New Forests (2025) 56:19
https://doi.org/10.1007/s11056-024-10088-0

RESEARCH

# Using spruces (*Picea* spp.) for Icelandic afforestation

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Received: 8 May 2024 / Accepted: 13 December 2024 / Published online: 24 December 2024


**Abstract**
Afforestation can help address climate change and biodiversity loss. Iceland is a valuable case study to assess afforestation at extreme locations at high latitudes (63–68°N). We used a ~23-year dataset of a provenance trial from the Icelandic Forest Service (now Land & Forest Iceland) to determine the best spruce species (*Picea* spp.) and provenances for afforestation. Sites were either frost-prone or protected (i.e., non-frost-prone) locations, and the latest height and survival data were assessed from six sites (out of nine) in 2018. Provenances were mainly from three spruce species from southwestern Canada and southern Alaska (53–61°N). Sitka spruce (*Picea sitchensis*) and its hybrids or introgressants with white spruce (*P. glauca*) survived and grew well in protected areas (≥60% and ≥275 cm), while white spruce and its hybrids or introgressants with Sitka spruce performed better in frost-prone areas (≥55% and ≥285 cm, based on combined frost-prone sites). The only provenance suitable for both frost-prone and protected places was a Sitka/Lutz spruce (*P. x lutzii*) introgressant from Iniskin Bay, Alaska. Additional genetic research would help guide afforestation in harsh areas at high latitudes (a distributional limit of many tree species) and inform forest management about novel environments and sustainable practices. Climate change should also be considered for afforestation efforts.

**Keywords** Survival · Growth · Provenance · Introgression · Frost · Non-native conifers

## Introduction

Afforestation is one nature-based solution to slow down climate change, restore biodiversity and ecosystem services, provide jobs, and address Sustainable Development Goals (SDGs) (FAO and UNEP 2020; United Nations 2022; IUCN 2023). For example, Ethiopia

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established the Green Legacy Initiative in 2019 where they created 120,000 nurseries and >700,000 jobs to plant 25 billion seedlings within four years to fight deforestation and improve land conditions (United Nations 2023). Although expanding forest cover is relatively easier at lower latitudes with warmer climates, such efforts are equally important at higher latitudes. Iceland, a Nordic country with a nascent forestry sector, is an ideal case study to look at afforestation in novel locations at high latitudes (≥63°N). Additionally, Iceland's short growing season due to extreme weather and harsh environmental conditions (Thórhallsdóttir 1998; Gretarsdottir et al. 2004) allows for research on performance limits of tree species.

Downy birch (*Betula pubescens* Ehrh.) covered at least 20% of Iceland prior to Norse settlement (874 CE) (Jónsson 2004). Overharvesting and sheep grazing led to deforestation (Jónsson 2004) and currently, Iceland has 1.5% native and 0.4% non-native woodland cover (Eysteinsson 2017). Free-range sheep grazing hinders seedling survival. Moreover, volcanic eruptions and soil erosion has led to degraded lands with nutrient loss (Arnalds 2008; Greipsson 2012). Presently, 37% of Iceland is extremely eroded (Marteinsdóttir and Stefánsson 2020). Native biodiversity and forest cover expansion are limited by Iceland's geographical isolation and high latitude, as well as unsustainable land management practices (e.g., sheep grazing) (Kristinsson 1975; Marteinsdóttir et al. 2017).

Given that downy birch is the only native tree that forms forests in Iceland, using non-native trees (e.g., conifers) can help increase forest cover faster (Blöndal 1987; Eddudóttir 2016). Additionally, most birches in Iceland struggle to grow into trees with a vertical form and grow as shrubs instead (Bragason 1995). Since 1899, there have been experimental plantings with non-native tree species sourced from various countries, including white spruce (*Picea glauca* (Moench) Voss), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), Norway spruce (*Picea abies* (L.) H.Karst.), mountain pine (*Pinus mugo* Turra), bristlecone pine (*Pinus aristate* Engelm.), Siberian stone pine (*Pinus sibirica* Du Tour), balsam fir (*Abies balsamea* (L.) Mill.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), European larch (*Larix decidua* Mill.), Siberian larch (*Larix sibirica* Ledeb.), common osier (*Salix viminalis* L.), gray alder (*Alnus incana* (L.) Moench), silver birch (*Betula pendula* Roth), and balsam poplar (*Populus balsamifera* L.) among others (Bragason 1995). Forest activities mainly used a trial-and-error approach until 1967 when the Icelandic Forest Service (now Land & Forest Iceland) started more structured research (Bragason 1995; Eysteinsson 2017). This led to identifying larches (*Larix* spp.), spruces (*Picea* spp.), pines (*Pinus* spp.), cottonwoods (*Populus* spp.), alders (*Alnus* spp.), and willows (*Salix* spp.) as the species with the highest survival, most of which came from North America except the larches. Current afforestation efforts have been most successful with Siberian larch, lodgepole pine (*Pinus contorta* Douglas ex Loudon), Sitka spruce (*Picea sitchensis* (Bong.) Carr.), black cottonwood (*Populus trichocarpa* Torr. & A. Gray ex Hook.), and alder (Blöndal 1987). Establishing conifer forests can also lead to a sustainable timber industry and increase carbon sequestration (Nijnik et al. 2013; Snorrason and Brynleifsdóttir 2018), but this can be expensive to implement (e.g., research and nursery costs). To guarantee afforestation success, selecting appropriate species, provenances, and locations are essential. Afforestation in Iceland would contribute to the country's aim of carbon neutrality by 2040 (Government of Iceland 2020).

Severe frost throughout Iceland in April 1963 significantly damaged numerous tree species and led to new collections of conifer seeds (e.g., *Pinus* spp. and *Picea* spp.) gathered abroad for growing experiments related to frost hardiness (Ragnarsson 1964; Blöndal

2004). In particular, Alaskan and Canadian sources at high latitudes with proximity to the ocean were chosen because they were more likely to be frost resistant and from a climate most similar to Iceland all year round. For example, the Icelandic Forest Service collected seeds from the Yukon, Canada and Alaska, USA in 1985. Furthermore, Dr. John Alden, a forest geneticist from the United States Forest Service in Alaska, gathered conifer seeds from 1988 to 1990 consisting of provenances and single-tree progeny that were later used in Iceland. In 1995–1996, a country-wide provenance trial was established to assess the growth of spruces at numerous sites in Iceland (Fig. 1) using origin seeds from a wider geographical distribution. These sites were either protected (i.e., less radiative frost during the active growing season) or frost-prone and were monitored every 1–4 years. Frost-prone sites in Iceland had a high likelihood of tree surfaces reaching freezing temperatures causing growth damage from ice crystals (hoar/radiation frost), particularly during cool nights with clear skies and low winds common in the fall and spring (Sakai and Larcher 1987; Geiger et al. 2003; Duong 2023).

Differences at the sites were detected for survival and growth between provenances and sites at the 4-year and 10-year marks (Jónsson 2000; Sigurgeirsson et al. 2006). When trees were ≤4 years, white spruce and Lutz (*Picea x lutzii* Little) showed greater frost damage resistance (particularly in fall) and grew taller than Sitka spruce. Whereas when trees were ≥10 years, Sitka spruce had notable advantage in protected areas and Lutz spruce survived better at frost-prone sites (Sigurgeirsson et al. 2006). Given these previous results, the aim of this research is to evaluate the survival and growth of spruces for afforestation around Iceland under different environmental conditions using long-term data (~23 years from site

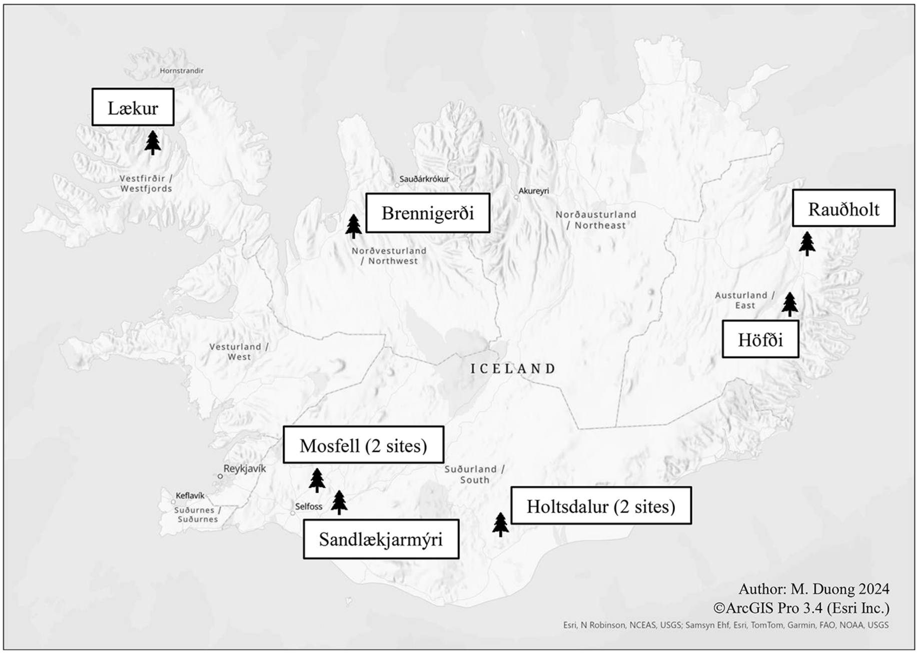


**Fig. 1** Provenance trial spruce planting sites (1995–1996) used for provenance survival and growth analyses. Note that only six of the nine sites were used for this study (Table 1). Source: Based on Fig. 3.1.1 in Duong 2023

planting) collected in 2018 from six sites. We identify spruce provenances and species that are most suitable in protected and frost-prone areas. At the ~23-year mark, we expect the same species performance seen at the 10-year mark. Although the Icelandic Forest Service is conducting research on other tree species that grow well in Iceland (e.g., downy birch, lodgepole pine, Siberian larch, and black cottonwood), they are beyond the scope of this study. Our research on spruces may lead to more sustainable afforestation in harsh areas at high latitudes (≥63°N) and help with the allocation of scarce resources. Furthermore, evaluating long-term spruce growth elucidates their distributional limits in novel habitats and their ecology within varying environmental conditions (e.g., protected and frost-prone).

## Materials and methods

### Site locations and experimental design

In 1994, seeds that were mostly from a project involving Nordic Forest Research and Dr. Alden (in Alaska) were grown into seedlings at a nursery and then planted (1995–1996) at 16 sites throughout Iceland (Skúlason et al. 2004; Sigurgeirsson et al. 2006). Only nine of 16 sites were viable for data analysis (Fig. 1) because they had sufficient survival and height measurements (Duong 2023). We compared spruce growth at six of these nine sites (Table 1) with data collected from one growing season in 2018 (22–23 years from site planting). These six sites captured a typical protected site and the variability of frost-prone sites in Iceland as well as having overlapping provenances (Duong 2023). The species planted were Sitka spruce (*P. sitchensis*), Lutz spruce (*P. x lutzii*), white spruce (*P. glauca*), Engelmann spruce (*P. engelmannii*), black spruce (*P. mariana* (Mill.) Britton, Sterns & Poggenb.), Sakhalin spruce (*P. glehnii* (F.Schmidt) Mast.), and Serbian spruce (*P. omorika* (Pančić) Purk.) (Table 2). Fertile introgressants of Lutz spruce (backcrosses to Sitka and white spruce) were also planted, and they are identified with the following notation: predominant species/secondary species (e.g., Lutz/white; Lutz/Sitka; white/Lutz; Sitka/Lutz). Pure species and introgressants were determined by (a) Dr. Alden with needle and cone morphology and (b) measuring the content of species-specific mitochondrial DNA with restriction fragment length polymorphism markers that showed to be either Sitka spruce or white spruce (see Sigurgeirsson et al. 1992).

Each site had a layout of 8–10 blocks where each block consisted of multiple rows of provenances (18–49) (Table 1) (Duong 2023). Blocks were randomized and every row had 10 seedlings from one provenance except for Lækur, a smaller and steeper area, which had seven seedlings per row. Rows were two meters apart with a two-meter distance between each seedling within a row. Overall, provenances consisted of 10 or more half-sib families and each progeny had a known maternal parent except for provenances from Iceland and species that were not comprised of Sitka, white, or Lutz spruce, which were from bulk seedlots (Duong 2023).

For the first analysis (Analysis 1), we compared Mosfell (frost-prone) and Holtsdalur95 (protected) (Table 1), typical sites present in Iceland, given their number of shared provenances (39) and higher amount of spruce species and introgressants (10) (Duong 2023). Frost-prone sites are usually flat, whereas protected sites tend to be sloped. At the end of summer and in early fall, there is more risk for radiation frost in flat landscapes. Mosfell

**Table 1** Study sites in Iceland. Approximated coordinates using Google Maps (2019). Table copied from Duong (2023; Table 3.1.1), which includes data from Jónsson (2000)

| Site | Site Description | Layout |
|---|---|---|
| Holtsdalur95 (63°45'N 18°14'W) | - Valley in Southeast Iceland<br>- Long steep slope<br>- Sheltered from wind<br>- Proximity to the ocean<br>Exposure to moisture with salt<br>- High level of precipitation<br>Low risk for frost<br>Longer growing season | – 8 blocks<br>– 40 provenances/block (All spruces)<br>– 10 seedlings/provenance row |
| Mosfell (64°07'N 20°39'W) | - South Iceland<br>- Drained peatland<br>- Very flat<br>- No wind protection<br>- Further from the ocean than Holtsdalur95<br>- Thick layer of grasses<br>Isolates soil temperature from surface area<br>Prone to frost<br>Shorter growing season | – 10 blocks<br>– 49 provenances/block (44 spruces, 5 pines)<br>– 10 seedlings/provenance row |
| Sandlækjarmýri (64°02'N 20°22'W) | - South Iceland<br>- Former farmland that use to be a marsh<br>- Flat with thick layer of grasses<br>Open to grazing<br>- Black cottonwood (*Populus trichocarpa*) experimental plot nearby | – 8 blocks<br>– 32 provenances/block (All spruces)<br>– 10 seedlings/provenance row |
| Höfði (65°14'N 14°23'W) | - Northeast Iceland<br>- Drained swamp<br>Upper flat portion that sometimes floods<br>Slightly sloped lower portion<br>- Patches of thick grasses | – 8 blocks<br>– 30 provenances/block (25 spruces, 5 pines)<br>– 10 seedlings/provenance row |
| Rauðholt (65°31'N 14°18'W) | - Northeast Iceland<br>- Flat drained moorland | – 8 blocks<br>– 18 provenances/block (14 spruces, 4 pines)<br>– 10 seedlings/provenance row |
| Lækur (66°00'N 22°56'W) | - Northwest Iceland (West Fjords)<br>- Drained grassy swamp<br>- In a narrow fjord just above sea level | – 10 blocks<br>– 27 provenances/block (All spruces)<br>– 7 seedlings/provenance row |

(drained peatland) was in the southern interior of Iceland on flat ground, while Holtsdalur95 was on a mountain slope in a valley in the southeast (Fig. 1; Table 1) (Duong 2023). Most of the provenances from these sites were Canadian or Alaskan white, Sitka, or Lutz spruces, however other species included first-generation Icelandic Sitka spruces, a first-generation Serbian spruce from Norway, Engelmann spruces from Canada and Colorado, a Japanese Sakhalin spruce, and an Alaskan black spruce (Table 2).

In our second analysis (Analysis 2), we compared spruce growth at five frost-prone sites vulnerable to radiation frost (late summer/early fall) (Duong 2023). These sites (Lækur, Höfði, Sandlækjarmýri, Mosfell, and Rauðholt) shared 14 Alaskan spruce provenances (Fig. 1; Table 1). The provenances were either white spruce, Sitka spruce, Lutz spruce, Lutz mixed with white spruce (Lutz/white), or Sitka mixed with Lutz spruce (Sitka/Lutz) (Table 2).

**Table 2** Spruce provenances. Origin refers to where the provenance seeds were collected; most came from the native range of the species, but not all. Coordinates and elevations were based on Jónsson (2000) and Skúlason et al. (2004), but some were approximated with Google Maps (2019) ([A]coordinates and [B]elevations). *Provenance 32 were first-generation clones from Iceland grafted onto new rootstocks in a seed orchard in Taraldsøy, Norway; seeds were then grown in Iceland. **These provenances have seedlings from two sources (i.e., 17+18 and 22+26). This table was copied from Duong (2023; Table A.1)

| Provenance Number | Species | Origin | Latitude (°N) | Longitude (°W) | Elevation (m) |
|---|---|---|---|---|---|
| 1 | *Picea sitchensis* | Chiniak, Alaska | 57°36' – 37' | 152°10' – 18' | 10–30 |
| 2 | *Picea sitchensis* | Duck Mountain, Alaska | 58°12' | 152°31' | 50–80 |
| 3 | *Picea sitchensis / Picea x lutzii* | Iniskin Bay, Alaska | 59°41' | 153°23' | 8–100 |
| 4 | *Picea sitchensis / Picea x lutzii* | Chinitna Bay, Alaska | 59°49' | 153°02' – 05' | 5–20 |
| 5 | *Picea sitchensis* | Port Chatham, Alaska | 59°11' | 151°43' | 30 |
| 6 | *Picea sitchensis* | Homer, Alaska | 59°38' | 151°28' – 34' | 5–30 |
| 7 | *Picea x lutzii / Picea glauca* | Ninilchik, Alaska | 59°58' – 59' | 151°33' – 35' | 91–122 |
| 8 | *Picea glauca* | Kenai, Alaska | 60°35' – 40' | 151°17' – 20' | 20–30 |
| 9 | *Picea sitchensis* | Resurrection River, Alaska | 60°09' – 11' | 149°27' – 32' | 15–61 |
| 10 | *Picea sitchensis* | Nash Road, Alaska | 60°05' – 08' | 149°20' – 24' | 3–61 |
| 12 | *Picea x lutzii / Picea sitchensis* | Cooper Lake, Alaska | 60°21' | 149°41' – 44' | 396 |
| 13 | *Picea x lutzii / Picea sitchensis* | Moose Pass, Alaska | 60°15' – 24' | 149°21' – 22' | 145–213 |
| 14 | *Picea glauca / Picea x lutzii* | Hope, Alaska | 60°54' | 149°36' – 37' | 30–69 |
| 15 | *Picea x lutzii* | Hope Road, Alaska | 60°54' | 149°36' – 37' | 30–69 |
| 17+18 ** | *Picea sitchensis* | Portage to Girdwood, Alaska | 60°47' – 51' | 149°44' – 55' | 23–76 |
| 19 | *Picea sitchensis* | Valdez, Alaska | 61°04' | 146°11' | 31 |
| 20[B] | *Picea sitchensis* | Cordova, Alaska | 60°32' | 145°45' | 122 |
| 21 | *Picea sitchensis* | Icy Bay, Alaska | 60°03' | 142°13' | 8 |
| 22+26 **, [A] | *Picea sitchensis* | Haines Highway, Alaska | 59°14' | 135°28' | 758 |
| 23 | *Picea sitchensis* | Discovery Bay, Alaska | 58°15' | 152°17' | 30 |
| 24 | *Picea x lutzii* | Snug Harbor, Alaska | 60°26' | 149°42' | 250 |
| 25 | *Picea x lutzii* | Knik River, Alaska | 61°35' | 149°15' | 10 |
| 28 | *Picea sitchensis* | Dyea, Alaska | 59°27' | 135°19' | 6 |
| 29 | *Picea sitchensis* | Yakutat, Alaska | 59°31' | 139°40' | 8.5 |
| 30 | *Picea sitchensis* | Cordova, Alaska | 60°32' | 145°45' | 8 |
| 31[B] | *Picea sitchensis* | Tatitlek, Alaska | 61°00' | 146°40' | 488 |
| 32 * | *Picea sitchensis* | Taraldsøy, Norway | | | |
| 33[B] | *Picea sitchensis* | Sitka, Alaska | 57°00' | 135°30' | 152 |
| 34[A, B] | *Picea sitchensis* | Ártúnsbrekka, Iceland | 64°07' | 21°50' | 8 |
| 35[A, B] | *Picea sitchensis* | Tumastaðir, Iceland | 63°44' | 20°03' | 100 |
| 36[A, B] | *Picea sitchensis* | Stálpastaðir, Iceland | 64°31' | 21°26' | 200 |
| 45 | *Picea sitchensis* | Phantom Road, Canada | 53°24' | 132°19' | 244 |
| 46 | *Picea sitchensis* | Queen Charlotte, Canada | 53°21' | 132°15' | 167 |
| 47 | *Picea sitchensis* | Porcher Island, Canada | 54°03' | 130°20' | 427 |

**Table 2** (continued)

| Provenance Number | Species | Origin | Latitude (°N) | Longitude (°W) | Elevation (m) |
|---|---|---|---|---|---|
| 48 | *Picea sitchensis* | Rennell Sound, Canada | 53°20’ | 132°18’ | 475 |
| 55[A, B] | *Picea glehnii* | Hokkaido, Japan | 43°16’ | 142°37’E | 700 |
| 56[A, B] | *Picea omorika* | Ringsaker, Norway | 60°54’ | 10°44’E | 200 |
| 57[B] | *Picea engelmannii* | Río Grande, Colorado | 38°00’ | 105°00’ | 2286 |
| 58[A, B] | *Picea engelmannii* | Bluejoint Mountain, Canada | 49°33’ | 118°31’ | 2200 |
| 60 | *Picea mariana* | Soldotna, Alaska | 60°30’ | 151°00’ | 25 |

## Data analysis

In Analysis 1, we compared protected (i.e., non-frost-prone) versus frost-prone sites regarding height and survival of common provenances (Duong 2023). A linear model was used for height and a generalized linear model with a logistic regression for survival (with factors as block and provenance for both models) (stats package 3.6.3 from R Foundation 2020). The logit link was used with the binomial survival data (dead = 0, alive = 1). The default (family link) was used for the height data (Duong 2023). The RStudio interface (RStudio Desktop 1.2.5042) with R software (R 3.6.3) was used to analyze the data (RStudio 2020; R Foundation 2020).

In Analysis 2, we focused on frost-prone sites and compared common provenances for survival and height (Duong 2023). Our five frost-prone sites had very different environmental conditions (Table 1). Preliminary analyses of variance (ANOVAs) and Pearson correlations indicated that four of them (Mosfell, Sandlækjarmýri, Rauðholt, and Höfði) could be combined as one frost-prone category, capturing the variability of frost-prone sites across Iceland (Type III ANOVAs ($p<0.001$); Pearson ($0.853<r_{height}<0.939$, $p<0.001$) (Duong 2023). The fifth site, Lækur, was kept separate for this analysis, because it had very low correlation to the other four sites (Pearson ($r_{height}<0.229$, $p<0.001$). We used car package 3.0–11 (Fox et al. 2021) for all ANOVAs, and the factors were provenance, site, and block nested within site. Pearson correlations were done with the Hmisc package 4.4-1 (Harrell and Dupont 2020) and stats package 3.6.3 (R Foundation 2020) (Duong 2023).

For both analyses, survival and height estimated marginal means were calculated using emmeans package 1.6.2-1 for every provenance (Lenth 2021). Given the large sample size ($n=7020$ trees for Analysis 1; $n=5740$ trees for Analysis 2), pairwise comparisons of the provenances (alpha level = 0.05) were used to create significant groupings (multcomp package 1.4–17 (Hothorn et al. 2021)). For every provenance, survival rate came from the number of surviving trees at each site, and then mean height was calculated from these trees (Duong 2023).

## Results

### Frost-prone and protected sites: Mosfell and Holtsdalur95 (Analysis 1)

Overall, there were significantly higher mean survival rates at Holtsdalur95 (>60%) than at Mosfell (<60%) (Fig. 2). Sitka spruce and introgressants (mainly Sitka with some Lutz spruce) had the best survival (>74%) (Fig. 2) at Holtsdalur95, the protected site (Duong

2023). For example, provenance 3 (Iniskin Bay, Alaska) had a significantly better survival (94±3%) than the lowest ten survival rates (<67%) (Fig. 2; Table 2).

At Mosfell, the frost-prone site, black spruce survived the best followed by Sitka and introgressants (mainly Sitka with some Lutz spruce) (>60% survival) (Fig. 2) (Duong 2023). Provenance 60 (black spruce; Soldotna, Alaska; 87±3% survival) and provenance 32 (Sitka spruce; Iceland/Taraldsøy, Norway; 76±4%) stood out with significantly greater survival compared to 65% of the other provenances (Fig. 2; Table 2). Provenance 32 came from a seed orchard in Taraldsøy, Norway established in the late 1970s with plus-tree clones selected from Iceland.

The species pattern for the heights at Holtsdalur95 was like the one for survival rates (Fig. 2) (Duong 2023). Sitka spruce and introgressants (mainly Sitka with some Lutz spruce) were generally taller (Fig. 2). For instance, provenance 21 (Icy Bay, Alaska; 461±15 cm) and provenance 28 (Dyea, Alaska; 459±14 cm) were significantly taller than 76% of the other provenances (Fig. 2; Table 2). Although not significantly different, sometimes trees that were mostly Lutz spruce (i.e., introgressant intermediates between Sitka and white spruce) were higher than Sitka spruce (>354 cm) (Fig. 2) (Duong 2023).

Lutz spruce and introgressants mainly with Lutz spruce were significantly taller (>216 cm) than the majority of Sitka spruces at Mosfell (Fig. 2) (Duong 2023). The heights for provenance 7 (Ninilchik, Alaska; 277±12 cm) and provenance 12 (Cooper Lake, Alaska;

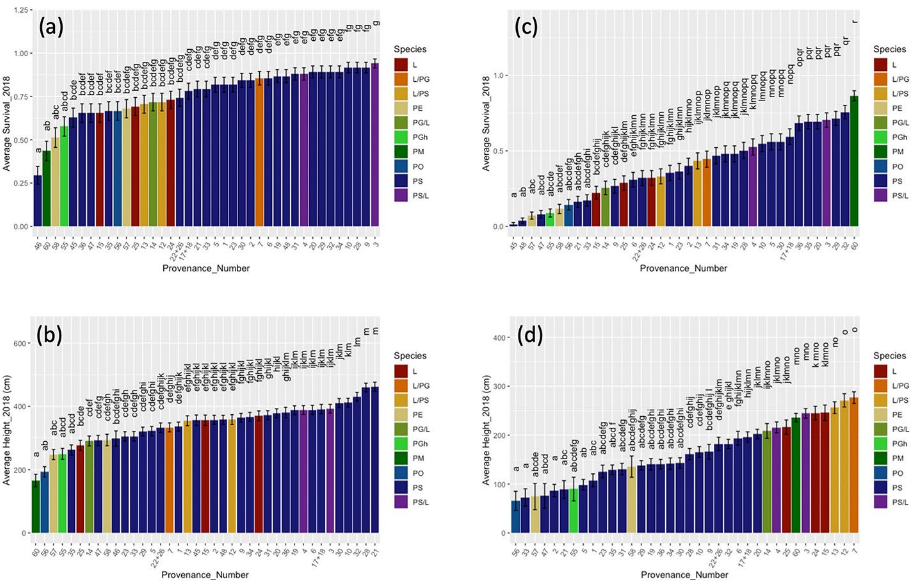


**Fig. 2** Mean survival rates and heights of the provenances in 2018 for Analysis 1. (**a**) and (**b**) are Holtsdalur95; (**c**) and (**d**) are Mosfell. Significant groupings and standard errors are shown. Two provenances are significantly different for survival and/or height if they do not share any of the same letters, e.g., provenances 19 and 55 in (**a**). Conversely, survival and/or height for two provenances are not significantly different if they have a letter in common, e.g., provenances 14 and 55 in (**a**) share a "**b**". Provenances 45, 46, and/or 48 were removed from Mosfell because of too much variability in survival and/or height. Otherwise, all 39 provenances are presented. Spruce species: PS = Sitka, L = Lutz, PM = black, PO = Serbian, PE = Engelmann, PGh = Sakhalin, PS/L = Sitka mixed with Lutz, PG/L = white mixed with Lutz, L/PS = Lutz mixed with Sitka, and L/PG = Lutz mixed with white. Note that PS/L, PG/L, L/PS, and L/PG are all introgressants. This figure is modified from Fig. 4.1.1-4 in Duong (2023)

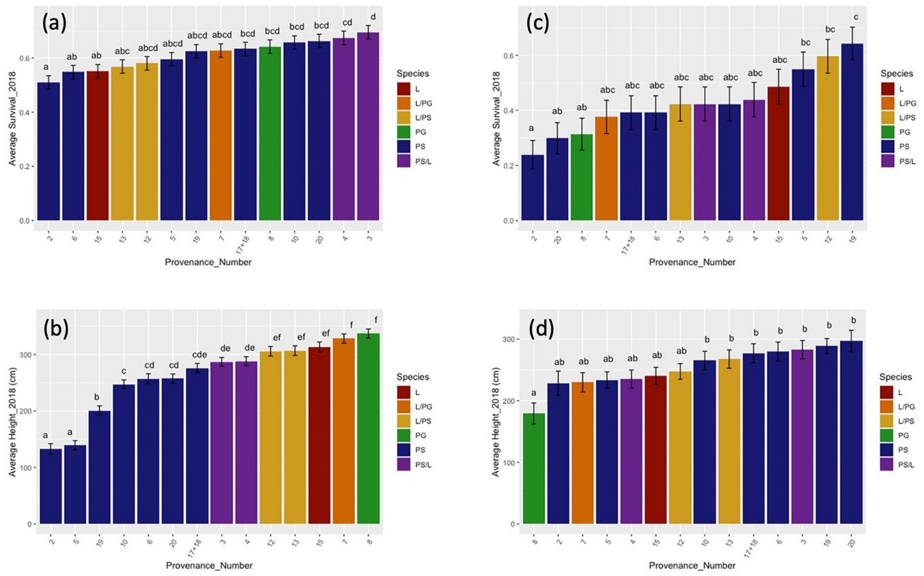


**Fig. 3** Mean survival rates and heights of the provenances in 2018 for Analysis 2. (**a**) and (**b**) are Mosfell, Sandlækjarmýri, Rauðholt, and Höfði combined; (**c**) and (**d**) are Lækur. Significant groupings and standard errors are shown. Two provenances are significantly different for survival and/or height if they do not share any of the same letters, e.g., provenances 3 and 13 in (**a**). Conversely, survival and/or height for two provenances are not significantly different if they have a letter in common, e.g., provenances 3 and 8 in (**a**) share a "**d**". All 14 provenances are presented in each graph. Spruce species: PS = Sitka, L = Lutz, PM = black, PO = Serbian, PE = Engelmann, PGh = Sakhalin, PS/L = Sitka mixed with Lutz, PG/L = white mixed with Lutz, L/PS = Lutz mixed with Sitka, and L/PG = Lutz mixed with white. Note that PS/L, PG/L, L/PS, and L/PG are all introgressants. This figure is modified from Fig. 4.2.1-4 in Duong (2023)

271±14 cm) were significantly greater than 70% of the other provenances (Fig. 2; Table 2). Overall, the trees at Holtsdalur95 were taller (>300 cm) than at Mosfell (<300 cm) (Fig. 2.) (Duong 2023).

## Frost-prone sites (five total) (Analysis 2)

The four sites that were combined into one frost-prone site were Mosfell, Sandlækjarmýri, Rauðholt, and Höfði. Sitka/Lutz survived well at frost-prone sites (>67%) (Fig. 3), although this was only significantly different with 25% of the other provenances (Duong 2023). In fact, the highest survival rates overall were the Sitka/Lutz trees from provenance 3 (Iniskin Bay; Alaska; 70±2%) and provenance 4 (Chinitna, Alaska; 67±2%) (Fig. 3; Table 2). Trees with any white spruce often had better survival (63–64±2%) over Lutz and Sitka spruces and their introgressants, though not significantly. It is important to note that the survival of Sitka spruce was variable (>60% or <55%) (Fig. 3) (Duong 2023).

Relative to the heights at frost-prone sites, most Sitka spruces grew significantly shorter (<258 cm) than the other spruce species, except for Sitka/Lutz (Fig. 3) (Duong 2023). Whereas trees with any white spruce grew significantly taller (>328 cm) than trees that were mostly Sitka spruce (<288 cm) (Fig. 3). For example, provenance 7 (Ninilchik, Alaska; 328±8 cm) and provenance 8 (Kenai, Alaska; 337±8 cm) were significantly taller than 75% of the other provenances (Fig. 3) (Duong 2023). However, trees with mostly white spruce were not significantly higher (>328 cm) than trees with some Lutz spruce (<313 cm) (Fig. 3).

At Lækur, a partially frost-prone site, only two provenances had significantly different survival rates to three of the 13 other provenances (Duong 2023). Specifically, provenance 2 (Sitka spruce; Duck Mountain, Alaska; 24±5%) had a significantly lower survival than provenances 5, 12, and 19, whereas provenance 19 (Sitka spruce; Valdez, Alaska; 64±6%) had significantly higher survival than provenances 2, 20, and 8 (Table 2; Fig. 3). Overall, trees that were mostly white spruce had poor survival (<38%), while trees with some Lutz spruce had better survival (42–60±6%) (Fig. 3). For height, pure white spruce (provenance 8) grew significantly shorter (179±17 cm) than 54% of the other provenances (Fig. 3) (Duong 2023). Trees that were mostly white spruce grew<230 cm, whereas some Sitka spruces grew somewhat taller (>265 cm) than most Lutz spruces and its introgressants (<248 cm) (Fig. 3). However, none of these comparisons were significant. In general, at Lækur, provenance 19 (Sitka spruce; Valdez, Alaska) had decent survival (64±6%) and height (289±12 cm) (Fig. 3).

## Discussion

After ~23 years of growth, Sitka spruce continued to perform the best at protected places (i.e., non-frost-prone). The most suitable provenances for protected areas (Holtsdalur95) are Sitka spruces and their introgressants originally from Alaska (provenances 3, 10, and 28) and Iceland/Norway (provenance 32) (Duong 2023). However, for frost-prone sites, not only did Lutz spruce perform well as it did at the 10-year mark, but so did white spruce, white spruce introgressants, and black spruce. Alaskan provenances with black spruce (provenance 60) or some white spruce (provenances 3, 4, 7, and 8) have the best survival and growth for locations that are flat with a risk of radiation frost (Rauðholt, Höfði, Sandlækjarmýri, Mosfell). Moreover, provenance 19 (Sitka spruce; Valdez, Alaska) seems to be the best suited for locations that are partially frost-prone (Lækur) (Duong 2023).

Average survival rates and height growths varied significantly among spruce provenances and the ranking of the provenances differed within some sites (Duong 2023). It is essential to consider survival and height together for afforestation at high latitudes (≥63°N) in novel habitats. In Iceland, for instance, provenance 3 (Sitka/Lutz; Iniskin Bay, Alaska) had both optimal survival (94±3%) and growth (392±14 cm) at protected sites (Holtsdalur95). Another important factor is a site's potential exposure to radiative frost because it has a strong influence on spruce performance (survival and growth). Sitka spruce can survive better and grow faster when there is a lower risk of radiative frost. For example, at Holtsdalur95, four provenances of Sitka spruce or its introgressants had significantly greater survival than 11–26% of the provenances and taller height than 29–74% of the provenances. These were provenances 3, 10 (Sitka spruce; Nash Road, Alaska), 28 (Sitka spruce; Dyea, Alaska), and 32 (Sitka spruce; Taraldsøy, Norway/Iceland). Increasing the number of protected sites would further confirm that Sitka spruce and its introgressants are best suited for afforestation at high latitude protected sites.

At sites with radiative frost (i.e., frost-prone; e.g., Rauðholt, Höfði, Sandlækjarmýri, Mosfell), provenance 3 and 4 (Sitka/Lutz spruce; Chinitna Bay, Alaska) were optimal for survival and height. The survival of provenance 7 (Lutz/white spruce; Ninilchik, Alaska) and 8 (white spruce; Kenai, Alaska) was slightly greater than some of the other provenances, but they both showed significantly greater growth than 69% of the other provenances. Among provenances 3, 4, 7, and 8, the common factor was white spruce (see Sigurgeirsson et al. 1992), making them the best spruce species in places with radiation frost. In addition, when comparing the frost-prone site Mosfell with the protected site Holtsdalur95 (Analysis 1), provenance 60 (black spruce; Soldotna, Alaska) had a significantly greater survival and growth than 84% and 58% of the other provenances, respectively, in frost-prone areas. Black spruce shows potential in frost-prone areas but needs further research as only one provenance has been planted in our study sites. Overall, provenance 3 was the only one that performed well in protected and frost-prone locations with significantly higher survival and growth ≥ 26% of the other provenances. Provenance 3 is a Sitka/Lutz introgressant (predominantly Sitka spruce with a lower Lutz spruce component), which gives it Sitka spruce traits to perform well in protected areas and white spruce traits from the Lutz to survive and grow well in frost-prone sites (Duong 2023). Lutz spruce is a natural hybrid of white and Sitka spruces in locations where their native ranges overlap or grow in proximity to each other, especially between maritime and continental transition zones (Hamilton and Aitken 2013; Byrne et al. 2022). Additionally, introgressants also result from the backcrossing of Lutz spruce with white or Sitka spruces (i.e., introgression) (Hamilton and Aitken 2013). Genetic analysis of provenance 3 with other well-performing white and Sitka spruces would help identify key traits beneficial for protected and frost-prone locations (Duong 2023).

For places that are partially frost-prone, Lækur provides important information on provenances that can be grown in such areas, especially since the survival and height were uncorrelated with the other frost-prone sites and were less than at Hotltsdalur95. Lækur is a gently sloping site in a narrow fjord in northwestern Iceland relatively near the coast with potentially more precipitation, making it a transitional site between protected and frost-prone. Provenance 19 had the best survival and height, which were significantly greater than 8–23% of the other provenances (Duong 2023). To accurately assess provenance performance in different locations, some areas for afforestation may need to be classified as partially frost-prone, especially with climate change impacting environmental conditions.

Understanding local environmental conditions is important for species and provenance selection in afforestation. Protected places have ideal conditions for Sitka spruce, which are similar to its native range, with high precipitation, low winds, and cool moderate temperatures (Burns and Honkala 1990). They have the most growth within a year because new needles and branches are less likely to be damaged by radiative frost (Duong 2023). Sites with higher soil moisture also have more occurrences of frost heaving that white and black spruces are more susceptible to because of their shallower and slower-growing roots (Burns and Honkala 1990). Furthermore, Sitka spruce has better tolerance to salt, and this is beneficial for places affected by sea spray (Burns and Honkala 1990; Sigurgeirsson et al. 1992).

However, in locations that are prone to frost (e.g., radiation frost), white spruces and their hybrids and introgressants, including Lutz spruce, are best-suited, particularly for height. The tissues of white spruces usually harden before those of Sitka spruces (Burns and Honkala 1990; Murray et al. 1994; Sebastian-Azcona et al. 2019), reducing the risk of height loss from autumn frost damage. They can maintain typical growth patterns with a shorter growing season in sites susceptible to radiation frost and trees with more white spruce genes seem to better withstand autumn frost events. These frost response patterns have been seen in spruce species in Iceland (Skúlason et al. 2004). However, Lutz and white spruces are more vulnerable to spring frost damage because they often bud and flush sooner than Sitka spruce (Cannell and Smith 1983; Burns and Honkala 1990; Murray et al. 1994). On rare occasions when spring frost causes tree damage, some white and Lutz spruces may die when young, allowing some Sitka spruces to survive better in frost-prone areas (Duong 2023). Autumn frost, however, is more problematic than spring frost given that it has a greater effect on productivity (Samuel et al. 2007).

Sitka spruces < 200 cm are noticeably impacted by fall frost damage at frost-prone sites. These smaller trees end up losing their top growth and have difficulty growing taller (Marquis et al. 2020). Once they reach the 200 cm threshold, Sitka spruces achieve stable height growth similar to spruces with white and/or Lutz spruce. Although Sitka spruce provenances with high survival (e.g., provenances 10 and 20) could be planted at frost-prone sites with additional sheltering measures, it is more feasible to use provenances that already have good survival and height.

Original latitude of the provenances, along with the species, plays a role in afforestation success. For example, in Iceland, the spruce provenances (Table 2) were largely from the most northerly latitudes in their distribution range where their acclimation to an earlier autumn frost provides greater frost hardiness (Cannell 1985; Lines 1987). Most of them were from coastal Alaska which has a climate similar to southern Iceland. Provenances from further south (e.g., ≤54°N in Canada, the continental United States, and Japan; Table 2) set their buds much later in the fall than northerly provenances, exposing them more to potential frost damage and making them poor candidates for afforestation in Iceland (Mimura and Aitken 2007; Skúlason et al. 2018). In contrast, southerly provenances (Washington and Oregon) of Sitka spruces perform better in Ireland than more northerly provenances (Canada) largely due to similar climate conditions (Thompson et al. 2005). Currently, Alaskan provenances already in Iceland are more suited for afforestation until Icelandic provenances have more time to adapt to local environmental conditions and become available for further research.

Climate change also needs consideration for afforestation, especially with Arctic amplification leading to warming three times faster than the average global rate (Zhou et al. 2024). To account for climate change, adaptation and migration (i.e., expansion of species range) strategies are essential for long-term success (Aitken et al. 2008). This means it is necessary to test provenances and species outside their environmental limits (e.g., temperature and elevation). For example, controlled experiments focusing on thermal tolerance (e.g., heatwave and drought conditions) of spruces would contribute to selecting trees resilient to climate change (Ouyang et al. 2023). Additionally, field research on assisted migration can be conducted on the Icelandic sites from our study using data about growth cycles and risk factors (e.g., life history events, pests, and frost) (Aitken et al. 2008; Sebastian-Azcona et al. 2019). A warmer climate may lead to a longer growing season with a greater risk of frost events (Marquis et al. 2020). Provenance selection, therefore, needs to examine the benefits of using southerly provenances that thrive with the longer growing season or northerly provenances that are more tolerant to frost. Additional studies on genetic variability among provenances can help identify more resilient candidates to climate change (Ledig and Kitzmiller 1992; Mimura and Aitken 2007; Aitken et al. 2008). Moreover, locations with natural hybridization and backcrossing of spruces (e.g., introgression zones) may yield trees with resilient traits (Sigurgeirsson et al. 1992; Hamilton and Aitken 2013; Byrne et al.

2022). Introgression zones have a diversity of genetic traits because of species divergence 28 million years ago in the genus *Picea*, temporal distribution of these species, and fertile offspring from the crossbreeding of contemporary species (Sigurgeirsson et al. 1992; Hamilton and Aitken 2013; Lockwood et al. 2013; Byrne et al. 2022).

In addition to climate change, implementing some of Brundu et al.'s (2020) guidelines related to the use of non-native trees in forestry would reduce potential negative impacts (e.g., invasive species, loss of ecosystems services) and address SDGs 13 and 15 (United Nations 2022). Non-native monoculture tree stands can reduce biodiversity (e.g., insect and plant communities), especially with improper forest management (e.g., too high tree densities) (Wallace et al. 1992; Humphrey et al. 1999). Over time, ecosystem changes by non-native trees (e.g., spruces raising soil acidity) may lead to an increase in generalist species and a decline of specialist ones (Thuille and Schulze 2006; Buscardo et al. 2008; Quine and Humphrey 2010). Sometimes, however, it may be necessary to have non-native trees supplement forestry efforts that use native trees, especially if native tree species are less abundant and/or unlikely to thrive in the face of changing environmental conditions (Duong 2023). Given this, monitoring and stakeholder collaborations are vital for planning the use of non-native trees and to minimize their spread beyond planting boundaries (Brundu et al. 2020). Current forest management practices can easily achieve this. For example, in Iceland, the Forest Service is on a trajectory of sustainable forestry fueled by scientific research using native and non-native trees, leading to economic advantages, social benefits, and environmental improvements. Our study contributes to the feasibility of using non-native trees (e.g., spruces) in novel habitats at high latitudes (e.g., Iceland) and provides a useful model system to incorporate climate change into forest management.

**Acknowledgements** The Agricultural Productivity Fund of Iceland (#18-033) and NordGen Forest & Nordic Forest Research (SNS) (#117012.5) partially funded the project. The Icelandic Forest Service provided financial and fieldwork support, especially from Edda Sigurdís Oddsdóttir, Brynja Hrafnkelsdóttir, Jóhanna Bergrúnar Ólafsdóttir, Kristján Jónsson, and Sæmundur Þorvaldsson.

**Author contributions** MD, BS, and MT conducted the data analysis. MD, MT, BS, and AS worked on writing and editing the manuscript.

**Data availability** Some data appears in Table 2. Additional data available upon request.

## Declarations

**Competing interests** The authors declare no competing interests.

**Financial and non-financial interests statement** The authors declare there are no financial or non-financial interests.

## References


Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S (2008) Adaptation, Migration or Extirpation: Climate Change Outcomes for Tree Populations. Evol Appl 1(1):95–111. https://doi.org/10.1111/j.1752-4571.2007.00013.x

Arnalds O (2008) Soils of Iceland. Jökull 58:409–421

Blöndal S (1987) Afforestation and Reforestation in Iceland. Arct Alp Res 19(4):526–529. https://doi.org/10.1080/00040851.1987.12002636

Blöndal S (2004) Innfluttu Skógartrén I: Sitkagreni (Picea sitchensis (Bong) Carr). Skógræktarritið 20041:10–29

Bragason A (1995) Exotic Trees in Iceland. Icelandic Agricultural Sci 9:37–45

Brundu G, Pauchard A, Pyšek P, Pergl J, Bindewald AM, Brunori A et al (2020) Global Guidelines for the Sustainable Use of Non-native Trees to Prevent Tree Invasions and Mitigate Their Negative Impacts. NeoBiota 61:65–116. https://doi.org/10.3897/neobiota.61.58380

Burns RM, Honkala BH, Technical C (1990) Silvics of North America: Volume 1, Conifers. Agriculture Handbook 654. Forest Service of the United States Department of Agriculture, Washington, DC

Buscardo E, Smith GF, Kelly DL, Freitas H, Iremonger S, Mitchell FJG, O'Donoghue S, McKee A-M (2008) The Early Effects of Afforestation on Biodiversity of Grasslands in Ireland. Biodivers Conserv 17:1057–1072. https://doi.org/10.1007/978-90-481-2807-5_7

Byrne T, Farrelly N, Kelleher C, Hodkinson TR, Byrne SL, Barth S (2022) Genetic Diversity and Structure of a Diverse Population of *Picea sitchensis* Using Genotyping-by-Sequencing. Forests 13(9):1511. https://doi.org/10.3390/f13091511

Cannell MGR (1985) Autumn Frost Damage on Young *Picea sitchensis* 1. Occurrence of Autumn Frosts in Scotland Compared with Western North America. Forestry: Int J For Res 58(2):131–143. https://doi.org/10.1093/forestry/58.2.131

Cannell MGR, Smith RI (1983) Thermal Time, Chill Days and Prediction of Budburst in *Picea sitchensis*. J Appl Ecol 20(3):951–963. https://doi.org/10.2307/2403139

Duong M (2023) *The Potential for Using Spruce (Picea) in Icelandic Forestry* [master's thesis, University of Iceland]. Skemman. http://hdl.handle.net/1946/43327

Eddudóttir SD, Erlendsson E, Tinganelli L, Gísladóttir G (2016) Climate change and human impact in a sensitive ecosystem: the Holocene environment of the Northwest Icelandic highland margin. Boreas 45(4):715–728. https://doi.org/10.1111/bor.12184

Eysteinsson T (2017) Forestry in a Treeless Land. Skógræktin, Egilsstaðir, Iceland. https://www.skogur.is/static/files/2017/Forestry_in_treeless_land_BKL_210x260mm.pdf

FAO and UNEP (2020) The State of the World's Forests 2020: Forests, Biodiversity and People. United Nations. https://doi.org/10.4060/ca8642en

R Foundation – R Core Team (2020) R Project for Statistical Computing for Mac OS X with the R Stats Package (R 3.6.3) [Software]. CRAN. https://cran.hafro.is. Accessed February 2020

Fox J, Weisberg S, Price B (2021) Companion to Applied Regression (car package 3.0–11). CRAN. https://cran.r-project.org/web/packages/car/car.pdf. Accessed 1 August 2021

Geiger R, Aron RH, Todhunter P (2003) The Climate Near the Ground, sixth edition. Rowman & Littlefield Publishers, Inc., Maryland, USA

Google Maps (2019) Google Maps Satellite Image – Iceland. Google. https://www.google.com/maps/@64.915517,19.6259013,647072m/data=!3m1!1e3. Accessed June 2019

Government of Iceland: Ministry for the Environment and Natural Resources (2020) Iceland's 2020 Climate Action Plan. https://www.government.is/library/01-Ministries/Ministry-for-The-Environment/201004%20Umhverfisraduneytid%20Adgerdaaaetlun%20EN%20V2.pdf. Accessed August 2021

Greipsson S (2012) Catastrophic Soil Erosion in Iceland: Impact of long-term climate change, compounded natural disturbances and human driven land-use changes. CATENA 98:41–54. https://doi.org/10.1016/j.catena.2012.05.015

Gretarsdottir J, Aradottir A, Vandvik V, Heegaard E, Birks H (2004) Long-Term Effects of Reclamation Treatments on Plant Succession in Iceland. Restor Ecol 12(2):268–278. https://doi.org/10.1111/j.1061-2971.2004.00371.x

Hamilton JA, Aitken SN (2013) Genetic and Morphological Structure of a Spruce Hybrid (*Picea Sitchensis* x *P. Glauca*) Zone Along a Climatic Gradient. Am J Bot 100(8):1–12. https://doi.org/10.3732/ajb.1200654

Harrell FE Jr, Dupont C (2020) Harrell Miscellaneous – Hmisc package 4.4-1. CRAN. https://cran.r-project.org/web/packages/Hmisc/index.html. Accessed 1 August 2021

Hothorn T, Bretz F, Westfall P (2021) Simultaneous Inference in General Parametric Models (multcomp package 1.4–17). CRAN. https://cran.r-project.org/web/packages/multcomp/multcomp.pdf. Accessed 1 August 2021

Humphrey JW, Hawes C, Peace AJ, Ferris-Kaan R, Jukes MR (1999) Relationships Between Insect Diversity and Habitat Characteristics in Plantation Forests. For Ecol Manag 113(1):11–21. https://doi.org/10.1016/S0378-1127(98)00413-7

IUCN (2023) Nature-based Solutions. https://www.iucn.org/our-work/nature-based-solutions. Accessed August 2021

Jónsson LÞ (2000) Proveniens og Familieforsøk på *P. sitchensis, P. x lutzii og P. glauca* i Etableringsfasen – 10 Forsøk på Island [master's thesis]. Norwegian University of Life Sciences, Ås, Norway

Jónsson TH (2004) Stature of Sub-arctic Birch in Relation to Growth Rate, Lifespan and Tree Form. Ann Botany 94(5):753–762. https://doi.org/10.1093/aob/mch200

Kristinsson H (1975) The Vegetation and Flora of Iceland. Am Rock Garden Soc Bull 33:105–111

Ledig FT, Kitzmiller JH (1992) Genetic Strategies for Reforestation in the Face of Global Climate Change. For Ecol Manag 50(1–2):153–169. https://doi.org/10.1016/0378-1127(92)90321-Y

Lenth R (2021) Estimated Marginal Means, aka Least-Squares Means (emmeans package 1.6.2-1). CRAN. https://cran.r-project.org/web/packages/emmeans/emmeans.pdf. Accessed 1 August 2021

Lines R (1987) Seed Origin Variation in Sitka Spruce. Proc Royal Soc Edinb Sect B: Biol Sci 93(1–2):25–39. https://doi.org/10.1017/S0269727000006254

Lockwood JD, Aleksić JM, Zou J, Wang J, Liu J, Renner SS (2013) A New Phylogeny for the Genus *Picea* from Plastid, Mitochondrial, and Nuclear Sequences. Mol Phylogenet Evol 69(3):717–727. https://doi.org/10.1016/j.ympev.2013.07.004

Marquis B, Bergeron Y, Simard M, Tremblay F (2020) Growing-season Frost is a Better Predictor of Tree Growth Than Mean Annual Temperature in Boreal Mixed-wood Forest Plantations. Glob Change Biol 26:6537–6554. https://doi.org/10.1111/gcb.15327

Marteinsdóttir B, Stefánsson JH (2020) GróLind: Stöðumat á ástandi lands og kortlagning beitarlanda [Presentation]. GróLind Kynningarfundur. https://grolind.is/wp-content/uploads/2020/06/Gr%C3%B3Lind-stodumat_beitarlond_18_06_2020.pdf. Accessed January 2022

Marteinsdóttir B, Barrio IC, Jónsdóttir IS (2017) Assessing the Ecological Impacts of Extensive Sheep Grazing in Iceland. Icelandic Agricultural Sci 30:55–72

Mimura M, Aitken SN (2007) Adaptive Gradients and Isolation-by-distance with Postglacial Migration in *Picea sitchensis*. Heredity 99:224–232. https://doi.org/10.1038/sj.hdy.6800987

Murray MB, Smith RI, Leith ID, Fowler D, Lee HSJ, Friend AD, Jarvis PG (1994) Effects of Elevated CO2, Nutrition and Climatic Warming on Bud Phenology in Sitka Spruce (*Picea sitchensis*) and Their Impact on the Risk of Frost Damage. Tree Physiol 14:691–706. https://doi.org/10.1093/treephys/14.7-8-9.691

Nijnik M, Pajot G, Moffat AJ, Slee B (2013) An Economic Analysis of the Establishment of Forest Plantations in the United Kingdom to Mitigate Climate Change. For Policy Econ 26:34–42. https://doi.org/10.1016/j.forpol.2012.10.002

Ouyang F, Sun M, Cui X, Tigabu M, Zhang H, Deng J et al (2023) *Picea pungens* exhibits greatest tolerance to short-time thermal stress compared to *Picea abies*, and *Picea omorika*. New Forests 55:769–784. https://doi.org/10.1007/s11056-023-10002-0

Quine CP, Humphrey JW (2010) Plantations of Exotic Tree Species in Britain: Irrelevant for Biodiversity or Novel Habitat for Native Species? Biodivers Conserv 19:1503–1512. https://doi.org/10.1007/s10531-009-9771-7

Ragnarsson H (1964) Trjáskemmdir vorið 1963. Ársrit Skógræktarfélags Íslands 1964:25–27

Sakai A, Larcher W (1987) Low Temperature and Frost as Environmental Factors. Frost Survival of Plants, Ecological Studies 62. Springer, Berlin, Heidelberg, Germany, pp 1–20. https://doi.org/10.1007/978-3-642-71745-1_1

Samuel CJA, Fletcher AM, Lines R (2007) Choice of Sitka Spruce Seed Origins for Use in British Forests (Bulletin 127). Edinburgh Forestry Commission (Forest Research). https://cdn.forestresearch.gov.uk/2007/03/fcbu127.pdf. Accessed June 2020

Sebastian-Azcona J, Hamann A, Hacke UG, Rweyongeza D (2019) Survival, growth and cold hardiness tradeoffs in white spruce populations: Implications for assisted migration. For Ecol Manag 433:544–552. https://doi.org/10.1016/j.foreco.2018.10.046

Sigurgeirsson A, Wang XR, Alden JN, Szmidt AE (1992) Patterns and extent of chloroplast gene exchange among *Picea* species in Alaska and British Columbia. In: Insights into the evolution of *Picea* inferred from chloroplast DNA (ISBN 91-576-4617-1) [Doctoral Dissertation]. Swedish University of Agricultural Sciences, Umea, Sweden, pp Appendix Paper VI

Sigurgeirsson A, Halldórsson G, Sverrisson H (2006) Rannsókn á Kvæmum Grenitegunda í Tveimur Landshlutum. Fræðaþing Landbúnaðarins 2006:235–238

Skúlason B, Sigurgeirsson A, Guðleifsson BE, Edvardsen ÖM (2004) Samanburður á Kvæmum og Systkinahópum Sitkagrenis, Hvítgrenis og Sitkabastarðs, með Tilliti til Frostþols að Vori og Hausti (Number 23 - ISSN 1608–3687). Mógilsá Forestry Research Center, Skógræktin (Icelandic Forest Service), Reykjavík, Iceland

Skúlason B, Hansen OK, Nielsen UB (2018) Provenance Variation in Phenology and Frost Tolerance in Subalpine Fir (*Abies lasiocarpa*) Planted in Denmark and Iceland. Forests 9(1):17. https://doi.org/10.3390/f9010017

Snorrason A, Brynleifsdóttir SJ (2018) Áhrif Fjórföldunar Nýskógræktar á Íslandi. Skógræktarritið 20181:34–45

Studio R (2020) RStudio Desktop: Open-Source Edition (1.2.5042) [Software]. https://rstudio.com/products/rstudio/older-versions/. Accessed February 2020

Thompson D, Lally M, Pfeifer A (2005) Washington, Oregon or Queen Charlotte Islands? Which is the best provenance of Sitka spruce (*Picea sitchensis*) for Ireland? Ir Forestry 62:19–34

Thórhallsdóttir TE (1998) Flowering phenology in the central highland of Iceland and implications for climatic warming in the Arctic. Oecologia 114:43–49. https://doi.org/10.1007/s004420050418

Thuille A, Schulze E-D (2006) Carbon Dynamics in Successional and Afforested Spruce Stands in Thuringia and the Alps. Glob Change Biol 12(2):325–342. https://doi.org/10.1111/j.1365-2486.2005.01078.x

United Nations (2022) Goal 13: Climate Action and Goal 15: Life on Land. Sustainable Development Goals. https://www.un.org/sustainabledevelopment/climate-change/ and https://www.un.org/sustainabledevelopment/biodiversity/. Accessed November 2022

United Nations (2023) Green Legacy Initiative. Department of Economic and Social Affairs. https://sdgs.un.org/partnerships/green-legacy-initiative. Accessed January 2023

Wallace HL, Good JEG, Williams TG (1992) The Effects of Afforestation on Upland Plant Communities: An Application of the British National Vegetation Classification. J Appl Ecol 29:180–194. https://doi.org/10.2307/2404360

Zhou W, Leung LR, Lu J (2024) Steady threefold Arctic amplification of externally forced warming masked by natural variability. Nat Geosci 17:508–515. https://doi.org/10.1038/s41561-024-01441-1

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