + e^{b\left(c - x_i\right)}} \right] +_i \tag{1}$$

where y_i is the observed value of the ith case of whole seedling damage, x is the temperature i, parameter d is the lower asymptote, b is the slope and c is the inflection point of the estimated curve. When there was some damage to unexposed seedlings (seedlings at the control temperature; see Fig. A1–3), and parameter d was needed, DT_{50} was calculated using the model

$$DT_{50} = c - \frac{log\left[\frac{0.5}{(0.5-d)}\right]}{b} \tag{2}$$

When there was no damage at the control temperature of + 5 or + 7 °C, parameter c described the temperature at which the probability of damage was 0.5 (DT_{50}).

It was assumed that the likelihood was proportional to $\mu^y(1-\mu)^{(1-y)}$ (see Usage Note 56992, SAS). In Experiment 1, the acclimation treatments were in the same analysis, and the DT_{50} estimates were statistically tested. In Experiment 2, the curves for all test occasions and acclimation treatments within a seedling lot were estimated in a single analysis. Within a test occasion, seedling lots were compared by estimating curves in the same analysis. The statistical significance of the differences between two estimated DT_{50} values were calculated using the delta method and significances between different treatments and occasions, or their combinations, using the Wald test statistics described by Lappi and Luoranen (2018). A difference with a p value of <0.05 was considered significant in all analysis.

Results

In January 2021, the frost hardiness of terminal buds and whole seedlings in Scots pine varied between acclimation treatments ($p<0.001$ for both organs). Both organs tolerated at least − 45 °C in the initial test (Fig. 2). During the deacclimation treatment, their hardiness

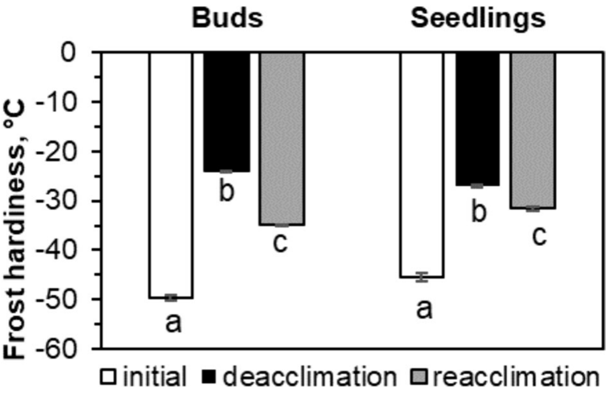

Fig. 2 Frost hardiness (DT_{50}) estimates for the terminal buds and whole seedlings (assessed as needle damage) of the one-year-old Scots pine seedlings after three acclimation treatments in the middle of January 2021. The frost hardiness was determined from samples collected from seedlings in overwintering conditions (initial), after a 7-day deacclimation treatment (+ 5 °C), and then after a 7-day reacclimation treatment (− 7 °C). The letters below the bars indicate the statistically significant differences between acclimation treatments within a plant organ. The vertical bars indicate the asymptotic standard errors of DT_{50} estimates. For the buds, the proportion of burst buds within three blocks and a test temperature, and for whole seedlings, 36 seedlings per test temperature, were used for DT_{50} estimations

reduced to about − 25 °C and then reacclimated by 5–10 °C during the following seven days, but their hardiness did not reach the initial state.

In the winter of 2022, the initial frost hardiness of the whole seedlings changed from February to late March in all conifer seedling lots ($p < 0.001$ for all lots compared between test occasions within a lot) and it differed between lots ($p < 0.001$ for lot-comparison in February and early March, $p = 0.020$ for late March). The initial frost hardiness of spruce seedlings was at least − 70 °C in February, and it decreased in both spruce seedling lots by early March (Fig. 3a, b). The reacclimation of the seedlings was continued in the one-year-old spruces in overwintering conditions until the end of March (Fig. 3a). There was some damage in all seedling lots, but especially in two-year-old Norway spruce seedlings under overwintering conditions in late March (Fig. S2). It was therefore impossible to calculate the DT_{50} value for the two-year-old spruce seedlings on that occasion. The DT_{50} values of the whole seedlings in Scots pines were about − 40 °C in February and early March, increasing to − 20 °C by the end of March (Fig. 3c).

The initial frost hardiness of the terminal buds differed between conifer seedling lots in February and early March (Wald test: $p < 0.001$ for both occasions), but not in late March ($p = 0.298$). However, no statistically significant differences between lots were found in pairwise comparison in February, and the hardiness was approximately − 50 °C in all lots (Fig. 3). The initial frost hardiness of buds in Norway spruce lots decreased

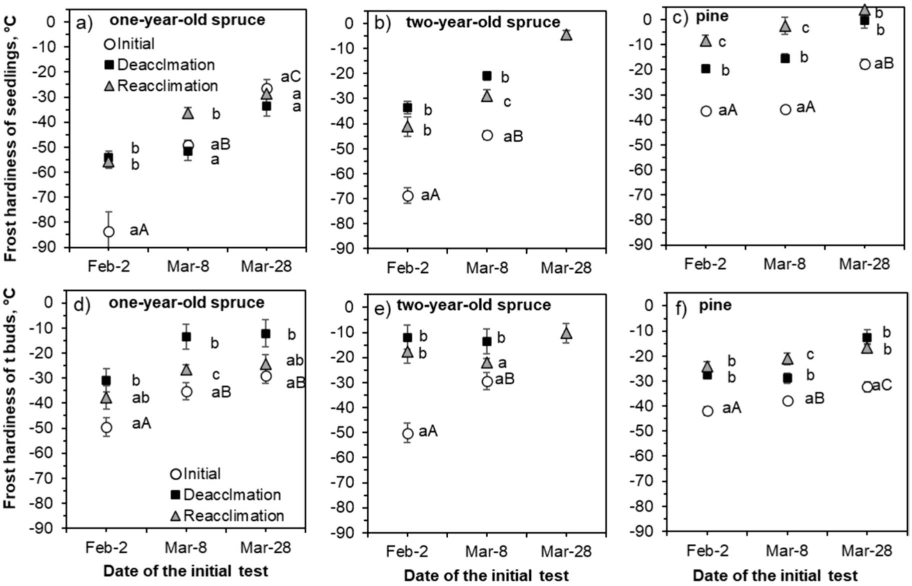

Fig. 3 Frost hardiness (DT_{50}) estimates for (**a**–**c**) whole seedlings and (**d**–**f**) terminal buds of (**a**, **d**) one-year-old or (**b**, **e**) two-year-old Norway spruce and (**c**, **f**)one-year-old Scots pine in early February and March and late March, when frost hardiness was assessed for seedlings sampled from three acclimation treatments: outdoor overwintering conditions (initial); after a 7-day deacclimation period; or a subsequent 7-day reacclimation period. Lowercase letters indicate statistically significant differences between acclimation treatments within a test date and seedling lot, and uppercase letters between test dates in the initial treatment within a seedling lot. Vertical bars indicate the asymptotic standard errors of DT_{50} estimates. For buds, the proportion of damaged buds within three blocks, a test temperature, a seedling lot, and a treatment, and for whole seedlings 20 samples per test temperature, a seedling lot, and a treatment were used for DT_{50} estimations

to − 30 °C by March (Fig. 3d, e). DT_{50} estimates for the buds of the one-year-old spruce seedlings between early and late March did not differ ($p = 0.167$; Fig. 3d). For the buds of the two-year-old spruce seedlings, it was impossible to estimate the DT_{50} value in late March (Fig. S3), but the initial frost hardiness decreased from February to early March ($p = 0.004$; Fig. 3e). In Scots pine, the changes in the initial frost hardiness of the terminal buds were smaller than in the spruce buds, still at − 38 °C in early March and − 32 °C in late March ($p < 0.001$ for the test occasion comparison; Fig. 3f).

Acclimation treatments affected the frost hardiness of both buds and whole seedlings in all conifer seedling lots and test occasions ($p < 0.001$ for all lots and occasions). In February, the frost hardiness of seedlings and buds in both one- and two-year-old Norway spruce decreased by at least 20 °C during the deacclimation treatment, and there were no statistically significant differences between de- and reacclimation treatments (Fig. 3a, b, d, e). In early March, the frost hardiness of seedlings in the one-year-old spruce did not change during deacclimation but decreased during reacclimation (Fig. 3a). However, the frost hardiness of buds in these seedlings decreased by more than 20 °C during the deacclimation treatment, but their frost hardiness increased during reacclimation treatment (Fig. 3d). At the same timepoint, in two-year-old spruces, the frost hardiness of both whole seedlings and buds decreased by more than 15 °C during deacclimation, and it increased by 8 °C during the reacclimation treatment (Fig. 3b, e). In late March, there were no statistically significant differences in the frost hardiness of whole seedlings of the one-year-old spruce between acclimation treatments in a pairwise comparison (Fig. 3a). The frost hardiness of the buds of these seedlings decreased by 17 °C during deacclimation and increased by 12 °C during the reacclimation treatment compared to the deacclimation treatment (Fig. 3d).

In the Scots pine, the deacclimation treatment decreased the frost hardiness of the whole seedlings and buds by 15–20 °C (except in early March in buds only by 9 °C) on all test occasions, and the trend was that the loss of frost hardiness continued during the reacclimation treatment (Fig. 3c, f). The frost hardiness of seedlings reduced by 28 °C and 18 °C in February and early March respectively, but there was no difference between the de- and reacclimation treatments either in whole seedlings or buds in late March. Deacclimation decreased the frost hardiness of buds by 9 °C in early March, and reacclimation decreased it by a further 8 °C.

Some of the silver birch seedlings and their terminal buds were damaged during overwintering since February (see Suppl. Fig. A4). In the February freezing tests, all silver birch seedlings in the initial treatment were alive at the control exposure temperature (+ 5 °C), but 48% and 51 % of the seedlings in the de- and reacclimation treatments were dead at this temperature. In the initial treatments in early and late March, 55% and 20 % of the birches were already dead at control temperatures. In February, 100%, 48% and 51 % of the terminal buds of silver birch seedlings were dead in control temperatures in the initial, de- and reacclimation treatments, respectively. In early and late March, 64, 35% and 52% and 34%, 64% and 38% of the terminal buds were dead in the respective treatments. The only reliable estimate of frost hardiness could be calculated for the first test occasion in February, when the initial frost hardiness of the silver birch seedlings was − 31(± 1.8) °C. In February, it was not possible to estimate the frost hardiness of silver birch seedlings in the de- and reacclimation treatments. At the same test temperatures, there was more damage in the deacclimation and reacclimation treatments than in the initial treatment. This would suggest that some deacclimation had occurred without reacclimation (Suppl. Fig. A4).

Discussion

Silver birch, Scots pine and Norway spruce seedlings all responded to the warm spells during winter and the ability of seedlings to reacclimate during the following cold spell decreased towards spring. If warm spells become more common during snowless winters in the future, as predicted (Laapas et al. 2012), young silver birch, Scots pine and Norway spruce seedlings may deacclimate earlier. At the same time, if very low temperatures still exist (Laapas et al. 2012), the risk of frost damage in seedlings and terminal buds of silver birch, Scots pine Norway spruce seedlings significantly increases. In fact, such conditions prevailed at the time of our study, when a warm spell occurred just before our tests in late March, followed by a rapid temperature decrease to -15 °C causing damage also in our experimental control seedlings. In the early winter, when the seedlings are in the endodormant stage, and when their chilling requirement has not been fulfilled, fluctuating temperatures are unable to de- and reacclimate plants (Nilsen and Rasmussen 2009). In our study, the chilling requirement needed for bud burst was achieved before our first tests in January and February, as all silver birch, Norway spruce and Scots pine seedlings in boreal conditions normally achieve this before the end of December (Li et al. 2005; Partanen et al. 2021). The seedlings were therefore in the ecodormant stage, and responses to the fluctuating temperature were possible on all test occasions, as the results showed.

The initial frost hardiness of the seedlings and buds of Norway spruce in early February was at least −50 °C, while the buds and seedlings of Scots pine in January and February tolerated a maximum of −40 °C and silver birches only about −30 °C. In midwinter, the frost hardiness of Norway spruce seedlings was in line with our previous results (Riikonen et al. 2023), when the maximum frost hardiness of the needles of two-year-old Norway spruce seedlings was −60 °C. However, Scots pine and silver birch seedlings have been much hardier in other studies. Previously, one-year-old Scots pine seedlings in November (Di et al. 2019) and 30-year-old Scots pine trees from January to March have tolerated −70 °C in Central Finland conditions (Leinonen et al. 1997). On the other hand, the differences in the hardiness levels between pine and spruce species are in line with a Canadian study, in which lodgepole and jack pine seedlings were less hardy than white and black spruce seedlings in the winter (Man et al. 2017). Although Scots pine seedlings were less hardy than Norway spruce seedlings in natural conditions in our study, they still tolerated temperatures from −30 to −35 °C, which occasionally occur in Central Finland in midwinter (the Finnish Meteorological Institute 2022). Our results in Norway spruce are in line with previous results, which showed that buds of several conifer species were less hardy in winter than other organs (Charrier et al. 2015). In our study, other parts of spruce seedlings were at least 14 °C hardier than buds. However, in Scots pine the differences between organs were smaller and buds were few degrees hardier than other parts of the seedlings in both study years in midwinter. The differences between Norway spruce and Scots pine may be linked to their differences in the supercooling: Buds of Scots pine can survive from extracellular freezing when vegetative buds of Norway spruce can be temporarily supercooled with the occurrence of intracellular freezing (Neuner et al. 2019). In the former type of species, the frost hardiness of buds is usually better than in the later type (Neuner et al. 2019).

In the first experiment, the seedlings were in the unheated greenhouse where temperatures were > −10 °C all the time and no damage was observed in the buds or needles at control temperatures. In the second experiment, overwintering temperatures were < −20 °C for a few days in December 2021 and January 2022 and could have damaged the root systems of the seedlings of all tree species. Previously Rikala and Konttinen (2010) have measured temperatures in the air and in root plugs of Plantek containers with air slits between the cells (used in our study). In that study, when the temperature at the seedling level was between − 16 and − 19 °C for several days without snow cover in outdoor storage, the temperature in the root plugs dropped to − 12 °C. Root deacclimation also starts earlier in late winter and at lower temperatures than in shoots (Bigras et al. 2001), which may have been exacerbated the root damage, especially as a result of a rapid drop in temperature after a natural warm period in our study. Damaged roots may then also exacerbate damage in aboveground parts, and especially in silver birch seedlings. Damage to conifer was assessed as damage to needles, but because of possible root damage, the observed damage is more indicative of the damage to the whole seedling including roots, stems and needles.

The frost hardiness of silver birch seedlings in February was clearly worse than that of Norway spruce seedlings and slightly worse than that of Scots pine, and worse than that observed in a previous study in Finnish conditions (Repo et al. 2021). A possible reason for the lower hardiness and damage observed in silver birch in our study is the natural freezing and thawing of thin birch stems in young seedlings before the first test occasion under overwintering conditions, together with the thawing of seedlings during the deacclimation treatment. As a result of these freeze-thaw cycles, the xylem sap of the seedlings was probably frozen, resulting in the formation of air bubbles in a water conduit during thawing (Sperry and Sullivan 1992). With repeated freeze-thaw cycles, these air bubbles can become large and prevent normal water transport. This xylem embolism is common in woody plants and in diffuse-porous trees, such as birch, the risk of this freezing response is higher than in conifers (Sperry and Sullivan 1992) and may explain why silver birch seedlings suffered more than conifers even in outdoor conditions. In yellow birch, freeze-induced embolism has been caused shoot dieback, especially when winter thaw followed by freezing has also caused root damage (Zhu et al. 2000). The risk of xylem cavitation also increases when thaw period lengthens (Zhu et al. 2000), as was the case during the deacclimation period in all test occasions and during the natural warm periods in March in our study. This embolism and root damage prevents normal water transport leading to the dried shoots (Zhu et al. 2000) but the dieback caused by xylem cavitation is not necessarily be the cause of freezing injury (Zhu et al. 2001). In our study, it is difficult to say what is the real cause of shoot drying in silver birch, and what was the real seedling frost hardiness, but it was related to the freezing and thawing of seedling tissues. Anyhow, in a future climate the risk of damage to young silver birches is likely to increase, whether the cause is air bubbles in the cells due to freezing and thawing of plant organs, or reduced frost hardiness.

In previous studies, temperatures above 0 °C have caused the deacclimation of needles in young Scots pines in natural conditions, although not until early April (Repo 1992; Leinonen et al. 1997). In our study, the temperatures increased above 0 °C during several days at the end of February before the second freezing test in 2022. This probably explains why the frost hardiness of Norway spruce decreased and of Scots pine seedlings slightly decreased already in early March under overwintering conditions. Furthermore, as our simulated acclimation treatments showed, the ability of seedlings to reacclimate after warm spells is low.

In the deacclimation treatments, the buds of Norway spruce seedlings responded more to the warm spells than the buds of Scots pine, but in the whole seedlings level Scots pine responded more strongly to warm spells than Norway spruce. The buds of Norway spruce seedlings probably started to deacclimate already during the natural warm spells before our freezing tests. The stronger response in Scots pine seedlings to warmer conditions are in line with Swedish results, in which two-year-old lodgepole pine and Scots pine seedlings were less hardy than two-year-old Norway spruce seedlings if they were kept at the similar temperature (+5.5 °C) as in deacclimation treatments in our study (Ögren et al. 1997). The buds and whole seedlings of Scots pine reacclimated by 5°–10 °C in January, but neither of the organs had the ability to reacclimate during the cold period from February onward. Similarly, the deacclimation of the Scots pine trees was rapid when the temperature was increased to 6 °C without the ability to reacclimate at a fluctuating temperature in the study of Leinonen et al. (1997). Sugar content and frost hardiness have been shown to be correlated and be lower in pine species than in spruce (Ögren et al. 1997). The respiration of spruce needles is also measured to be lower than in pine needles (Ögren et al. 1997). Scots pine seedlings therefore probably respirated more during the deacclimation treatment in our study, which may have reduced sugar content and therefore also frost hardiness. Furthermore, the low sugar content of pines probably prevented their reacclimation in the cold treatment. Similarly, the natural warm spells before our freezing tests probably caused respiration and a reduction in sugar content, thus damaging the seedlings in the late March tests.

In addition to warm spells, solar radiation, especially in two-year old Norway spruce seedlings, may explain seedling damage during overwintering conditions. The seedlings were in an open-walled shelter that allowed the afternoon sun to shine on the seedlings. The two-year-old seedlings were taller than the seedlings in the other seedling lots. All the seedlings had been mixed in the same containers. The tall two-year-old seedlings probably overshadowed the others. In addition, the seedling shoots were probably exposed to strong sun radiation and warm temperatures, which increased transpiration and may have led to desiccation when water uptake by the roots from frozen root plugs was impossible (Larcher 1995).

There were no big differences between one- and two-year-old Norway spruce seedlings in their initial frost hardiness, and they deacclimated from the beginning of March onward. Two-year-old spruce seedlings responded more to the reacclimation treatment than one-year-old seedlings in early March since only the two-year-old seedlings reacclimated. In our study, one- and two-year old Norway spruce seedlings with different origins were used although both suitable to Central Finland conditions. This may have had a slight impact on the results. To our knowledge, there have been no studies of the responses of different genotypes of either Scots pine or Norway spruce to fluctuating winter temperatures. However, it has been observed that autumn frost hardening of one-year-old Norway spruce seedlings varies between genotypes when growing season temperatures increase (Levkoev et al. 2018). In addition, the two-year-old seedlings received a short day treatment in July, but the one-year-old seedlings did not, which may have led to differences in responses to acclimation treatments.

We used seven days for both de- and reacclimation periods for practical reasons (e.g., the capacity of air-cooled chambers). From previous studies we know that the duration of these periods can affect the responses of seedlings to fluctuating temperatures. A spell of a few days may have some effect, but if it lasts at least six days, it can deacclimate seedlings more effectively (Nielsen and Rasmussen 2009). On the other hand, reacclimation needs a longer period (Kalberer et al. 2006). In our climate simulation, where a seven-day warm spell was followed by a seven-day cold spell, reacclimation did not occur. The reason may be that the cold period was too short for reacclimation. Namely, the foliage of adult montane red spruce (*Picea rubens* Sarg) deacclimated by 3°–14 °C during a natural three-day-warm spell in January, and 10–20 days were needed to reacclimate to the original level of frost hardiness (Strimbeck et al. 1995). However, in natural conditions air temperature changes may be very rapid, as happened in late March in our study, and if seedlings cannot reacclimate even in seven days, the risk of damage is high. Further studies of the effects of shorter warm spells are needed.

A stronger response of Scots pine and silver birch seedlings to the simulated warm spells and lower initial frost hardiness in midwinter expose them to harsh temperature conditions during a snowless winter in outdoor winter storage conditions in nurseries, as well as on the planting sites, especially if they are planted in the fall. In nurseries, seedlings can be protected by covering them with artificial snow or by storing them in a freezer. However, on planting sites, seedlings will be exposed to winter weather conditions. In snowless winters, Scots pine seedlings can be damaged more than Norway spruce seedlings by cold temperatures, and these frost hardiness differences may explain, as we speculated earlier, the poorer field performance of Scots pine seedlings after fall planting, observed in a previous Finnish study (Luoranen et al. 2018) In Scots pine, whole seedlings also deacclimated more towards spring than buds. The buds of Scots pine are therefore better able to withstand rapidly changing temperatures than the other parts of the seedling. In Scots pine, the whole seedlings also deacclimated more than the buds towards the spring. The buds of Scots pine therefore have a better ability to survive from rapidly fluctuating temperatures than their other parts. However, minor frost damage in needles and roots may reduce the growth of seedlings in the subsequent year (Lindström 1986; Man et al. 2021). Scots pine seedlings have been shown to suffer more from defoliation than Norway spruce (Långström and Hellqkvist 1989), and the strong tendency to deacclimation in Scots pine seedlings can therefore be fatal. Shoot injury in silver birch seedlings will result in reduced growth and may lead to multiple leading shoots if only part of the shoot is killed. If both buds, roots, stem and needles are damaged, seedlings may die, resulting in planting failure, increased replanting requirements and regeneration costs.

Norway spruce seedlings are predicted to suffer more from climate change than silver birch and Scots pine seedlings in northern European boreal forests (Kellomäki et al. 2018). Norway spruce is particularly sensitive to drought (Jansons et al. 2016). Based on our results, Scots pine and silver birch appeared to be more vulnerable to fluctuating winter temperatures than Norway spruce, at least during their first winter. Norway spruce seedlings also have the ability to acclimate after warm periods in late winter and early spring, which was not observed for Scots pine. Due to the embolism, the results for silver birch are uncertain and more research is needed in this species. Further studies are needed to determine how serious these risks are in a warming climate, whether these results can be generalized to older, planted and established seedlings, whether it is possible to influence seedling responses to fluctuating temperatures through nursery management practices, and to what extent the sensitivity of Scots pine and silver birch seedlings to warm spells may influence regeneration decisions.

Conclusions

In conclusion, Scots pine and especially silver birch seedlings are at high risk of frost damage during snowless winters and are highly sensitive to fluctuating winter temperatures. Norway spruce seedlings can tolerate typical Nordic boreal winter temperatures in midwinter, but their frost hardiness may be reduced during warm spells in March, when temperatures below −10 °C can damage seedlings. This can lead to a risk of planting failure in regeneration sites and damage in outdoor winter storage conditions in nurseries if seedlings are not protected, for example, by artificial snow cover.

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Data Availability Data will be available upon reasonable request via contact with JL

Declarations

Conflicts of interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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