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Recovery of planted spruce seedlings from abiotic damage caused by exceptional weather conditions in the boreal forest: Identification of risks associated with site selection and regeneration practices

Jaana Luoranen [a,*], Aura Salmivaara [b], Jari Miina [c]

[a] Natural Resources Institute Finland, Natural resources, Juntintie 154, Suonenjoki 77600, Finland
[b] Natural Resources Institute Finland (Luke), Natural resources, Latokartanonkaari 9, Helsinki 00790, Finland
[c] Natural Resources Institute Finland (Luke), Natural resources, Yliopistokatu 6 B, Joensuu 80100, Finland

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ABSTRACT

Extreme weather events are predicted to increase in the Nordic boreal region with climate change, and stress conditions can damage newly planted seedlings and affect future stand development. The aim of the study was to investigate the recovery of Norway spruce (*Picea abies* (L.) Karst.) container seedlings from winter and drought damage in southern and central Finland (60–64°N) and the effect of damage on regeneration outcome three growing seasons after damage. Abiotic damage reduced the number of planted spruces (over 1600 trees ha^{-1}) to an average of 1500 planted crop trees ha^{-1} three years after damage. Natural regeneration supplemented the stands and regeneration outcomes were good (>1600 trees ha^{-1}) in most of the stands. Abiotic damage reduced planted spruces quality, increased the number of multiple stems, and further reduced planted tree growth. Weather conditions had an effect on the recovery of drought-damaged seedlings, but not on the recovery of winter-damaged seedlings. Fall planting, packing growing seedlings in closed cardboard boxes during summer and fall, and planting growing seedlings from outdoor winter storage in dry conditions in early summer reduced seedling recovery from abiotic damage. The use of open geospatial data is promising to identify regeneration sites at high risk of abiotic damage (dry sites and high topographic position). In conclusion, good regeneration results in a changing climate can be achieved by making the right decisions during the regeneration process and by using natural regeneration to supplement planted spruce stands.

1. Introduction

Extreme weather events are projected to increase with climate change. In the boreal zone, snowless winters with variable temperatures (Räisänen, 2016; Luomaranta et al., 2019) and droughts, especially in spring and early summer, will become more frequent (Ruosteenoja et al., 2018). Drought associated with rising temperatures may increase tree mortality worldwide, with seedlings being particularly vulnerable (Adams et al., 2017). Weather conditions are particularly important for Norway spruce (*Picea abies* (L.) Karst.; hereafter spruce) seedlings, as mature spruce has been observed to be highly sensitive to drought (Jansons et al., 2016) and changing temperature and snow conditions (Suvanto et al., 2017) among commercially important tree species in the northern boreal region. The predicted extreme weather conditions have already occurred in Finland in some recent years, and both drought and winter injury have already been observed in practical plantations as damaged shoots and increased mortality in recently planted stands (Luoranen et al., 2018, 2022a, 2023). Extensive winter damage has been observed also in Canada (Man et al., 2013; Lamhamedi et al., 2022). Knowing how planted seedlings recover, grow, and perform after abiotic damage would be useful in predicting future stand development. Most importantly, site conditions and current regeneration practices that increase the risk of abiotic damage in extreme weather conditions should be identified and avoided in the regeneration process.

There are several mechanisms that can damage seedlings in winter. If temperatures are below the frost hardiness of a plant organ, the organ can be damaged regardless of the season (Sutinen et al., 2001). Native tree species are normally sufficiently hardened enough in the boreal forest zone (Bigras et al., 2001 and references therein), but the fluctuating temperatures, especially during the snowless winter and early

* Corresponding author.
E-mail address: jaana.luoranen@luke.fi (J. Luoranen).

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spring, increase the risk of damage, especially to young seedlings (Luoranen et al., 2024a). Warm periods can deacclimate plant organs, but they have the ability to reacclimate at lower temperatures. The reacclimation process is slower than deacclimation process, and the ability to reacclimate decreases toward spring (Kalberer et al., 2006). Under these conditions, plant organs can be damaged by the rapidly drop in temperature after winter warm spells (Kalberer et al., 2006). In winter desiccation, strong sunlight and warm daytime temperatures increase transpiration, but frozen soil in late winter and early spring prevents root water uptake, leading to above-ground desiccation (Larcher, 1995). Luoranen et al. (2022a) observed winter damage in spruce seedlings planted in the previous growing season, and based on winter and spring weather conditions, the most likely cause of damage was winter desiccation.

Continuous uptake of water and nutrients and the growth of roots are essential for the survival of seedlings (Burdett, 1990; Grossnickle, 2012). Newly planted seedlings are always exposed to varying degrees of planting stress (Grossnickle, 2000). High temperatures and dry soil at the time of planting increase the risk of stress (Grossnickle and Ivetić, 2022 and references therein). Plants need continuous water movement from the soil to the roots and from the roots to the needles. Drought damage occurs when the soil is dry, water movement to the root system is restricted, and the plant is unable to take up enough water from the surrounding soil to meet the evaporative needs of the shoot (Grossnickle, 2018). This can then lead to reduced growth and even damaged seedlings as observed by Luoranen et al. (2023) during a warm and dry summer in Finland in 2021.

Abiotic damage caused by weather conditions, such as winter desiccation and summer drought, is usually observed as partial or complete drying out of shoots or discoloration or death of needles. Before visible symptoms appear, plants undergo several physiological changes due to water stress, such as decreased water potential and reduced photosynthesis (Grossnickle, 2000), which can also affect seedling development. Damaged seedlings may produce new shoots from dormant buds lower on the stem or just above the ground. This can often result in multiple stems and reduced growth (Krasowski and Simpson, 2001). Multiple and twisted stems on seedlings can lead to poor wood quality in the future.

It is not possible to predict final regeneration outcomes from surveys conducted immediately after abiotic damage. Observed damage may be exacerbated by subsequent summer or winter conditions (Krasowski et al., 1996; Luoranen et al., 2018, Malmqvist et al., 2018; Luoranen et al., 2022a). A more realistic assessment of the ability of seedlings to recover from abiotic damage can be made three or four years after planting (Johansson et al., 2015). This is the standard time in Finland for the evaluation of planting success (Kankaanhuhta et al., 2009). Luoranen et al. (2022a), (2023) inventoried damaged stands immediately after damage, but these inventories do not indicate how well seedlings recover from damage. The remeasurement of seedling stands, from which we know damage levels (Luoranen et al., 2022a, 2023), allows us to study seedling recovery three or four growing seasons after planting and three growing seasons after abiotic damage, and the factors that influence it.

Several silvicultural practices during the regeneration process and seedling characteristics have an impact on the survival potential and planting stress of seedlings (Grossnickle, 2000). In the Nordic countries, conifer seedlings are grown in containers. In Finland, the planting season is the entire period of unfrozen soil, from spring to fall. Seedlings are either overwintered outdoors in the nurseries or packed in cardboard boxes in the late fall and stored in the freezer. Cardboard boxes have been developed for storage in the freezer (Landis et al., 2010). However, at least in Finland, for logistical reasons, some operators want seedlings to be packed in boxes also during the growing season, regardless of the growth stage of the seedlings. During the growing season, seedlings delivered directly from the nursery or outdoor winter storage, are either actively growing (June-July plantings) or still in winter hardening (fall plantings in August and September). These types of seedlings require sunlight for proper development (Grossnickle, 2000). Freezer-stored seedlings can be safely stored in boxes for two weeks in cool spring weather (Helenius et al., 2004), but the storage period for seedlings packed from the field is about one week in spring and only a few days at other times (Luoranen et al., 2019). Seedling size at planting, month of planting, packaging and overwintering methods, and duration of field storage prior to planting influence the risk of immediate abiotic damage to newly planted spruce seedlings (Luoranen et al., 2022a, 2023). We do not know how the above-mentioned operational factors affect the recovery and quality of planted seedlings in the long run and if there is a need to change the guidelines of the regeneration process.

The risk of abiotic damage to spruce seedlings is increased by the location of a sample plot on a hilltop, in dry and poor site types (Luoranen et al., 2022a, 2023). Such risk sites should be identified in advance and, for example, Scots pine (*Pinus sylvestris* L.; hereafter pine) should be planted instead of spruce. Open geospatial data have been found to be useful in providing details on site conditions suitable for selecting the tree species and regeneration methods to achieve the best possible regeneration results in boreal forests (Miina et al., 2024). By identifying sites susceptible to winter and drought damage, seedling material and other operational decisions could be optimized to reduce the risk of damage at these sites.

In planted stands, natural regeneration is used to supplement planted seedlings. Supplemented, seed-born seedlings are especially important in stands with increased planted seedling mortality or poor seedling quality due to the abiotic damage. Seedlings that had been accepted for further growth are called crop trees. Crop trees can be either planted trees or natural, seed-born, supplemental trees. The criteria for supplemental crop trees are based on tree species, distance from other crop trees, and height. The natural crop trees are selected in such a way that they are expected to reach a merchantable stem size at the time of the first commercial thinning (Korhonen et al., 2010). The species used for natural regeneration depends on site conditions. According to Miina and Saksa (2013), natural spruces supplemented planted spruces, especially on wet and peat soils and unprepared regeneration sites, while the number of natural crop-tree pines was higher on drier sites. On rich, moist sites, the number of natural seedlings was low, so they supplemented planted seedlings less often than on medium, sub-mesic sites. Seed-born birches were most abundant on fine-textured and peat soils.

The objectives of the study were to investigate whether abiotic damage caused by extreme weather events during the first year after planting affected i) the regeneration outcome (including both planted and seed-born seedlings) and ii) the recovery, growth, and quality of planted spruce seedlings assessed three growing seasons after the damage, and iii) whether other factors related to site conditions, planting material, or the regeneration process could explain seedling recovery and quality and potentially help mitigate the effects of extreme weather events. Hypothesis 1 is that the number of crop-tree spruce seedlings assessed three years after damage will coincide with the number of spruce seedlings assessed as healthy or predicted to recover immediately after the damage. Our expectation is that the recovered seedlings would have quality defects, especially multiple stems, and lower height growth (Hypothesis 2). We also hypothesize that the same factors that explained the immediate abiotic damage, such as planting date, winter storage conditions, packaging method, site type, soil texture, and weather (Luoranen et al., 2022a, 2023), would also explain the probability of reduced quality of planted spruce trees three growing seasons later (Hypothesis 3). Hypothesis 4 suggests that site-specific geospatial data (e.g., topographic variables) can help to predict the sites susceptible to abiotic damage.

2. Material and methods

2.1. Study sites

We remeasured part of the regeneration sites that were inventoried after winter damage (Luoranen et al., 2022a; hereafter referred to as winter damage survey) and summer drought (Luoranen et al., 2023; drought survey). The timing of abiotic damage and measurements is described in Fig. 1. In the first survey conducted in 2020, large participating companies selected 10 regeneration sites, while smaller companies selected 5, all exhibiting winter damage symptoms (brown or dropped needles and/or dead shoots) in central Finland (Luoranen et al., 2022a). Another criterion was to select sites that were planted in different planting seasons, i.e. spring, summer and fall. For the first drought survey in 2021, each participating company randomly selected sites in its area of operation, with larger companies selecting the required number of sites in a certain geographic area rather than their entire area of operation (Luoranen et al., 2023). The aim was to collect sites from as wide a geographical area as possible, covering all of Finland except the northernmost part (Lapland). The geographic coverage was influenced by the operating areas of the companies involved in the project.

Regeneration sites were remeasured three (drought-damaged stands, and fall-planted winter-damaged stands) or four (winter-damaged stands planted in early summer 2020) growing seasons after planting and three growing seasons after abiotic damage. The initial surveys determined the abiotic damage (yes or no) and condition (healthy, slightly weakened, dying, or dead) of the planted seedlings and predicted the recovery of a seedling from the damage (healthy and slightly weakened).

The criteria for remeasurement were that more than 5 % of the planted spruce seedlings were found to be damaged during the initial surveys and that all necessary background information was available. Sites where seedlings taken from freezer storage were planted in July (planting in 2021) were not remeasured because at least some of the damage was frost damage due to the late planting date. The growing season after planting was too short for proper growth and cold acclimation before fall and winter, resulting in frost damage (Hänninen et al., 2009) rather than drought. We also excluded regeneration chains that are rarely used in Finland. In total, 37 sites from the winter damage survey and 41 sites from the drought survey were selected for re-inventory (Fig. 2).

2.2. Field measurements

The inventory method used in the initial surveys and described by Luoranen et al. (2022a), (2023) was used. Briefly, 8–15 circular sample

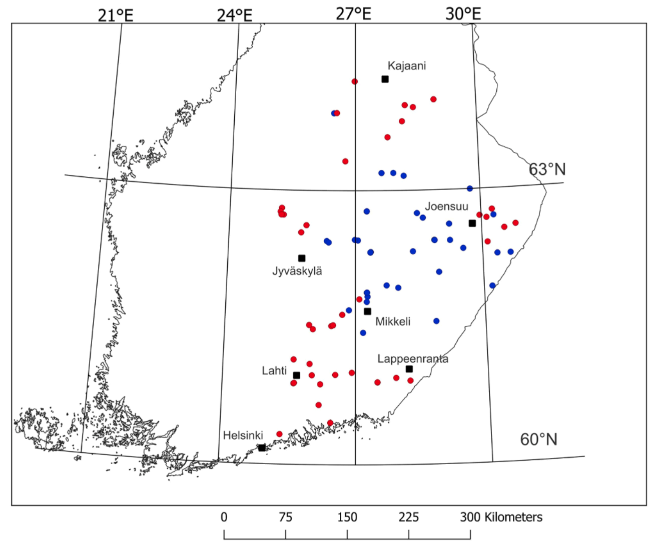

Fig. 2. Location of three- or four-year-old spruce stands inventoried three growing seasons after abiotic damage in central and southern Finland. Blue symbols are winter-damaged stands (n = 37), and red symbols are drought-damaged stands (n = 41).

plots (radius 3.0 m, 28 m^2) were systematically sampled at each regeneration site. Winter-damaged and drought-damaged stands were remeasured in May and early June in 2023 and 2024, respectively.

On each sample plot on mineral soils, site type was classified into four categories based on Tonteri et al. (1990) and Cajander (1949): very rich, moist (*Oxalis-Maianthemum* type; OMaT); rich, moist (*Oxalis-Myrtillus* type; OMT); medium, sub-mesic (*Myrtillus* type; MT); rather poor, sub-dry (*Vaccinium* type; VT). The same fertility levels were applied to peat soils as classified by Laine et al. (2012). The podzol soil texture type was defined by visual inspection and feel test based on the major fraction as coarse mineral soil (>0.2 mm, particle size easily observable), medium coarse mineral soil (0.02–0.2, individual particles are distinguishable, grains detached), or fine mineral soil (<0.02, individual particles are not visible). The fourth soil type category was peat. Stoniness was classified into three categories according to visible stoniness, ranging from few stones (proportion of stones < 30 % of surface soil volume), through normal stoniness (30–60 %), to very stony (> 60 %), using the method developed by Viro (1952).

On each sample plot, all original and supplemental planted spruce seedlings were identified. The health status of each planted spruce was assessed using the following categories: healthy seedling, slightly damaged (some needles damaged without affecting further development

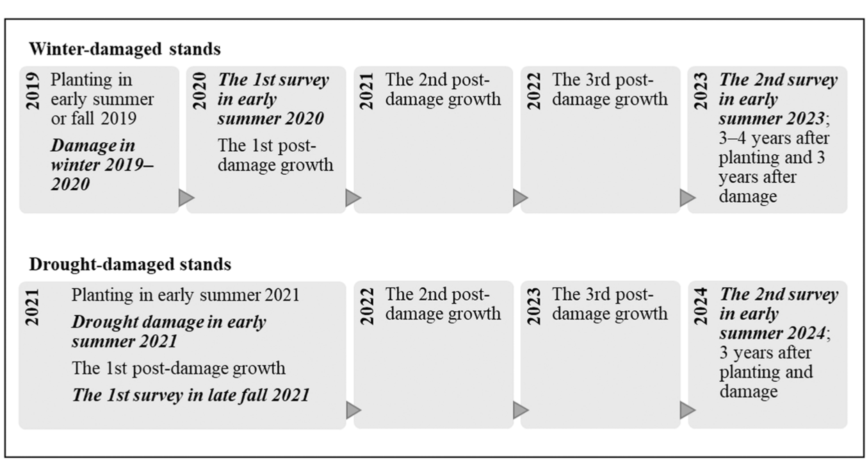

Fig. 1. Timing of spruce planting, abiotic damage, and survey of winter- and drought-damaged stands.

of the seedling), weak (seedling likely to survive but some effect on further development likely), severely damaged (seedling still alive but likely to die), and dead. Healthy and slightly damaged planted spruce trees were classified as viable crop trees.

If there were not enough planted crop-tree spruce seedlings, supplemental natural crop trees were selected, with a maximum of eight crop trees per plot. The height of the natural crop trees had to be at least half and at most 1.5 times the height of the planted spruces, and the distance between the crop trees had to be at least 1 m. From the identified natural crop trees, conifers (spruce or pine) were selected first, then silver birch (*Betula pendula* Roth), and finally downy birch (*Betula pubescens* Ehrh.).

Each planted spruce (crop tree or not) and natural crop tree on the sample plot was recorded by tree species, origin (originally planted, supplementary planted, or natural), and the structure of the growing point (unprepared soil, good quality mound, mound made on slash or stones, humus mound, patches (including those of spot mounds), or other topsoil disturbance such as the wheel groove of a driving machine). The heights of the planted spruces were measured at the end of the last four growing seasons, as was the total height of the natural crop trees. For the planted spruces, the last three annual increments (i.e., first-, second-, and third-year growths after winter and drought damage) were calculated. The condition of the leader shoot of each planted spruce was classified as follows: one original leader shoot; previous (third) year's growth dry or dead, but new growth in the lower part of the shoot; multiple stems in the previous (third) year's growth; leader shoot changed in the second year's growth, but one leader shoot in the current shoot; leader shoot changed in the first year's growth, but one leader shoot in the current shoot; and no clear leader shoot, shrub-like seedling. Planted spruce with a change in the leader shoot and multiple stems formed in the first or second year after abiotic damage were classified as damaged spruce with reduced quality. The causes of damage were also identified (drought, waterlogging, pine weevil (*Hylobius abietis* L.) damage (no damage, new or old feeding damage), insects other than pine weevil, animals (e.g. birds, moose, voles, deer), early season frost, fall frost, planting failure, competition with field vegetation, winter drought, other known or unknown reasons).

2.3. Open geospatial data

Several topographic and climatic variables available from open data sources were used to analyze the probability of reduced quality of planted spruce in the damaged stands (Table 1).

The terrain-derived variables included the topographic wetness index at 16 m resolution (TWI in thousands; the higher, the wetter; Salmivaara, 2016) and the depth-to-water index with thresholds of 0.5, 1, 4, and 10 ha at 2 m resolution (DTW; the higher, the drier; Salmivaara, 2020). Elevation, slope, aspect, topographic position index (TPI; elevation difference between a central grid cell and the mean of its surrounding cells) and terrain ruggedness index (TRI; root mean square deviation of elevation differences between a central grid cell and its surrounding cells) variables were calculated based on the 2 m digital elevation model (National Land Survey of Finland, 2023). Zonal statistics for each variable (mean, standard deviation, median, minimum, maximum, and majority) were calculated for each circular sample plot and used as potential predictors in the modeling. Depending on the resolution of the input data (2 m or 16 m), the number of values contributing to the sample plot statistics varied between 9 and 16 at 2 m resolution and 1–4 at 16 m resolution.

Climatic variables such as daily minimum, maximum and mean temperature, precipitation and potential evaporation were extracted from the closest grid (1 km × 1 km) in the gridded datasets of the Finnish Meteorological Institute (2022). Monthly values were calculated from the daily values, and monthly climate variables were used in the modeling.

Table 1
Descriptive statistics of open-source and field-assessed variables of sample plots (28 m^2) in a total of 37 winter-damaged and 41 drought-damaged planted spruce stands in central and southern Finland. Monthly climatic variables in June and July of the years following the abiotic damage are presented.

	Winter-damaged stands n = 331		Drought-damaged stands n = 348	
Open-source variables[a]	Mean ± SD	Range	Mean ± SD	Range
Digital elevation model, m	117.7 ± 17.8	83.0–151.4	118.8 ± 50.3	2.6–231.9
TWI (in thousands)	7.4 ± 1.5	4.6–14.6	7.4 ± 1.5	5.0–13.2
DTW with 0.5 ha threshold, m	0.8 ± 0.9	0.0–4.4	0.9 ± 1.1	0.0–6.5
TPI, dm	0.0 ± 0.2	−1.1–0.9	0.0 ± 0.1	−0.3–0.7
TRI, dm	3.7 ± 2.8	0.8–20.1	3.6 ± 2.1	1.0–11.6
Precipitation sum in June 2020, mm	68.2 ± 14.1	40.7–101.6	–	–
Mean temperature in June 2020, °C	17.5 ± 0.5	15.9–18.1	–	–
Precipitation sum in July 2020, mm	112.9 ± 26.3	79.2–172.0	–	–
Mean temperature in July 2020, °C	15.7 ± 0.5	14.7–16.6	–	–
Max temperature in July 2020, °C	26.3 ± 0.2	25.6–26.6	–	–
Precipitation sum in June 2021, mm	68.2 ± 14.1	40.7–101.6	41.2 ± 19.6	17.6–95.5
Mean temperature in June 2021, °C	18.9 ± 0.4	17.3–19.4	18.8 ± 0.7	17.1–19.8
Precipitation sum in July 2021, mm	44.3 ± 12.9	20.9–67.8	36.3 ± 11.5	21.6–66.4
Mean temperature in July 2021, °C	20.1 ± 0.6	18.7–21.0	20.1 ± 0.8	18.6–21.3
Max temperature in July 2021, °C	31.9 ± 0.3	31.1–32.4	31.8 ± 0.6	30.7–32.8
Precipitation sum in June 2022, mm	71.6 ± 10.3	51.2–100.8	58.0 ± 21.1	26.7–98.8
Mean temperature in June 2022, °C	15.8 ± 0.3	15.0–16.2	15.9 ± 0.6	14.8–16.9
Precipitation sum in July 2022, mm	85.0 ± 20.4	46.1–125.5	74.6 ± 23.5	32.9–121.0
Mean temperature in July 2022, °C	17.7 ± 0.5	16.4–18.6	17.5 ± 0.7	15.9–18.2
Max temperature in July 2022, °C	30.2 ± 0.5	29.4–30.9	29.9 ± 0.7	28.4–31.4

Field-assessed variables		N	%	N	%
Site type	Rich (*Oxalis-Myrtillus* type)	8	2.4	113	31.7
	Medium (*Myrtillus* type)	276	83.4	228	64.0
	Rather poor (*Vaccinium* type)	47	14.2	15	4.2
Soil texture	Fine	90	27.2	115	32.3
	Medium	206	62.2	186	52.2
	Coarse	1	0.3	15	4.2
	Peat	34	10.3	39	11.0

[a] TWI = topographic wetness index; DTW = depth-to-water index; TPI = topographic position index; TRI = terrain ruggedness index. All terrain-derived variables at 2 m resolution, except TWI at 16 m resolution.

2.4. Data analysis

The regeneration result was analyzed by calculating the number of originally planted crop-tree spruce seedlings ha^{-1} and the total number of crop trees ha^{-1}. The regeneration result was classified as moderate (1200 ha^{-1}), good (1600 ha^{-1}) and excellent (1800 ha^{-1}) based on the future wood production of the stand.

The number of originally planted crop-tree spruces in the second survey (N_2) was compared to the number of planted spruces that were healthy or predicted to recover from damage in the first survey (N_1) (Fig. 3). Recovery of spruce trees from abiotic damage was defined as the ratio of spruce trees in the second and first surveys (N_2/N_1). Note that the total number of spruce trees originally planted in the first and second surveys may not be the same due to sampling error (the sample plots from the first surveys were not located and therefore not remeasured),

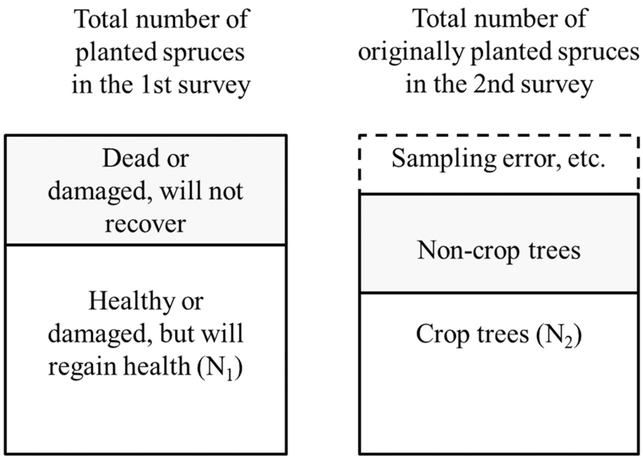

Fig. 3. Recovery of originally planted spruce seedlings from abiotic damage was defined as the ratio of the number of originally planted spruce seedlings that were crop trees at the second survey (N_2) to the number of planted spruce seedlings that were healthy or predicted to recover from abiotic damage at the first survey (N_1).

and some of the dead trees may have been completely destroyed, and it was not possible to know for empty mounds if they were unplanted or if the seedlings died and disappeared until the second survey. In addition, planted spruce trees that were predicted to recover may not have recovered and/or may have been damaged by other agents, and therefore, the number of planted crop-tree spruces in the second survey would be lower than expected. Conversely, if more spruce trees had recovered, more planted crop-tree spruces would be observed in the second survey.

The effects of exceptional weather conditions on the leader shoot, i.e. multiple stems, were expected to be observed in the first or second year of growth after abiotic damage. Pearson's chi-squared test for homogeneity (the function chisq.test in the R package stats; R Core Team, 2024) was used to test for differences between non-crop and crop-tree spruce trees, and spruce trees with respect to the condition of the leader shoot and the cause of damage. Spruce seedlings were defined as damaged if multiple leaders were formed in the first or second year after abiotic damage.

The post-damage height development of healthy and damaged crop-tree spruce seedlings was compared by fitting a multilevel normal model. The lmer function in the R package lme4 was used for fitting (Bates et al., 2015). The response variables (annual height growth and total height) were square root transformed to normalize the distribution. Due to the hierarchical and unbalanced data structure, the random, normally distributed between-stand and between-plot effects were included in the intercept of the model. The Anova function in the R package stats was used to compare healthy and damaged crop-tree spruce seedlings.

The probability of reduced quality of planted spruce (i.e., seedlings with multiple stems in the first or second year of growth after abiotic damage) was modeled using a multilevel binomial model with a logit link function (McCulloch and Searle, 2001). The random, normally distributed between-stand and between-plot effects were included in the intercept of the model. The glmmPQL function in the R package MASS (Venables and Ripley, 2002) was used to fit the model. Packaging (box, open) and storage (freezer-stored, fresh) methods and planting periods (May, June, July, September), as well as plot-level field-assessed variables (site type, soil texture, stoniness) and open-source variables (topographic and climatic variables) were included in the models as potential predictors. Also, the fixed observer effect was included to account for the between-observer variation in determining the reduced quality of planted spruce (two observers in 2023 and 2024). Comparisons between groups of categorical variables (e.g. planting periods) were based on statistically significant differences ($p < 0.05$) between group-specific parameters, evaluated using the linearHypothesis function in the R package car (Fox et al., 2013). Pseudo-R2 values were calculated using the function r.squaredGLMM in the R package MuMIn (Bartoń, 2020) and only fixed predictors (i.e. marginal models).

3. Results

3.1. Regeneration outcome 3–4 years after planting

In the winter-damaged and drought-damaged stands, 96 % (range 77–100 %) and 92 % (range 68–100 %) of the originally planted spruce seedlings, respectively, were determined to be crop trees (Table 2). The number of originally planted crop-tree spruce seedlings in both the winter- and drought-damaged stands averaged about 1500 trees ha^{-1}. In

Table 2
Main characteristics of the winter-damaged (n = 37) and drought-damaged (n = 41) spruce stands, initially surveyed after damage and re-surveyed three growing seasons later.

Variable	Winter-damaged stands		Drought-damaged stands	
	Mean ± SD	Range	Mean ± SD	Range
The first survey[a]				
Total number of planted spruce seedlings, ha^{-1}	1756 ± 167	1429–2188	1630 ± 248	992–2009
Number of planted healthy or recovered spruce seedlings (N_1), ha^{-1}	1250 ± 442	71–1875	1464 ± 286	794–1964
Percentage of planted healthy or recovered spruce seedlings, %	71 ± 24	4–99	90 ± 10	62–100
The second survey				
Total number of originally planted spruce seedlings, ha^{-1}	1549 ± 266	865–2034	1633 ± 221	1017–1989
Number of originally planted crop-tree spruce seedlings (N_2), ha^{-1}	1491 ± 256	865–1989	1509 ± 255	752–1945
Percentage of originally planted crop-tree spruce seedlings, %	96 ± 5	77–100	92 ± 8	68–100
Percentage of originally planted crop-tree spruce seedlings with one leader, %	65 ± 19	25–95	73 ± 11	46–90
Percentage of originally planted crop-tree spruce seedlings with winter or drought damage[b], %	27 ± 18	0–65	10 ± 6	0–30
Number of supplementary planted crop-tree spruce seedlings, ha^{-1}	52 ± 138	0–575	9 ± 55	0–354
Number of natural crop-tree spruce seedlings, ha^{-1}	104 ± 118	0–442	75 ± 117	0–354
Number of natural crop-tree pine seedlings, ha^{-1}	105 ± 135	0–542	90 ± 128	0–486
Number of natural crop-tree silver birch seedlings, ha^{-1}	194 ± 159	0–629	138 ± 172	0–707
Number of natural crop-tree downy birch seedlings, ha^{-1}	136 ± 161	0–747	96 ± 119	0–531
Total number of planted and natural crop trees, ha^{-1}	2082 ± 304	1547–2751	1916 ± 267	1415–2476
Conifers as a percentage of all crop trees, %	85 ± 11	51–100	88 ± 10	56–100
Originally planted crop-tree spruce seedlings as a percentage of all crop trees	75 ± 13	37–92	79 ± 12	47–100
Recovery of originally planted spruces (N_2/N_1), %	204 ± 378	79–2179	106 ± 23	57–151

[a] In the first survey, the recovery of planted spruce seedlings from abiotic damage was predicted.
[b] Damage was determined if there had been a change in the leader shoot in the first or second year after exceptional weather conditions.

a total of nine stands, less than 1200 originally planted crop-tree spruce seedlings ha^{-1} were found, due to low planting density and abiotic damage (Fig. 4A). One third of the winter-damaged stands and half of the drought-damaged stands had more than 1600 originally planted crop-tree spruce seedlings ha^{-1}, which is the limit for successful regeneration in spruce plantations in Finland. The planting density measured in the first survey had a positive and significant effect on the number of planted crop-tree spruce seedlings in the second survey (Fig. 4A).

When naturally regenerated and supplementally planted crop trees (found in nine winter-damaged and one drought-damaged stand) were included, the total number of crop trees averaged about 2080 trees ha^{-1} (range 1550–2750) in the winter-damaged stands and 1920 trees ha^{-1} (range 1420–2480) in the drought-damaged stands (Table 2). More than 1600 crop trees ha^{-1} were found in 97 % and 80 % of the winter- and drought-damaged stands, respectively, (Fig. 4B). The proportion of conifer crop trees (planted spruce and seed-born pine and spruce) in the winter and drought damaged stands was 85 % (range 51–100 %) and 88 % (range 56–100 %), respectively, which means that all stands are likely to be dominated by conifers in the future.

3.2. *Recovery and damage of planted spruce seedlings 3 years after abiotic damage*

The recovery of planted spruces from abiotic damage varied considerably among stands and damaging agents (Fig. 5). In the first survey, the recovery of spruce from winter damage was more often underestimated than the recovery from drought damage. For example, in two winter-damaged stands, only about 100 spruce seedlings ha^{-1} were predicted to recover in the first survey, but almost 1600 originally planted crop-tree spruce seedlings ha^{-1} were found in the second survey.

The winter- and drought-damaged stands differed in the causes of damage for both non-crop spruce seedlings ($\chi2(6) = 14.4$, $p = 0.026$) and crop tree spruce seedlings ($\chi2(6) = 122.0$, $p < 0.001$). In planted non-crop spruce seedlings, the most common causes of damage were drought, waterlogging, insects (mainly pine weevil) and animal pests, and competition with ground vegetation and unwanted broadleaves (Fig. 6A). Of the non-crop spruce seedlings, 21 and 26 % were dead, 4 and 8 % were severely damaged, and 67 and 65 % were weak in the winter- and drought-damaged stands, respectively. Spring or fall frost and competition with other plants caused minor damage to the crop trees, and the drought was also considered to have caused minor damage in the drought-damaged stands. Pine weevil feeding damage was assessed in all planted spruce trees (non-crop and crop trees combined) and was found in 19 % and 22 % of the seedlings inventoried in winter- and drought-damaged stands, respectively. In the second survey of the winter- and drought-damaged stands, only 0.3 % and 0.1 % of the originally planted and inventoried spruce seedlings, respectively, were dead due to pine weevil feeding. Of the seedlings with pine weevil feeding scars, 4 % and 7 % were slightly damaged and 13 % and 13 % were healthy.

Abiotic damage was still visible in the leader shoots of originally planted crop-tree spruce seedlings, i.e. the leader shoot had changed in the first or second year after exceptional weather conditions. Among the originally planted crop-tree spruce seedlings, the proportion of spruce seedlings with such a change in the leader shoot was on average 27 % (range 0–65 %) in the winter-damaged stands and 10 % (range 0–30 %) in the drought-damaged stands (Table 2). Considering all leader shoot damage during the three post-damage growing seasons, the proportion of crop-tree spruce seedlings with one leader was on average 65 % (range 25–95 %) and 73 % (range 46–90 %) in the winter- and drought-damaged stands, respectively.

The poor condition of the leader shoot and especially the multiple stems was the main reason for classifying planted spruce seedlings as non-crop trees (Fig. 6B). Approximately 40 % of the non-crop trees had multiple stems that had been formed over three growing seasons following abiotic damage. In addition, non-crop spruce seedlings had dead leader shoots, especially in winter-damaged stands. Based on the homogeneity test (Pearson's chi-square), the condition of leader shoots of non-crop and crop spruce seedlings after three post-damage growing seasons was different in both winter-damaged ($\chi2(5) = 339.8$, $p < 0.001$) and drought-damaged stands ($\chi2(5) = 87.8$, $p < 0.001$). The winter- and drought-damaged stands differed in the condition of the leader shoots of both non-crop spruce seedlings ($\chi2(5) = 31.9$, $p < 0.001$) and crop tree spruce seedlings ($\chi2(5) = 255.8$, $p < 0.001$).

In the winter-damaged stands, the proportion of planted spruce seedlings damaged in the first survey correlated significantly and negatively with the proportion of planted crop-tree spruce seedlings with a leader shoot and with the mean height of planted crop-tree spruce seedlings in the second survey (Fig. 7). The higher the proportion of originally planted crop-tree spruce seedlings with leader shoot damage, the lower the height growth of these spruce seedlings (Fig. 8). In the drought damaged stands the correlations were also negative, but not statistically significant.

Annual height growth and total height of damaged crop-tree spruce seedlings were significantly lower than those of healthy crop-tree spruce seedlings, except for growth in the third year after drought damage ($\chi2(1) = 1.0$, $p = 0.323$) (Fig. 9). Crop-tree spruce seedlings were defined as damaged if multiple stems were formed in the first or second year after abiotic damage.

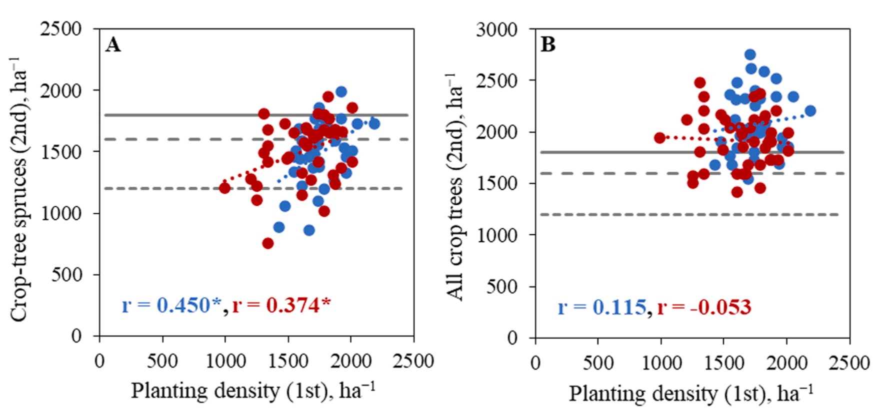

Fig. 4. The number of crop-tree spruce seedlings originally planted (A) and all crop trees, both planted and naturally regenerated (B) in the second survey in relation to the planting density observed in the first survey. Blue and red colors indicate winter and drought damaged stands, respectively. Horizontal dotted, dashed and solid lines indicate the limits of 1200, 1600 and 1800 trees ha^{-1}, respectively. Statistically significant ($p < 0.05$) Pearson's correlation coefficients (r) are indicated with asterisks (*).

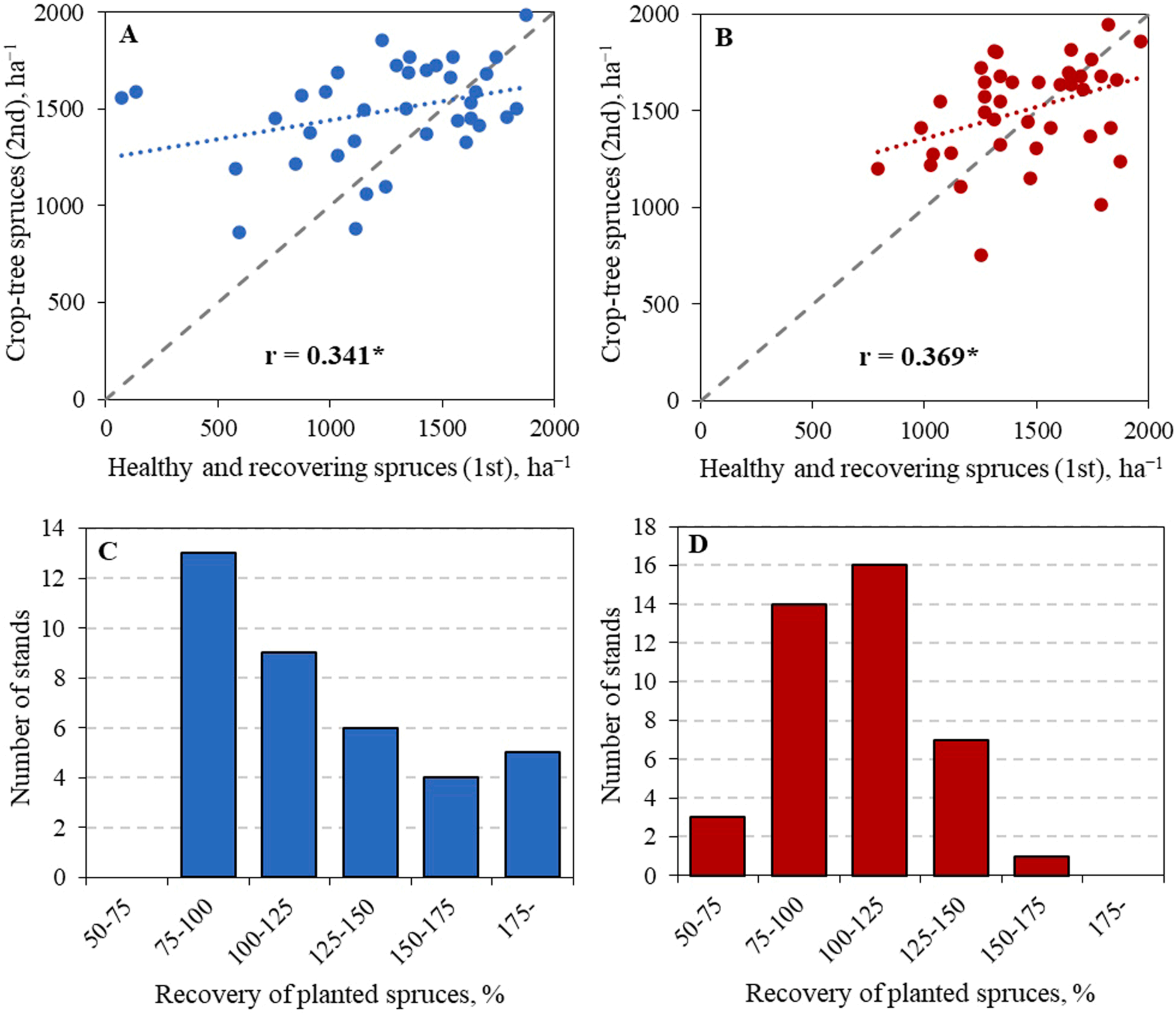

Fig. 5. Recovery of planted spruce seedlings from winter (A, C) and drought (B, D) damage. Above: The number of planted crop-tree spruce seedlings in the second survey relative to the number of spruce seedlings that were healthy or predicted to recover from damage in the first survey (A, B). Statistically significant ($p < 0.05$) Pearson's correlation coefficients (r) are indicated by asterisks (*). Histogram of recovery, i.e. the ratio between the number of crop-tree spruce seedlings in the second survey and the number of planted spruce seedlings that were healthy or predicted to recover in the first survey (C, D).

3.3. *Factors influencing the quality of planted spruce seedlings*

In winter-damaged stands, site type, the interaction of packaging method and planting month, and the topographic position of a sample plot (topographic position index) significantly predicted the probability of reduced quality of planted spruce seedlings (Table 3). The pseudo-R^2 of the model was 19.0 %. Packaging method and month of planting ($\chi 2$ (7) $= 32.65$, $p < 0.001$) were the most important predictors in the model. Compared to open trays, the risk was higher when spruce seedlings were packed and stored in a closed package and planted in June or July (Fig. 10A). Regardless of the packaging method, the risk of reduced quality was high for fall planting. The risk of reduced quality was higher for seedlings planted on top of hills and on poor sites (VT) (Fig. 10B).

In the drought-damaged stands, the probability of reduced quality of planted spruce seedlings was influenced by the storage method; the risk of damage was lower for seedlings stored in the freezer than for fresh seedlings packed in boxes or open trays. (Table 4; Fig. 11A). However, more important predictors were the weather conditions during the growing season of the planting year 2021 and the following growing season in 2022. A high precipitation sum in June and July 2021 decreased (Fig. 11C) and a high mean temperature in July 2022 (Fig. 11D) increased the risk of reduced quality. The temperature sum of the stand had a significant effect on the probability of reduced quality of planted spruce trees; the higher the temperature sum, the lower the risk (Fig. 11B). The temperature sums probably described the south-north orientation of the stands or other location-dependent effects that could not be accounted for. The pseudo-R^2 value of the model was only 5.2 %. Both in the winter- and drought-damaged stands, the observer effect was insignificant ($p > 0.05$), indicating that the reduced quality of planted spruce seedlings was interpreted similarly by two observers.

4. Discussion

When comparing the prediction made immediately after damage with the recovery three years later, spruce seedlings recovered better from winter damage than from drought damage. In the drought-

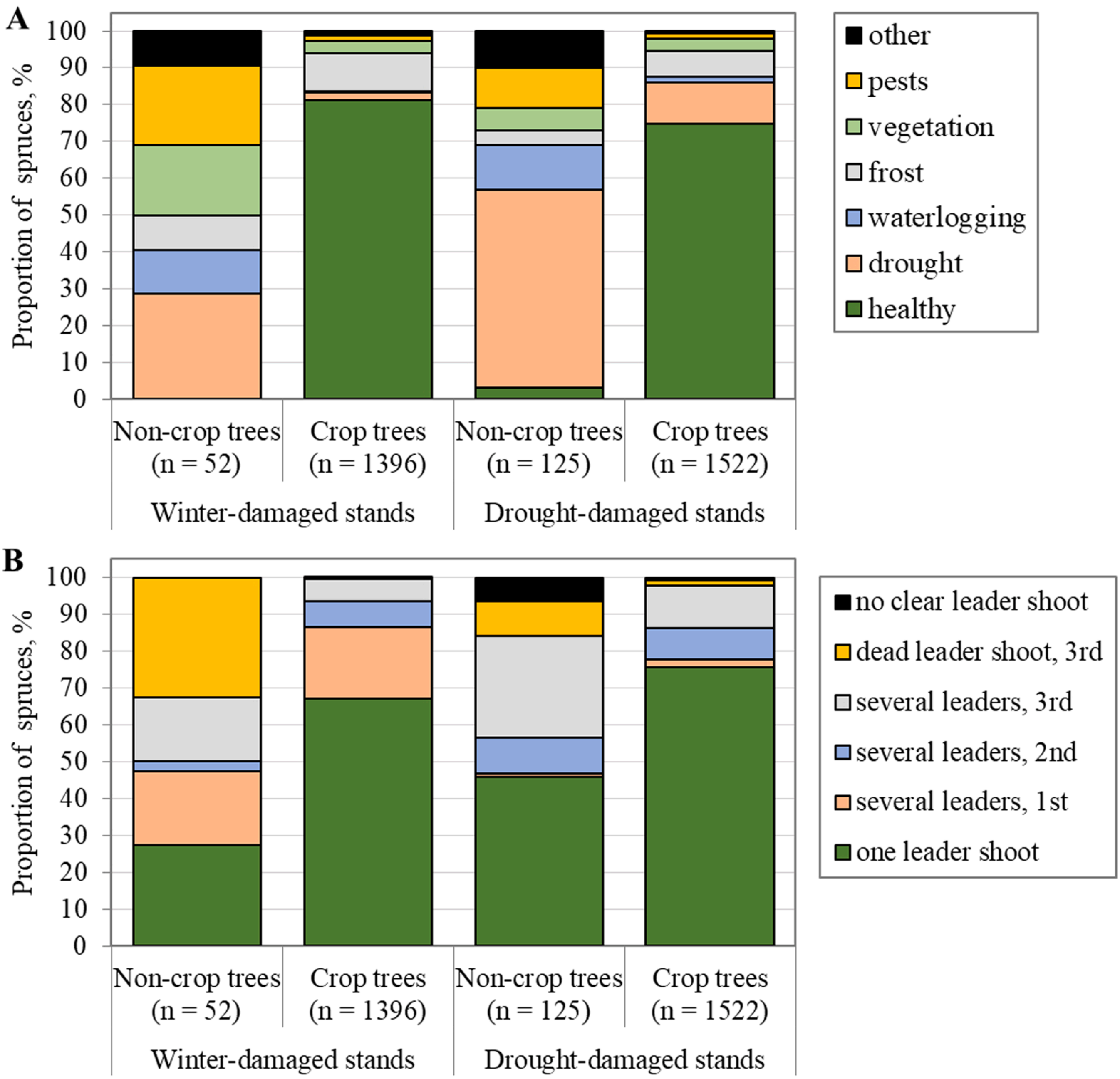

Fig. 6. Cause of damage (A) and condition of the leader shoot (B) of non-crop and crop-tree spruce seedlings in winter- and drought-damaged stands examined 3 years after damage. Multiple stem formation was detected in the first, second and third year after abiotic damage.

damaged stands, the number of crop-tree spruce seedlings assessed three years after damage was on average close to the number of spruce seedlings assessed as healthy or predicted to recover from damage immediately after damage, whereas spruce recovery from winter damage was more often underestimated. The nature of the winter and drought damage was different. This affected the further development of the seedlings. In winter-damaged stands, the main cause of damage was most likely due to desiccation or frost injury of shoots during the winter (Luoranen et al., 2022a). During winter, air temperatures are about 10 °C lower and temperature fluctuations are stronger than in soil temperatures in mounds (Lindström and Troeng, 1995), so shoots are more exposed to temperature fluctuations than roots. In addition, fluctuating air temperatures and high solar radiation during clear, windy days in late winter and early spring increase transpiration and lead to needle and stem desiccation when root water uptake is prevented in frozen soils in late winter or early spring (Larcher, 1995; Krasowski and Simpson, 2001). The root system of planted seedlings was protected by the frozen soil in winter-damaged stands, the roots and lower parts of the stems were not damaged, and growth started from dormant buds at the base of the stem. At the time of the first inventory of winter-damaged stands, seedling growth had not begun in stands inventoried in late spring and early summer (Luoranen et al., 2022a), and thus recovery of damaged seedlings could not be reliably predicted.

The other reason for differences in recovery is related to differences in root growth and root system size of seedlings. Water availability and root growth immediately after planting are essential for the successful establishment and development of newly planted seedlings (Burdett, 1990). At the time of drought stress, newly planted seedlings were not rooted in the drought-damaged stands. However, in the winter-damaged stands, seedlings planted in the spring and summer were well-rooted at

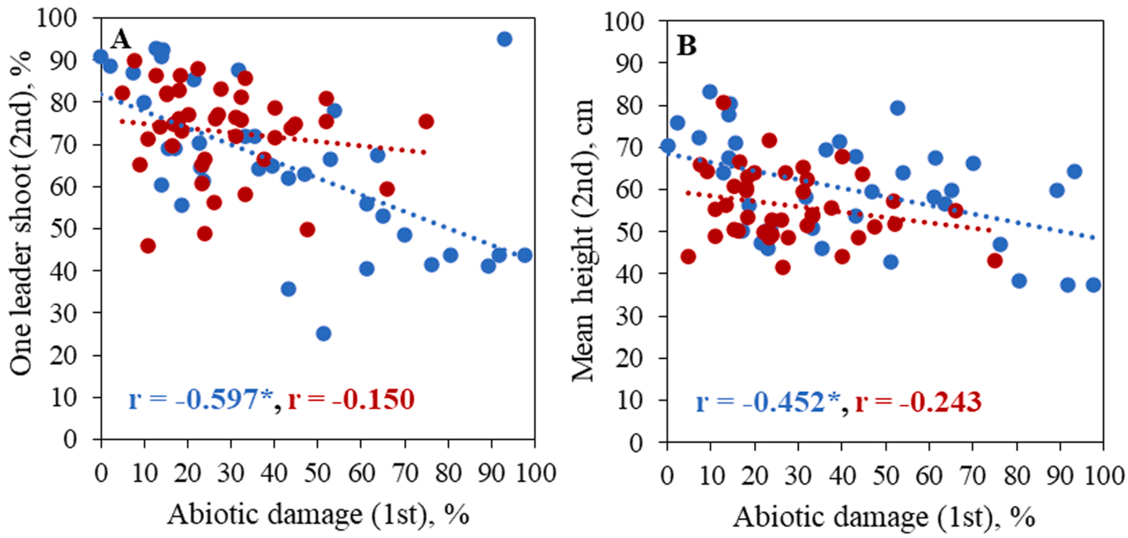

Fig. 7. The proportion of originally planted crop-tree spruce seedlings with a leader shoot (A) and the mean height (B) of originally planted crop-tree spruce seedlings in the second survey in relation to the proportion of damaged spruce seedlings in the first survey. Winter- and drought-damaged stands are indicated by blue and red colours, respectively. Statistically significant ($p < 0.05$) Pearson's correlation coefficients (r) are indicated by asterisks (*).

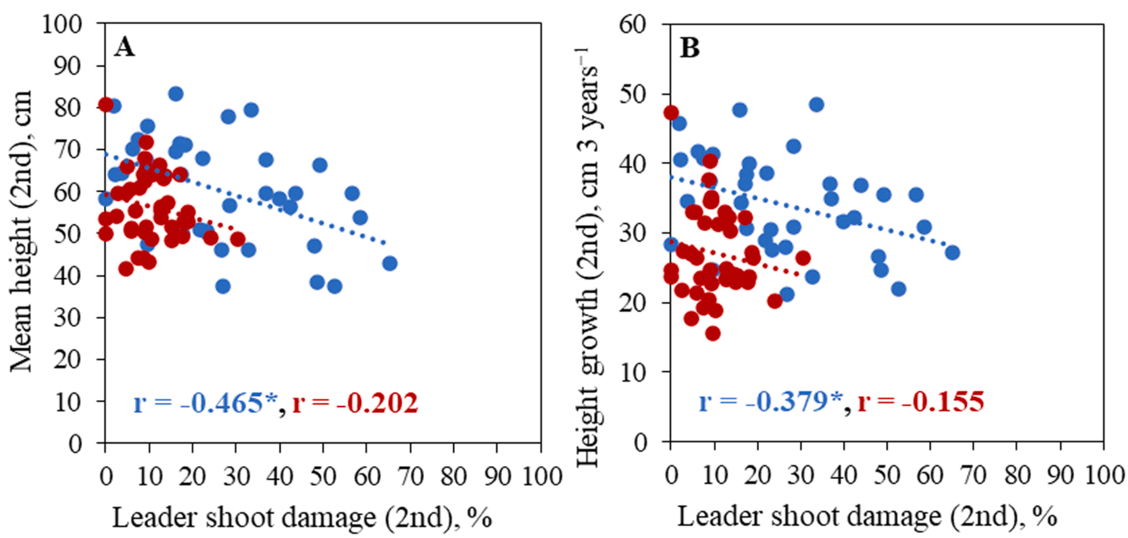

Fig. 8. Mean height (A) and three-year height growth (B) of originally planted crop-tree spruce seedlings in relation to the proportion of originally planted crop-tree spruce seedlings with leader shoot damage in the second survey. Winter- and drought-damaged stands are indicated in blue and red, respectively. Statistically significant ($p < 0.05$) Pearson's correlation coefficients (r) are indicated by asterisks (*).

the end of the planting summer and had adapted to their site prior to the extreme winter weather events. Seedlings with well-developed root systems at the time of injury had a better ability to recover from injury than poorly rooted seedlings (Grossnickle and Ivetić, 2022). Wallertz et al. (2016) observed this in fall-planted spruce seedlings, which recovered more poorly from pine weevil feeding damage than earlier-planted, better-rooted seedlings. Similarly, the poor rooting of fall-planted seedlings likely explains why they did not recover from winter injury as well as earlier-planted seedlings. When spruce seedlings are planted in September in central Finland, the seedlings do not have root growth in the planting year (Luoranen, 2018). Shoot injury further reduces root growth in the growing season following the injury (Colombo and Glerum, 1984). Poorly rooted seedlings then start their root growth later (Luoranen, 2018) and may not recover from damage as well as earlier planted, better-rooted seedlings.

Although seedlings recovered from damage, abiotic damage had an impact on regeneration outcomes through reductions in seedling quality and height growth. The number of crop-tree spruce seedlings was lower than required for successful regeneration (i.e. >1600 crop trees ha^{-1}) at most sites and decreased with decreasing planting density. Compared to recent studies in Finland, the number of crop-tree spruce seedlings was slightly lower, as in previous studies > 1500 planted spruce seedlings ha^{-1} were observed to be alive three years after planting in the mounded mineral soil site (Luoranen and Viiri, 2021; Luoranen et al., 2022b). Based on the Finnish National Forest Inventory (NFI) data, the average number of crop-tree spruce seedlings planted just before the inventory was 1660 seedlings ha^{-1}, but in 2–5-year-old spruce stands the number of seedlings decreased to 1350 seedlings ha^{-1} (Korhonen et al., 2010). Thus, the spruce regeneration results were better than average in southern Finland, despite the known abiotic damage. In Sweden, Holmström et al. (2019) observed that the number of planted spruce seedlings decreased from 2000 to 1500 seedlings ha^{-1} in three years.

Multiple stems were the main reason for the classifying planted spruces as non-crop trees. In the Finnish NFI (Korhonen et al., 2010), the

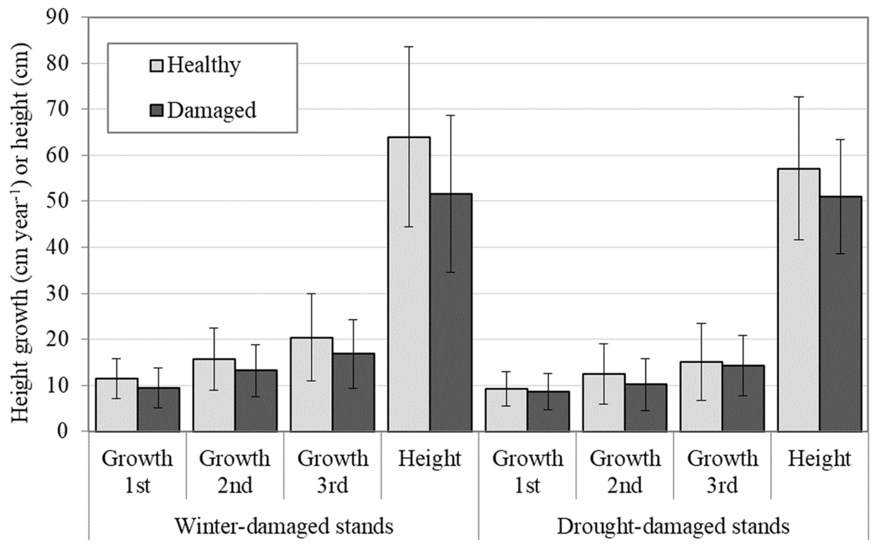

Fig. 9. Mean (± SD) height growth in the first, second and third year after damage and total height of healthy and damaged crop-tree spruce seedlings in winter- and drought-damaged stands. A spruce was defined as damaged if multiple stems were formed in the first or second year after abiotic damage. Bars of healthy and damaged spruce seedlings marked with * * ($p < 0.01$) and * ** ($p < 0.001$) are significantly different (type III Wald $\chi2$ test).

Table 3
Parameter estimates of the multilevel binomial model estimated for the probability of reduced quality of planted spruce seedlings (i.e., leader shoot had changed in the first or second growth) in winter-damaged stands. χ^2 is the combined Wald χ^2 test of categorical fixed effects (type III test), degrees of freedom in parentheses. The modeling data consist of 1436 originally planted spruce seedlings, of which 378 spruce seedlings with a change in the leader shoot (26 %).

Variable	Estimate[a]	Std error	t-value	p
Intercept	−1.811	0.672	−2.70	0.007
Topographic position index (TPI)	4.104	2.015	2.04	0.043
Site type (ref. OMT)		$\chi^2(2) = 6.44$		0.040
MT	−0.267[a]	0.506	−0.53	0.598
VT	0.524[b]	0.591	0.89	0.376
Packaging: Planting month (ref. Box: May)		$\chi^2(7) = 32.65$		< 0.001
Box: June	0.333[bc]	0.930	0.36	0.723
Box: July	1.394[a]	0.559	2.49	0.019
Box: September	1.165[ab]	0.514	2.26	0.031
Open: May	−0.299[c]	0.566	−0.53	0.602
Open: June	−2.748[d]	1.133	−2.43	0.022
Open: July	−0.211[c]	0.579	−0.36	0.719
Open: September	0.932[b]	0.537	1.73	0.093
Random effects	Variance			
Stand (n = 37)	0.390			
Sample plot (n = 328)	0.409			

[a] Estimates for the fixed effect with different letters are significantly different ($p < 0.05$).

symptom 'leader shoot change' reduced the quality of 11 % of the total area of young spruce stands (mean height < 1.3 m), which is comparable to the level observed in the drought-damaged stands, but the probability of multiple stems was higher in the winter-damaged stands.

In addition, there were stressors other than winter and drought damage that affected regeneration outcome, and reduced seedling quality, and may have increased the proportion of seedlings with multiple stems. Pine weevil feeding damage was found in both surveys, but the effect of feeding on seedling health was small. Only a few seedling mortalities due to pine weevil feeding were found, which is comparable to the previous experimental studies in Finland (Luoranen et al., 2017, 2022b). However, pine weevils can cause minor damage even to over 60 % of spruce seedlings planted in mounds and protected from feeding by either insecticides or other protective methods prior to planting (Luoranen et al., 2017, 2022b, 2024b). Similar to abiotic damage when the root system is alive pine weevil feeding damage can also result in multiple stems (Luoranen et al., 2017). Browsing by cervids and voles is also a known cause of multiple stems and quality defects in seedlings (e.g. Bergquist et al., 2003; Huitu et al., 2013), and some browsing damage (species unknown) was observed in the first inventory of winter-damaged stands (Luoranen et al., 2022a). Night frosts during the growing season can also kill buds and leader shoots, cause multiple stems in seedlings, and reduce growth (Langvall et al., 2001). In the winter-damaged stands, some seedlings were so severely damaged by competition that they were classified as non-crop trees. Seedlings are less able to compete with other vegetation, either herbaceous or seed-born broadleaves, when damage reduces the growth of seedlings,

Planting date played an important role in explaining the reduced quality in both damage types, packaging method interacted with planting date in winter-damaged stands, and packaging and storage methods played a minor but significant role in drought-damaged stands. Immediately after drought damage, the difference in damage risk between freezer-stored and fresh seedlings was particularly pronounced for June plantings (Luoranen et al., 2023). In June, fresh seedlings delivered from the field are actively growing and their stress resistance and ability to root under drought stress is poorer than that of dormant seedlings stored in freezer (Helenius et al., 2005), which probably explains why the risk of abiotic damage and reduced quality was higher for fresh seedlings, regardless of the type of packaging, than for boxed seedlings stored in the freezer. Fresh seedlings suffered more from drought and damage was more severe (Luoranen et al., 2023), resulting in reduced quality even three years after damage. In July, at least some of the seedlings in the winter-damaged stands were probably stored in freezers and were dormant at planting. The growing season for these seedlings was too short for proper hardening before the first fall frosts and winter (Hänninen et al., 2009), and some of the damage was caused by frost rather than winter desiccation. Similar regeneration processes were observed in the drought survey, but these sites were excluded due to the above results in winter-damage stands. For summer and fall plantings, even the short periods in closed boxes can reduce root growth and frost hardiness of planted seedlings (Luoranen et al., 2019), increasing the risk of planting stress immediately after planting and winter damage the following winter.

Weather conditions during or after the damage season explained the reduced quality only in drought damaged stands. The winter-damaged

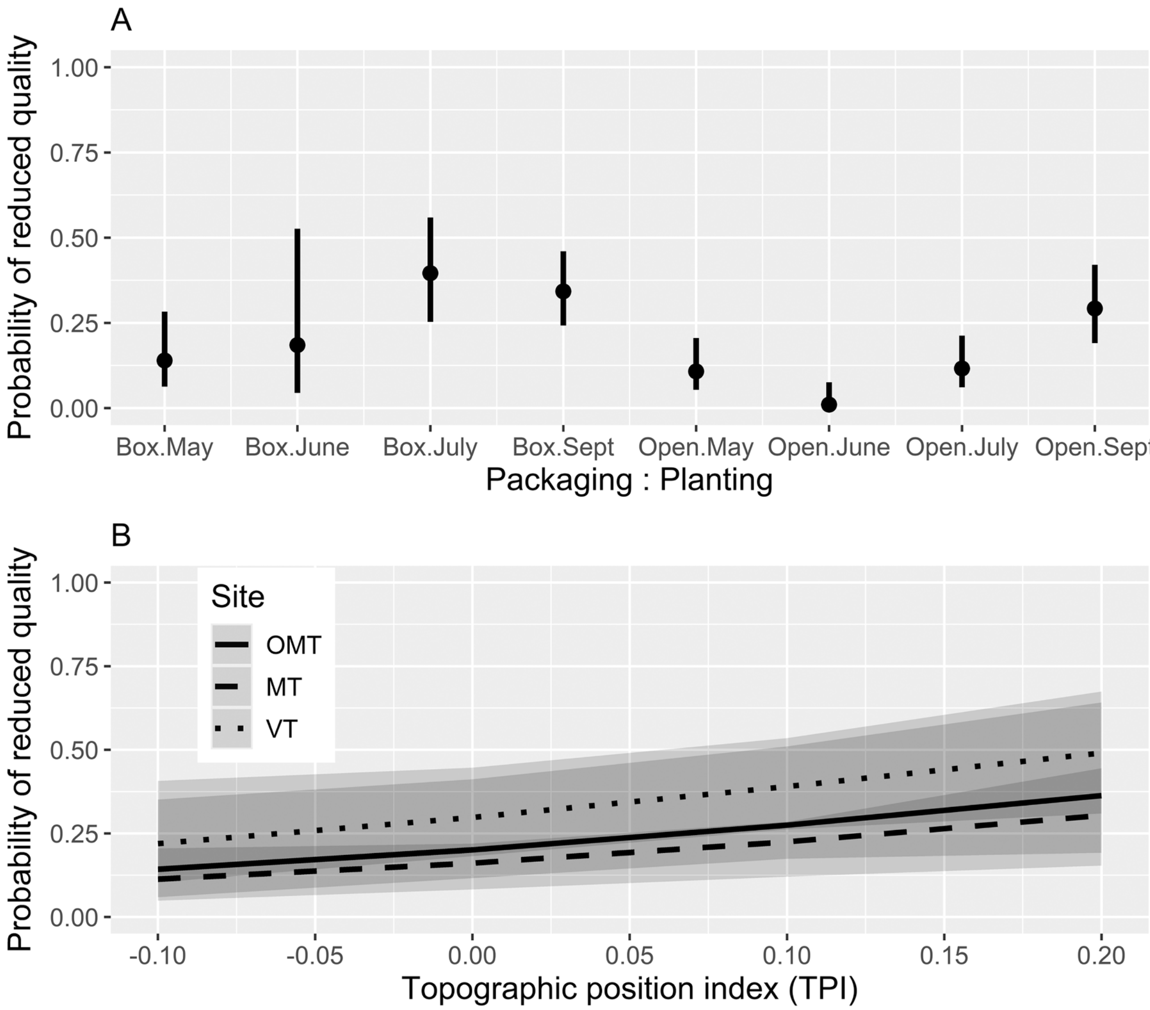

Fig. 10. Predicted tree-level response and 95 % confidence intervals of the probability of reduced quality of planted spruce seedlings in winter-damaged stands to (A) packaging method (Box, Open) and planting month (May, June, July, September), and (B) site type (OMT, MT, VT) and topographic position index (TPI) on the sample plot.

Table 4
Parameter estimates of the multilevel binomial model estimated for the probability of reduced quality of planted spruce seedlings (i.e., leader-shoot change in the first or second growth) in drought-damaged stands. χ^2 is the combined Wald χ^2 test of categorical fixed effects (type III test), degrees of freedom in parentheses. The modeling data consist of 1614 originally planted spruce seedlings, of which 171 spruce seedlings with a leader-shoot change (11 %).

Variable	Estimate[1]	Std error	t-value	p
Intercept	1.757	3.539	0.50	0.620
Packaging: Storage (ref. Box: Freezer)		$\chi^2(2) = 9.90$		0.007
Box: Fresh	0.949[a]	0.321	2.95	0.001
Open: Fresh	0.537[a]	0.243	2.21	0.034
Temperature sum 2021, dd	−0.010	0.002	−4.77	< 0.001
Precipitation sum in June-July 2021, mm	−0.054	0.011	−4.93	< 0.001
Mean temperature in July 2022, °C	0.871	0.230	3.79	< 0.001
Random effects	Variance			
Stand (n = 41)	< 0.001			
Sample plot (n = 354)	1.050			

[1]Estimates for the fixed effect with different letters are significantly different ($p < 0.05$).

stands were located in a narrow geographical area in central Finland, and the weather conditions were quite similar in all of them (Luoranen et al., 2022a). In contrast, the drought damaged stands were in the southernmost part of Finland, covering the region from the southern coast 400 km to the north, and weather conditions varied more between sites (Luoranen et al., 2023). In these stands, reduced precipitation sum in June and July of the planting summer explained the reduced seedling quality. Low precipitation sum immediately after planting means that the soil is dry and the planted seedlings are dependent on capillary water in the mounds, and the uninterrupted movement of water from the soil to the roots is threatened, especially in newly planted seedlings with poor root-soil contact (Örlander, 1986), and the seedlings are at high risk of planting stress (Grossnickle and Ivetić, 2022). Lack of water can further reduce the root growth, which later affects seedling recovery, and shoot growth.

In the first inventory, elevated temperatures two weeks after planting increased the risk of drought damage (Luoranen et al., 2023), but temperature conditions in June or July were not significant predictors of reduced quality. However, increasing in temperature sum throughout the growing season reduced the risk. This variable probably indicates the geographic location of the drought damaged stands, as the more southerly a site was, the higher the temperature sum in 2021. The higher temperature sum also means a longer growing season and, for example, more time for root growth in the fall of the year in which the damage occurred. Seedlings with larger root systems are better able to

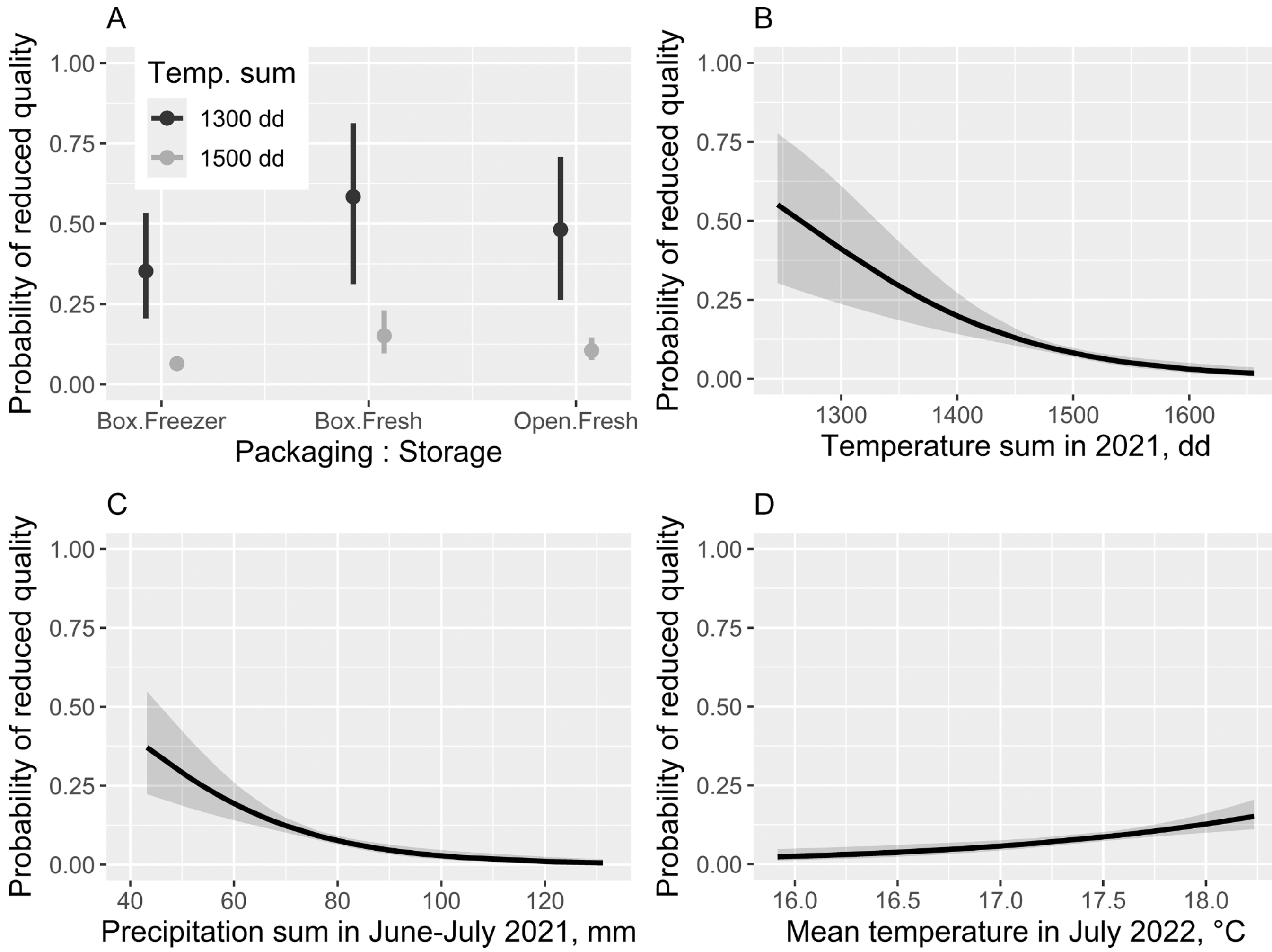

Fig. 11. Predicted tree-level response and 95 % confidence intervals of the probability of reduced quality of planted spruce seedlings in drought-damaged stands to (A) seedling packaging (Box, Open) and storage (Freezer, Fresh) methods, (B) temperature sum in 2021, (C) precipitation sum in June-July 2021, and (D) mean temperature in July 2022.

absorb water and recover from damage, as discussed above. The importance of soil moisture conditions, annual variation in available water, precipitation and temperature conditions for seedling survival after planting has been demonstrated in many studies, for example in Sweden (Holmström et al., 2019) and USA (Chen and Nelson, 2020).

Among the climatic factors, the warm weather in the following summer (July 2022) after the drought damage also increased the risk of reduced quality. This probably indicates that there was some kind of weather stress in the second year as well, and under these conditions, the initial damage can be exacerbated or prevent recovery of the leader shoot. A similar situation was observed by Luoranen et al. (2018), where low spring and early summer precipitation sums after winter damage increased the risk of leader shoot damage in summer and fall planted spruce seedlings.

The same site factors predicted a reduction in seedling quality both immediately after the damage and three years later. For example, both winter and drought damage were more likely to occur at the top of the hill (Luoranen et al., 2022a) and on slopes (Luoranen et al., 2023), and the topographic position index (TPI) predicted the risk of reduced quality three years later. Based on our results, open geospatial data can be used to calculate indices such as TPI, which can be used to predict the risk of damage, especially winter damage, and thus identify site conditions that may affect regeneration outcomes.

Naturally regenerated seedlings, where available, were selected to supplement poor quality or missing planted seedlings. As a result, nearly all winter-damaged stands and 80 % of drought-damaged stands were successfully regenerated. On the sample plots of the drought-damaged stands, drought conditions (i.e., high values for depth-to-water and topographic position indices) reduced the number of natural seedlings for a given number of planted seedlings (data not shown). In these dry conditions, the risk of poor regeneration results may also be higher if the high topographic position also increases the risk of poor quality of planted seedlings. In pre-commercial thinning of damaged spruce stands, naturally regenerated seedlings can be used to establish mixtures by allowing more admixed species, especially broadleaves, as potential crop trees (Huuskonen et al., 2021).

In the initial surveys, there were several variables that described the microtopography and quality of the planting spots and predicted the risk of damage. The risk of abiotic damage is reduced when seedlings are planted in good quality planting spots covered with mineral soil, especially in mounds (Luoranen et al., 2018, Luoranen et al., 2022, Luoranen et al., 2023; Wallertz et al., 2018). The previous studies (Örlander, 1986; Luoranen and Viiri, 2016; Luoranen et al., 2018) also found that sufficient planting depth reduced both drought and winter damage, as well as pine weevil feeding damage. We also evaluated the structure of the growing point, but it was not a statistically significant predictor in the model three or four years after planting. However, this does not diminish the importance of these factors for the establishment of the planted seedlings in regeneration sites.

The damage reduced the number of spruce seedlings with a leader shoot, and consequently the shoot damage reduced the height development of the seedlings. Growth reduction of drought- or winter-damaged spruce seedlings was already observed in the first inventories (Luoranen et al., 2022a, 2023) and this reduction continues several years after the damage. Decreased growth following multiple leadering has also been observed in other studies (e.g. Luoranen et al., 2006). Growth reduction of damaged, low quality seedlings was evident in all growing seasons after planting. Although the differences were a few centimeters per year, they multiplied over time and were 10 cm after four-year-old spruces in winter-damaged stands. This difference in the establishment phase may persist into young stands. According to the Johansson et al. (2013), height differences between seedlings planted in differently prepared soils become in the establishment phase can still be seen after 18 years. In addition, dead and severely damaged planted seedlings are replaced with naturally regenerated seedlings. Genetic gains of first and 1.5-generation seedlings of Norway spruce are 20.6 % and 36.9 % in stem volume growth, respectively (Haapanen, 2020). Natural seedlings are at least partly in unprepared soil, and there seedling growth is poorer than in prepared soil, especially in mounds (Harrington et al., 2003; Mjöfors et al., 2017; Uotila et al., 2022). Thus, a significant loss of growth and carbon stock in future forests can be result from the loss of the original planting stock due to abiotic damage.

Damage to seedlings can be expected to increase the cost of young stand management in the future. Early tending and pre-commercial thinning will probably require more time than usual, as the remaining stems will need to be selected and consideration given to removing damaged planted seedlings and leaving naturally regenerated seedlings.

In conclusion, abiotic damage reduces the number of planted crop trees, but natural regeneration supplements the damaged stands, shifting spruce stands towards mixed stands still dominated by conifers. Abiotic, and biotic, damage reduces the quality of planted spruce by increasing the number of multiple stems in damaged stands, which then reduces tree growth. Abiotic damage can be prevented to some extent by avoiding planting spruce on poor, drought-prone sites with coarse-textured soils and on hilltops. In addition to soil texture and site type, which are currently used in decision making, geospatial data such as TPI could be used in the selection of regeneration tree species and methods. With proper planning and timing of regeneration operations from nursery to planting site, it is possible to improve the regeneration outcome of spruce plantings and ensure rapid development of fully-stocked seedling stands in a warming climate with fluctuating winter temperatures.

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CRediT authorship contribution statement

Salmivaara Aura: Writing – review & editing, Data curation. **Luoranen Jaana:** Writing – original draft, Validation, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Miina Jari:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Formal analysis, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

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Data availability

Data will be made available on request.

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