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RESEARCH

Inter- and intraspecific variation in seed germination traits of Arctic plant species

Majken Pagter[1] · Line Holm Andersen[1] · Jakob Deichmann Aagaard[1] · Charlotte Anni Damsgaard Andreasen[1] · Toke Thomas Høye[2] · Nanna Kåstrup Müller[1] · Maja Eline Bak Pedersen[1] · Sara Nørris Christoffersen[1] · Simon Bahrndorff[1]

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Abstract

Cold adapted plant species often dependent on seed dormancy breakage for successful germination, yet the effects of climate-driven changes in soil temperature on this process remain unclear. To improve our understanding of temperature impacts on seed dormancy breakage of Arctic plant species and populations, we investigated how different durations of cold-moist stratification at 0 °C or -5 °C affected seed germination of three Greenlandic plant species: *Luzula spicata*, *Juncus trifidus*, and *Luzula multiflora*. Seeds were collected from natural populations at low (0 m a.s.l) and high (500 m a.s.l.) elevations. Germination patterns differed between species, however, in general germination percentages were significantly higher for low elevational seeds compared to high elevational seeds for all three species. Elevation affected day of first germination only in *J. trifidus*. Stratification temperature, however, affected both day of first germination for *J. trifidus* and *L. multiflora* and the germination rate of *L. spicata.* Several species-specific interactions among stratification duration, elevation, and stratification temperature were identified. These findings show that Arctic plant species, and even their individual populations, exhibit different dormancy patterns. Climate change may thus affect populations and species differently, with important consequences for future Arctic plant community dynamics.

Keywords Greenland · Adaptation · Climate change · Day of first germination · Seed dormancy · Cold stratification

Introduction

As a result of climate change the Arctic is rapidly warming, with temperature increases nearly four times the global average during the past four decades (Hansen et al. 2010; Rantanen et al. 2022). Rising temperatures and increased precipitation are reducing snow cover and causing earlier snow melt (AMAP 2017; Box et al. 2019), which strongly alters ground thermal regimes because snow functions as thermal insulation, keeping the ground from freezing and sheltering the organisms beneath it (Wipf et al. 2015; Körner 2021). Arctic plant communities are already shifting in species abundance, composition, and distribution (Elmendorf et al. 2012; Myers-Smith and Hik 2018; García Criado et al. 2020), and continued warming is expected to reduce floral diversity as cold-adapted species decline (Niskanen et al. 2019; Elmendorf and Hollister 2023).

Genetic diversity, phenotypic plasticity, and effective seed dispersal are key traits enabling species to adapt to new environmental conditions or migrate to more suitable habitats. Arctic plants have traditionally been viewed as relying mostly on vegetative reproduction, due to low viable seed production, low germination rates and high seedling mortality (Billings 1987; Hermanutz et al. 1989). However, according to recent studies, sexual recruitment may occur more frequently than previously believed (Watts et al. 2019), and many species maintain high genetic diversity (Bills et al. 2015).

One important aspect of cold adapted plant species' survival in the extreme Arctic is seed dormancy and dormancy breakage. Seed dormancy allows species to delay germination until environmental conditions favor seedling survival.

✉ Majken Pagter
mp@bio.aau.dk

[1] Department of Chemistry and Bioscience, Aalborg University, Fredrik Bajers Vej 7H, Aalborg 9220, Denmark

[2] Department of Ecoscience, Aarhus University, C. F. Møllers Allé 8, Aarhus C 8000, Denmark

Dormancy is typically broken by external cues that coincide with those favorable conditions, thereby increasing the likelihood of successful establishment (Finch-Savage and Leubner-Metzger 2006; Moreira and Pausas 2012). In arctic-alpine plants, more than 70% of species produce dormant seeds, exhibiting mainly physiological dormancy, which requires cold and moist conditions (i.e., cold stratification) to be released (Baskin and Baskin 2004). This mechanism aligns germination with snowmelt and minimizes the risk of frost damage to emerging seedlings (Cavieres and Sierra-Almeida 2018). However, temperature effects on dormancy breakage have been studied in only few Arctic species (Graae et al. 2008; Kellmann-Sopyła and Giełwanowska 2015) and it is largely unknown how alterations in ground thermal regimes will impact germination across species and populations.

Temperature during cold stratification is an important factor influencing dormancy alleviation. Temperatures between 0 and 10 °C are generally effective for dormancy release (Cavieres and Arroyo 2000; Cotado et al. 2020), and many studies on alpine plants have applied stratification temperatures between 3 and 5 °C (Sayers and Ward 1966; Milbau et al. 2009; Cavieres and Sierra-Almeida 2018). The duration of cold stratification also influences dormancy release (Cavieres and Arroyo 2000), and the optimal length of this period varies among species (Bell and Amen 1970).

In alpine plant species, seeds from high-elevation populations, where long snow cover and harsh winter conditions prevail, tend to exhibit deeper dormancy and require longer periods of cold stratification for germination than seeds from lower-elevation populations exposed to milder winters (Cavieres and Arroyo 2000; Cavieres and Sierra-Almeida 2018; Cotado et al. 2020). This pattern highlights substantial variation in germination traits across a relatively short environmental gradient. These results also suggest selection for dormancy breakage, not only across species, but also populations. Yet little is known about whether similar selective pressures shape dormancy traits of Arctic plant seeds across altitudinal gradients.

The aim of this study is to increase our understanding of temperature effects on dormancy breakage of cold adapted plant species and populations in view of climate change. Specifically, we investigate whether different durations of cold stratification at 0 °C or -5 °C, representing conditions under current and future snow cover, respectively, affect seed germination of three perennial plant species commonly found in Greenland: *Luzula spicata* (L.), *Juncus trifidus* (L.), and *Luzula multiflora* (Erhr.). Seeds were collected from natural populations at low (0 m a.s.l) and high (500 m a.s.l.) elevations. We hypothesized that (1) high elevation seeds have deeper dormancy and require longer periods of cold stratification for germination than low elevation seeds. (2) Seeds stratified at 0 °C will germinate more rapidly and have an increased germination percentage compared to seeds stratified at -5 °C, and (3) longer cold stratification will accelerate germination and increase the germination percentage compared to a short cold stratification period.

Materials and methods

Seed collection

Seeds were collected in 2023 from the area around Narsarsuaq, southern Greenland. Low-elevation collections were made at sea level in Hospital Valley for *L. multiflora* (61°11'17"N, 45°21'10"W), and in Igaliku for *J. trifidus* and *L. spicata* (60°59'28"N, 45°25'45"W). High-elevation seeds were collected at 500 m a.s.l. in Mellemlandet, Narsarsuaq (61°09'27"N, 45°22'12"W). Mature seeds were collected on 19 August at the high-elevation site and between 19 and 21 August at the low-elevation sites from >25 individual plants of each species. Seed production of *J. trifidus* was for most plants limited to a maximum of three seeds per plant and in general seed collection was complicated by sparsely distributed plants, limiting the number of seeds available for stratification treatments. After collection, seeds were dried to a moisture content of ca. 30% at room temperature. Dry seeds were stored in airtight containers at 5 °C in the dark for approximately four months until start of the experiment.

Before the experiment started, the seed mass of each population was determined by weighing six times 10 dry seeds for each population on a Sartorius Quintix35-1 S scale ($n=6$).

Stratification treatments

Seeds were exposed to one of two stratification temperatures (−5 °C or 0 °C) for 0, 4, 8, or 12 weeks. The -5 °C treatment represents reduced snow cover associated with climate warming, whereas 0 °C reflects temperatures beneath a thick snowpack, as this corresponds to temperatures typically found under present snow cover (Milbau et al. 2009). The selected temperatures and stratification durations were based on(Milbau et al. 2009) and local records from Narsarsuaq (Hollesen et al. 2024), and are well aligned with the thermal conditions in the study areas (Online Resource Table S1 and Fig. S1). Because seeds of *L. spicata* exhibit physical dormancy(Sayers and Ward 1966), they were scarified at the micropylar end (Bell and Amen 1970) under a stereomicroscope prior to stratification.

Seeds were placed in 9 cm petri dishes with two layers of filter paper soaked in demineralized water. For each species and each combination of population, stratification

temperature, and duration, seeds were divided among 10 replicate petri dishes, except for *L. multiflora*, where the number of seeds only allowed for 9 replicates. Due to varying numbers of seeds from each species, the number of seeds in each replicate differed between species. Replicates of *J. trifidus* contained six seeds each, and replicates of *L. multiflora* and *L. spicata* contained five seeds each.

The replicates were handled according to stratification period and temperature and placed in temperature-controlled chambers at 0 °C or -5 °C in darkness. Seeds which did not receive any stratification treatment (None) were not placed in temperature-controlled chambers. After stratification, seeds were moved to a growth chamber (Snijders Microclima MC1750E) at constant 12 °C with a 16/8 h day/night cycle and a light intensity of 138 $\mu molm^{-2}s^{-1}$ during the day. A 16-h photoperiod reflects the natural day length in the study area in early May, immediately following snowmelt.

Germination was monitored daily or every second day for 21 days, with germination defined by radicle emergence. Fungal infections were noted (Online Resource Table S2). As soon as contaminated seeds were observed they were removed and the filter papers replaced by new papers. The filter papers in each petri dish were watered when dry. Day of first germination was counted from the first day after stratification.

Data analysis

A GLM was used to analyze seed weight, with quantile-quantile plots confirming a Gaussian distribution. Explanatory variables included elevation (factor with two levels), species (factor with three levels) and their interaction. Significant effects were followed by least square means with a Tukey correction (Lenth 2025).

The germination percentages were analyzed using a binomial model with a logit-link with germinated versus ungerminated seeds as response variable. Mold infected seeds were registered as dead and were not included in the non-germinated seed count. In 7 replicates, all seeds within a petri dish were infected with fungus, and it was not possible to estimate the number of germinated versus ungerminated seeds. These replicates were excluded from the model. Explanatory variables included species (factor: *L. multiflora*, *L. spicata* and *J. trifidus*), elevation (factor: 0 vs. 500 m), stratification temperature (factor: None, 0˚C and -5˚C), stratification duration (factor: None, 4, 8 and 12 weeks) and all two-, three-, and four-way interactions. Significant differences were examined using least square means with a Tukey correction.

Model checking was done using package DHARMa (Hartig 2024), where both residual testing, dispersion test, outlier test and Kolmogorov-Smirnov test showed that the model was a good fit.

For day of first germination, a negative binomial model fitted the right-skewed data best. Model fit was tested by residual testing, dispersion test, outlier test and Kolmogorov-Smirnov test from package DHARMa, with some deviations detected in the Kolmogorov-Smirnov test and the dispersion test. The model was fitted using glmmTMB (Brooks et al. 2017). Initially, explanatory variables included species (factor: *L. multiflora*, *L. spicata* and *J. trifidus*), elevation (factor: 0 vs. 500 m), stratification temperature (factor: None, 0˚C and -5˚C), stratification duration (factor: None, 4, 8 and 12 weeks) and all two-, three-, and four-way interactions. However, this model was rank-insufficient, and the available data was insufficient to support a 4-way-interaction model. Therefore, we fitted separate models for each species, thereby reducing model complexity. In these models, explanatory variables included elevation (factor: 0 vs. 500 m), stratification temperature (factor: None, 0˚C and -5˚C) and stratification duration (factor: None, 4, 8 and 12 weeks). No interaction terms were included. Significant differences were assessed using post hoc pairwise comparisons based on estimated marginal means, implemented in the *emmeans* package (Lenth 2025).

To calculate t50, defined as the median time to reach 50% of final germination, we used the Germinationmetrics package. The Farooq method was applied to estimate t50, which was calculated for each species–treatment combination (Farooq et al. 2005; Aravind et al. 2026).

All data analysis was performed in R version 4.5.0 (R Core Team, Vienna 2025), with figures produced in ggplot2 (Wickham 2016) and combined using cowplot (Wilke 2024).

Results

Seed mass

Significant differences in seed mass were found among species (GLM, $F=64.28$, $df=2$, $p<0.0001$) and between elevations (GLM, $F=11.27$, $df=1$, $p<0.01$), supported by a significant species-by-elevation interaction (GLM, $F=8.02$, $df=2$, $p<0.01$) (Fig. 1). Least square means test indicated that *L. multiflora* seeds were significantly heavier at low elevation than at high elevation ($p<0.001$), while no significant altitudinal differences were found between the other species. Seed masses also differed significantly between species with *J. trifidus* having significantly lower seed mass than *L. multiflora* ($p<0.0001$) and *L. spicata* ($p<0.0001$).

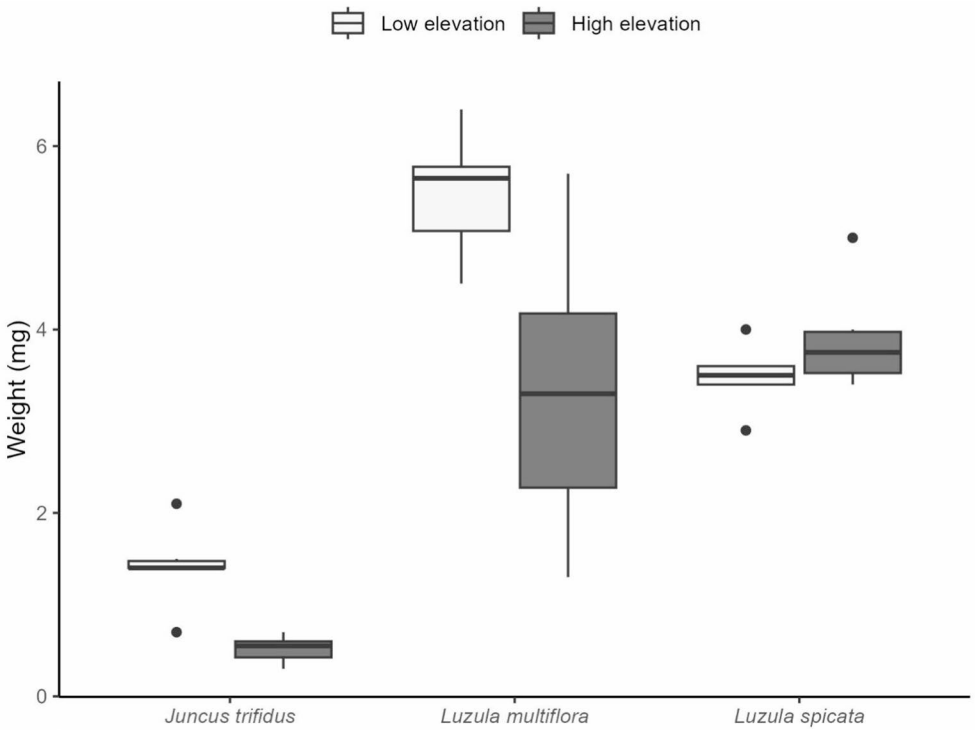


Fig. 1 The seed mass of *Juncus trifidus*, *Luzula multiflora*, and *Luzula spicata*, across high-elevation and low-elevation populations ($n=6$). The plot depicts the median, the upper and lower hinges (corresponding to the 75th and 25th percentiles), and the whiskers showing the largest values within 1.5 times the interquartile range. Dots are outliers

Table 1 Results of the binomial GLM with logit link for germination percentage. Values in bold are significant

Species (S)	df	*p*
	2	<0.0001
Elevation (E)	1	**<0.0001**
Stratification duration (D)	3	**<0.0001**
Stratification temperature (T)	1	**<0.001**
S*E	2	**<0.0001**
S*D	6	**<0.0001**
E*D	3	**<0.001**
S*T	2	**<0.0001**
E*T	1	>0.05
D*T	2	>0.05
S*E*D	6	**<0.001**
S*E*T	2	>0.05
S*D*T	4	>0.05
E*D*T	2	>0.05
S*E*D*T	4	>0.05

Germination percentages

Germination percentages were significantly affected by species, elevation, stratification duration and stratification temperature (Table 1, binomial GLM, Fig. 2). Further there were significant interactions between species and elevation, species and stratification duration, species and stratification temperature, elevation and stratification duration, as well as a significant three-way interaction between species, elevation and stratification duration (Table 1, binomial GLM). Together, these results indicate substantial differences in germination traits among species (Online Resources Table S3).

Across species, seeds from low elevations exhibited a significantly higher percentage of germination than those from high elevations (Fig. 2, Online Resources Table S4). However, the magnitude of this difference was species-specific. For *J. trifidus*, germination percentages were significantly higher for low-elevation seeds than high-elevation seeds, irrespective of stratification treatment (Fig. 2A, Online Resources Table S4). Low-elevation seeds consistently exhibited high germination rates, whereas high-elevation seeds showed uniformly low rates across all treatments. In *L. multiflora* and *L. spicata*, seeds from low-elevation populations stratified at 0 °C consistently exhibited higher germination percentages than those from high-elevation populations stratified at 0 °C, regardless of stratification duration (Fig. 2B and C, Online Resources Table S4). For seeds stratified at -5 °C, a significantly higher germination rate in low-elevation populations compared to high-elevation populations was observed only after 4 weeks of treatment in *L. spicata* and after 12 weeks of treatment in *L. multiflora*.

Stratification temperature had no effect on the germination percentage of *J. trifidus* or *L. multiflora* (Fig. 2A and B, Online Resources Table S5). However, in low-elevation populations of *L. spicata*, 0 °C was more effective for dormancy release than -5 °C following 8 or 12 weeks of stratification as indicated by higher germination percentages at 0 °C (Fig. 2C, Online Resources Table S5). A similar

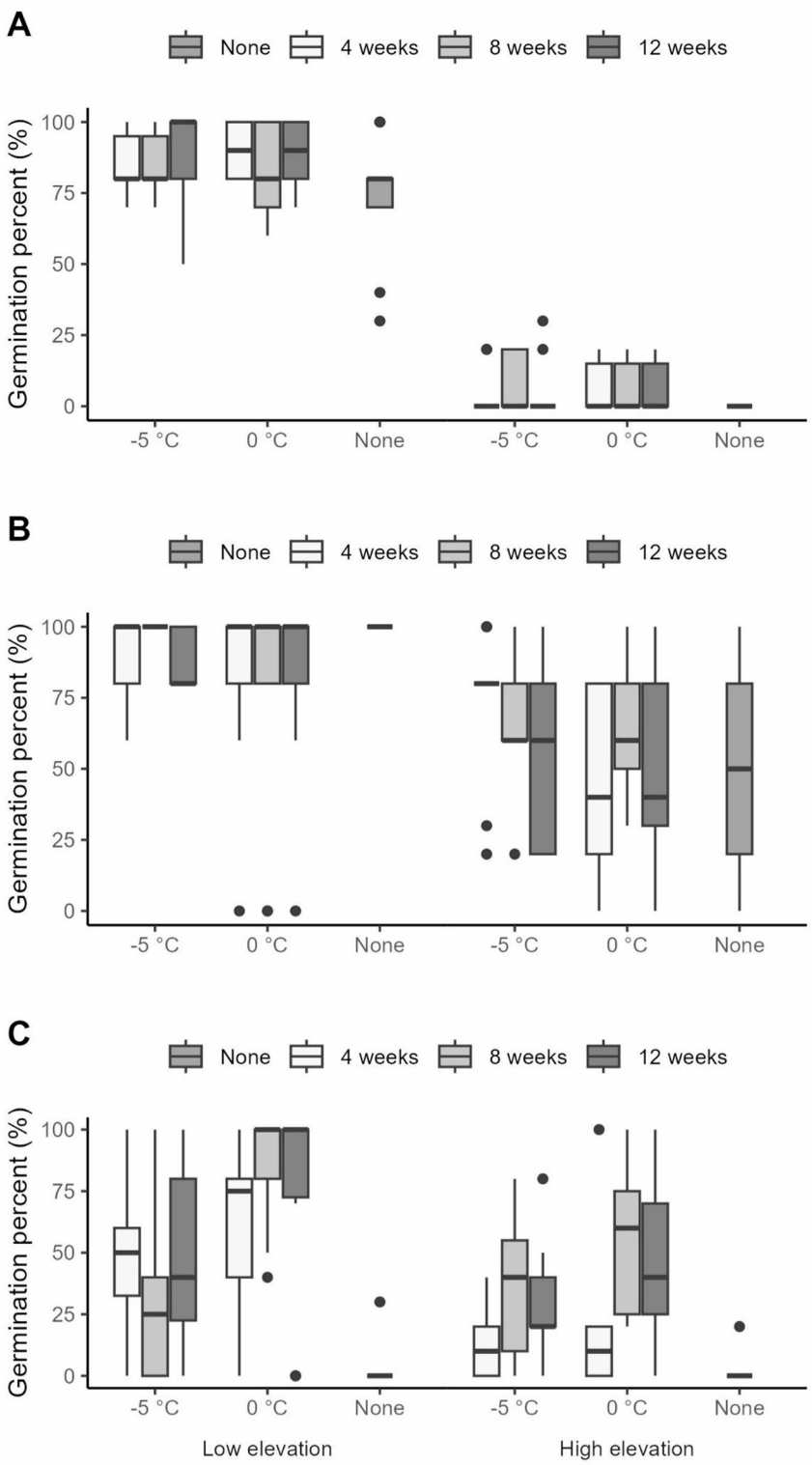


Fig. 2 Median germination percentage for (**A**) *Juncus trifidus*, (**B**) *Luzula multiflora*, and (**C**) *Luzula spicata*. Values are shown for seeds collected from low-elevation or high-elevation populations and across different stratification temperatures (-5 °C, 0 °C) and stratification durations (4, 8, 12 weeks). None represents non-stratified seeds. Boxes represent 25th and 75th percentiles, whiskers are the smallest/largest value within 1.5 times the interquartile range below/above the 25th/75th percentiles. Dots are outliers

tendency was observed for high-elevation seeds, although the differences were not statistically significant.

Stratification duration had a significant effect only for *L. spicata* (Fig. 2, Online Resources Table S6). In high-elevation seeds, stratification for 8 weeks at -5 °C or for 8 or 12 weeks at 0 °C resulted in higher germination percentages compared with a shorter 4-week stratification period.

Day of first germination and t50

For *J. trifidus*, both elevation, stratification temperature, and stratification duration had a significant effect on day of first germination (negative binomial GLM, Table 2; Fig. 3A). High-elevation seeds took 1.59 times longer to germinate than low-elevation seeds (estimated marginal means, $p<0.01$), and seeds stratified at 0 °C germinated sooner than seeds stratified at -5 °C (estimated marginal means, $p<0.0001$). Regardless of stratification temperature and duration, non-stratified seeds of *J. trifidus* from both elevations had a significantly later day of first germination than stratified seeds. The t50 for *J. trifidus* ranged from 4.7 days for low-elevation seeds stratified at 0 °C for 12 weeks to 13.0 days for high-elevation seeds stratified at -5 °C for 4 weeks (Table 3). Non-stratified seeds from high elevation failed to germinate, while non-stratified seeds from low elevation had a t50 of 12.9 days (Table 3; Fig. 3A).

The day of first germination for *L. multiflora* was significantly affected by stratification duration (negative binomial GLM, $p<0.0001$) and stratification temperature (negative binomial GLM, $p<0.01$) (Table 3; Fig. 3B). Stratified seeds germinated earlier than non-stratified seeds, with those stratified at 0 °C germinating significantly faster than those stratified at -5 °C (estimated marginal means, $p<0.01$). High-elevation seeds stratified at 0 °C for 4 weeks had the lowest t50 (5.3 days), whereas the highest t50 (15.8 days) was observed in non-stratified seeds from low elevation (Table 3; Fig. 3B).

For *L. spicata*, day of first germination was only significantly affected by stratification duration (negative binomial GLM, $p>0.0001$, Table 3; Fig. 3C). Seeds stratified for 4 weeks took 1.32 times longer to germinate than seeds stratified for 8 weeks (estimated marginal means, $p<0.05$). The t50 *for L. spicata* ranged from 4.78 days for low-elevation seeds stratified at 0 °C for 12 weeks to 16.50 days for non-stratified high-elevation seeds (Table 3).

Differences in germination percentages, as well as in the day of first germination and t50 across species, elevations and stratification treatments were also evident in the germination curves (Online Resources Figs. S2-S4). For example, the germination percent for *L. multiflora* after 21 days of monitoring was greater for low-elevation seeds than high-elevation seeds, and stratified seeds began germinating earlier than non-stratified seeds.

Table 2 Results (p values) from the negative binomial models on day of first germination. Values in bold are significant

Elevation	*Juncus trifidus*	*Luzula spicata*	*Luzula multiflora*
	<0.0001 (df=1)	>0.05 (df=1)	>0.05 (df=1)
Stratification duration	**<0.0001 (df=3)**	**<0.0001 (df=3)**	**<0.0001 (df=3)**
Stratification temperature	**<0.05 (df=1)**	>0.05 (df=1)	**<0.01 (df=1)**

Discussion

Climate change is expected to strongly affect Arctic plants (Elmendorf et al. 2012; Myers-Smith and Hik 2018; García Criado et al. 2020), as rising temperatures and shorter winters will impact the length of the seed dormancy period and cold stratification temperatures, which will affect seed dormancy break and the germination temperature required (Shimono and Kudo 2005).

The three species examined in this study displayed somewhat different responses to stratification temperature and duration, indicating different germination strategies. *Luzula spicata* showed limited seed germination without cold stratification and although low-elevation seeds of *J. trifidus* germinated readily without cold stratification, the germination rate of high-elevation seeds of *J. trifidus* was also increased by cold stratification at 0 °C. Moreover, stratification accelerated seed germination in all three species. This suggests that a cold period is important for promoting germination in *L. spicata* and *J. trifidus*, consistent with findings from alpine populations in the Northern Apennines, where germination mainly occurred after prolonged exposure to low non-freezing temperatures (Orsenigo et al. 2015). In contrast, germination of *L. multiflora* was less dependent on cold stratification with a moderate germination percentage for high-elevation seeds and a high germination percentage for low-elevation seeds, regardless of treatment, indicating that seeds of *L. multiflora* were non-dormant or in non-deep physiological dormancy. This differs from previous work (Orsenigo et al. 2015), showing that a prolonged period of low, non-freezing temperatures stimulates seed germination of alpine *L. multiflora*. Overall, these results demonstrate that cold stratification is important for dormancy release in some species but not others, aligning with patterns observed in other Arctic plant species (Kellmann-Sopyła and Giełwanowska 2015). Differences among species, and even among studies of the same species, may, in addition to duration of stratification, reflect population differences in dormancy breakage. Divergent observations of dormancy status within the same species may be caused by differential

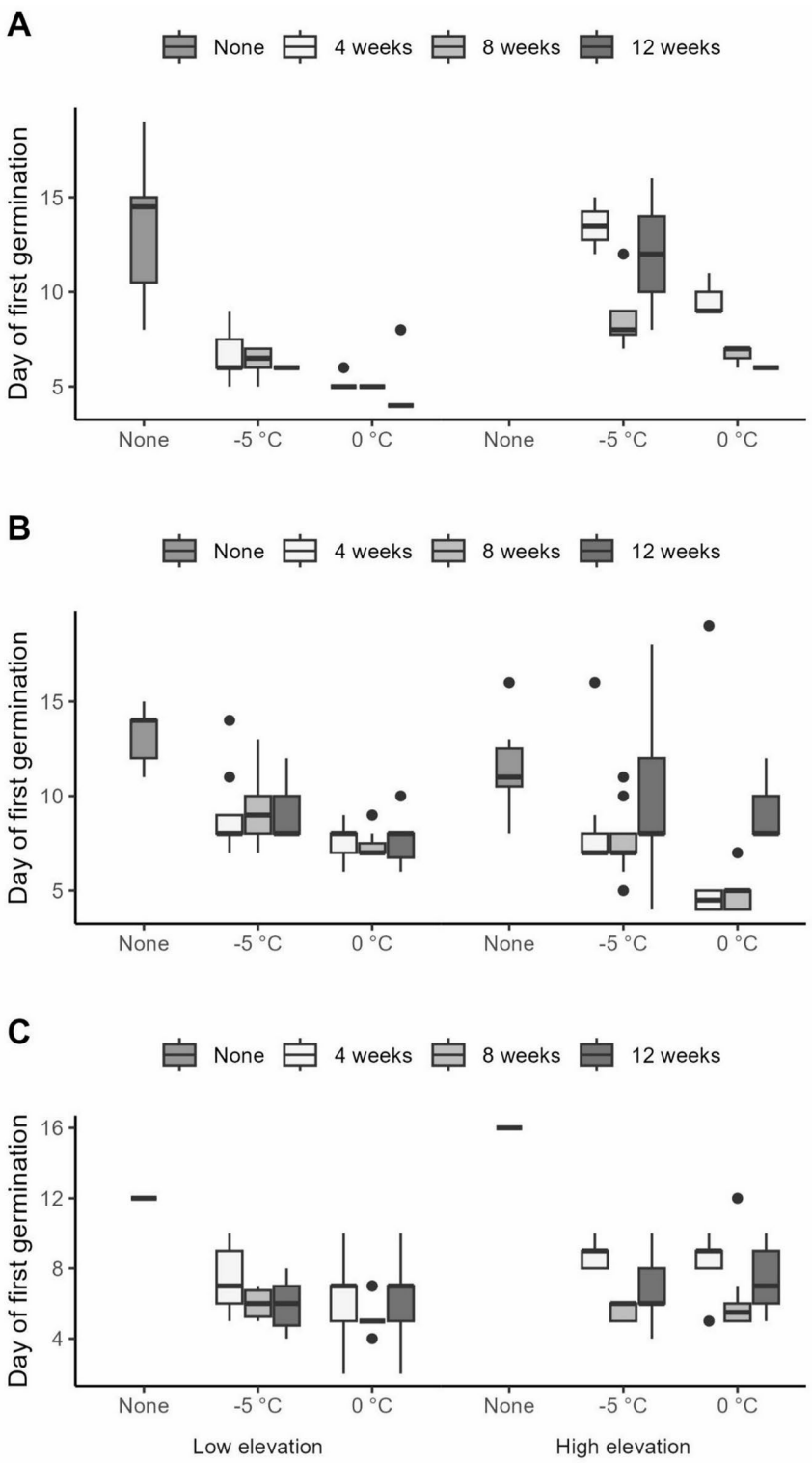


Fig. 3 Median first day of germination for (**A**) *Juncus trifidus*, (**B**) *Luzula multiflora*, and (**C**) *Luzula spicata*. Values are shown for seeds collected from low-elevation or high-elevation populations across different stratification temperatures (-5 °C, 0 °C) and stratification durations (4, 8, 12 weeks). None represents non-stratified seeds. Boxes represent 25th and 75th percentiles, whiskers are the smallest/largest value within 1.5 times the interquartile range below/above the 25th/75th percentiles. Dots are outliers

importance of various environmental cues and responses in distinct ecotypes that may also have different depths of dormancy (Finch-Savage and Leubner-Metzger 2006). For example, Mondoni et al. (2018) documented different germination and dormancy patterns in alpine and sub-arctic populations of the same species, with these differences presumably being driven by an interplay of geographical and climatic factors.

Interestingly, we found a strong effect of population on the germination rates of all three species, with seeds collected at low elevation exhibiting higher germination rates than those from high elevation. Low-elevation seeds of *J. trifidus* also

Table 3 The number of days to 50% germination (t50) for each species-treatment combination. Seeds of *Juncus trifidus*, *Luzula multiflora*, and *Luzula spicata* were collected from low- or high-elevation populations and subjected to different stratification temperatures (-5 °C, 0 °C) and stratification durations (4, 8, 12 weeks). None represents non-stratified seeds. The t50 is based on seeds that germinated within 21 days. No estimate was found when no seeds had germinated

Species	Elevation	Temperature (˚C)	Duration (weeks)	t50 (days)
Juncus trifidus	High	0	4	8.8
Juncus trifidus	High	0	8	6.3
Juncus trifidus	High	0	12	6.0
Juncus trifidus	High	-5	4	13.0
Juncus trifidus	High	-5	8	7.5
Juncus trifidus	High	-5	12	8.5
Juncus trifidus	High	None	0	NA
Juncus trifidus	Low	0	4	5.1
Juncus trifidus	Low	0	8	NA
Juncus trifidus	Low	0	12	4.7
Juncus trifidus	Low	-5	4	6.3
Juncus trifidus	Low	-5	8	6.2
Juncus trifidus	Low	-5	12	6.8
Juncus trifidus	Low	None	0	12.9
Luzula multiflora	High	0	4	5.3
Luzula multiflora	High	0	8	6.4
Luzula multiflora	High	0	12	7.2
Luzula multiflora	High	-5	4	9.1
Luzula multiflora	High	-5	8	10.7
Luzula multiflora	High	-5	12	9.3
Luzula multiflora	High	None	0	13.5
Luzula multiflora	Low	0	4	10.5
Luzula multiflora	Low	0	8	9.7
Luzula multiflora	Low	0	12	8.8
Luzula multiflora	Low	-5	4	12.5
Luzula multiflora	Low	-5	8	13.4
Luzula multiflora	Low	-5	12	10.8
Luzula multiflora	Low	None	0	15.8
Luzula spicata	High	0	4	8.5
Luzula spicata	High	0	8	5.7
Luzula spicata	High	0	12	6.1
Luzula spicata	High	-5	4	8.3
Luzula spicata	High	-5	8	6.3
Luzula spicata	High	-5	12	7.0
Luzula spicata	High	None	0	16.5
Luzula spicata	Low	0	4	7.3
Luzula spicata	Low	0	8	6.5
Luzula spicata	Low	0	12	4.8
Luzula spicata	Low	-5	4	8.4
Luzula spicata	Low	-5	8	6.3
Luzula spicata	Low	-5	12	7.6
Luzula spicata	Low	None	0	12.5

germinated more rapidly. For *L. spicata* and *J. trifidus* this pattern may reflect deeper dormancy of high-elevation seeds relative to low-elevation seeds and a corresponding requirement for a longer period of cold stratification. Consistent with this interpretation, longer cold stratification increased the germination percentage in high-elevation populations of *L. spicata*, whereas stratification duration had no effect on the germination rate of low-elevation seeds. In alpine plants species, temperatures during seed maturation can alter seed dormancy, with warmer temperatures resulting in reduced dormancy and enhanced germinability (García-Fernández et al. 2015; Bernareggi et al. 2016). Similarly, water availability during seed development leads to changes in seed dormancy (Fenner 1991). Another, non-exclusive, explanation may be differences in seed viability and vigour. Low temperatures, short growing seasons and/or reduced water availability can reduce seed production, while also decreasing seed germination and seedling establishment (Cavieres and Sierra-Almeida 2018; Panchen et al. 2022). Supporting this, *L. multiflora* seeds from low elevation were on average heavier relative to high-elevation seeds and a similar tendency was observed for *J. trifidus*. This suggests that more favorable climatic conditions at low elevation allow plants to produce larger seeds that provision the embryo and seedling with greater resources. Some studies investigating variation in seed weight within single alpine species have reported a reduction in seed weight with increasing elevation(Totland and Birks 1996; Wirth et al. 2010) although this pattern is not universal (Pluess et al. 2005; Daco et al. 2021). Where present, it is often attributed to more stressful environments, which may decrease the availability of resources to plants, and thus reduce allocation of resources to individual seeds (Qi et al. 2014). One implication of increased seed size and germinability in response to increased growing season temperatures is increased reproductive success of Arctic plants as the climate warms. Hence, there is some evidence that recent climate warming has improved seed viability in the Arctic, if not offset by increasing climate extremes (Alsos et al. 2013; Panchen et al. 2022). However, because only two populations were included along the elevational gradient, it is not possible to draw firm conclusions about the effect of elevation. The differences observed between the high- and low-elevation seeds may instead reflect microhabitat variation in temperature and other environmental factors. Given the large differences observed between the two populations, future studies should include multiple populations across the elevation gradient to more reliably disentangle the effects of elevation and site-specific conditions.

In accordance with our second hypothesis, the germination rate of low-elevation seeds of *L. spicata* was significantly higher for seeds stratified at 0 °C than for those stratified at -5 °C. Additionally, in *J. trifidus* and *L. multiflora* germination proceeded more rapidly following stratification at 0 °C than at -5 °C. These results indicate that, for some species, 0 °C is more effective for dormancy release than −5 °C. Consequently, lower soil temperatures associated with a thinner snow cover may diminish germination

of *L. spicata* and delay germination of *J. trifidus* and *L. multiflora.* Previous work shows generally higher germination rates and earlier germination in seeds stratified at constant 0.5 °C compared to seeds stratified at temperatures varying between 0.5 and -10 °C across 23 subarctic species (Milbau et al. 2009). In contrast, Graae et al. (2008) reported little effect of stratification temperature on the germination of *Empetrum nigrum* and *Vaccinium uliginosum* seeds collected from arctic, boreal and alpine sites. Together, these contrasting results suggest that the effectiveness of stratification temperature is species-specific.

We did not, as hypothesized, detect a consistent effect of stratification duration on germination. However, longer cold stratification accelerated day of first germination and increased germination percentages in high-elevation populations of *L. spicata*, indicating that stratification duration is indeed important in populations with deeper dormancy. Such population differences in stratification requirements likely reflect adaptations to local variation in snow-cover duration and winter temperatures.

Although low-elevation seeds of *L. spicata* exhibited higher germination percentages overall, they appeared more susceptible to pathogen attack than high-elevation seeds, leading to the removal of a substantial number of *L. spicata* seeds (Online Resources Table S2). Fungal diversity is strongly shaped by climatic conditions (Jarvis et al. 2015) and according to Halliday et al. (2021), who studied foliar levels of fungal diseases along a 1100-m elevational gradient, increasing temperature associated with lower elevation can directly increase pathogen growth and reproduction, thereby elevating disease risk at low elevation. Across a larger spatial gradient, Graae et al. (2008) found that Arctic seeds of *V. uliginosum* were more vulnerable to fungal infection than boreal seeds of the same species, a pattern attributed to poorer seed development in colder climates or reduced antifungal defenses in populations adapted to very cold climates. Across species, the rate of fungal infection also appeared larger in seeds stratified at 0 °C as compared to -5 °C. This is consistent with previous observations for *V. uliginosum* seeds and may indicate that low temperatures play an important role in preventing fungal infection during winter (Graae et al. 2008).

In conclusion, we found strong effects of species, population, and stratification temperature on seed germination, alongside several complex species-specific interactions involving stratification, stratification duration, elevation, and temperature. These findings indicate that climate warming and associated shifts in ground thermal regimes will influence germination patterns in Arctic plants in ways that vary among species and populations. Projected decreases in winter soil temperatures may reduce germination rates and slow germination in species for which cold exposure promotes dormancy release.

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Author contributions SB collected the seeds. MP, JDA, CADA, NKM, MEBP and SB conceived and designed research. JDA, CADA, NKM, SNC, TTH and MEBP obtained data and conducted germination experiments. LHA analyzed and visualized the data. MP wrote the manuscript with all the authors contributing to the interpretation of the data, review and editing of the manuscript. All authors read and approved the manuscript. SB and MP were responsible for supervision.

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Data availability The data supporting the findings of this study are available upon request from corresponding author.

Declarations

Competing interests The authors declare no competing interests.

Ethics declaration Not applicable.

Statement on inclusion Plant seeds were collected and necessary permits obtained in accordance with Home Rule Greenland (license no. GE23-001).

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