Seed Science Research

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Can alpine species take the heat? Impacts of increased temperatures on early life stages

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Short Communication

Cite this article: Seglias AE, DePrenger-Levin M (2024). Can alpine species take the heat? Impacts of increased temperatures on early life stages. *Seed Science Research* 1–5. https://doi.org/10.1017/S0960258524000096

Received: 30 November 2023
Revised: 22 February 2024
Accepted: 12 March 2024

Keywords:
alpine; climate change; conservation; rare plants; seed germination; seedling

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Abstract

Alpine plant species are particularly vulnerable to climate change. Temperature fluctuations are projected to be most severe at high elevations. Even small shifts in temperature have major consequences on phenology, reproduction, and community composition. Early life stages are arguably the most important processes in the fitness of an individual plant and the dynamics and persistence of plant populations. These initial developmental stages are expected to be more vulnerable to changes in climate than adult life stages. To understand how early life stages of alpine plant species will respond to warming temperatures, seeds and seedlings of two species were exposed to three different temperature regimes. Temperatures were based on current and projected conditions under low and high emission scenarios. Two rare alpine species performed better under warmer temperatures at both the germination and seedling stages. The results show that early life stages of alpine plants may not be at high risk from warming temperatures; however, there are many other shifting climatic factors to consider, resulting from climate change beyond temperature alone.

Introduction

Climate change threatens plant biodiversity worldwide, but alpine plants are particularly vulnerable to climate change. Warming in alpine regions over recent decades has been outpacing the average global warming rate (Pepin et al., 2015), with annual mean temperatures from 1961 to 2010 increasing about 1.2 times faster in high-elevation areas (Wang et al., 2016). Warming in the alpine triggers earlier snowmelt, thereby advancing and increasing the length of the growing season (Inouye, 2008). Alpine plants have adapted to low temperatures, meaning that even a small increase in temperature may have a larger impact in high-elevation systems compared to less climatically extreme systems.

Early life stage processes (seed germination and seedling survival) are arguably the most important in population dynamics. Early life stages drive individual fitness, population persistence and the ability to disperse and establish in more suitable habitats. These initial developmental stages are expected to be more vulnerable to changes in climate than adult life stages (Walck et al., 2011) and thereby represent a major bottleneck to recruitment and population responses as climate change increases in severity. Temperature is one of the most important climatic cues for germination because it signals that the environmental conditions are suitable for emergence and seedling establishment (Briceño et al., 2015). Climate change is altering temperature and other environmental cues that seeds need to germinate, impacting phenology, germination rate and seedling establishment.

Alpine species were thought to persist primarily through clonal reproduction. However, recent studies have shown that many alpine species reproduce sexually (Forbis, 2003; Schwienbacher et al., 2011; Fernández-Pascual et al., 2020). Strict alpine plants are characterized by physiological seed dormancy, germination under warm temperatures, a positive response to alternating day/night temperatures and a positive response to light (Fernández-Pascual et al., 2020). Most alpine species are classified as physiologically dormant, meaning that a period of cold is required to break dormancy and germinate (Schwienbacher et al., 2011; Baskin and Baskin, 2014; Gremer et al., 2020). Alpine species disperse seeds in the autumn, which overwinter under insulated snow protection and germinate in the spring when environmental conditions are favourable for seedling survival (Rosbakh and Poschlod, 2015).

Rare and threatened species have additional constraints on distribution and survival. The niche-breadth hypothesis suggests that rarity is caused by a narrow range of habitats and environmental conditions required for persistence, thereby limiting their range (Slatyer et al., 2013). Rare species, or those with a narrow niche breadth, are less tolerant to changes in climate than more widespread species (Vincent et al., 2020). As the climate continues to change at an unprecedented rate, rare alpine species with narrow niches and sensitivity may be one of the most at-risk groups.

This study quantifies the impact of increasing temperatures on the germination and seedling stages of two rare alpine Colorado endemics. In knowing the impacts of warmer temperatures on early life stages, we can prioritize conservation actions for at-risk alpine species.

https://doi.org/10.1017/S0960258524000096 Published online by Cambridge University Press

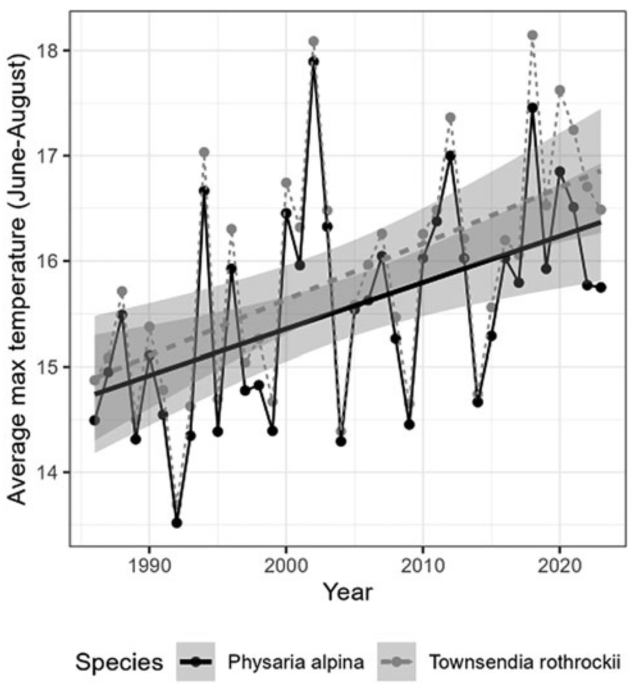

Figure. 1. Maximum temperature (°C) averaged over the months of June to August from 1986 to 2023 for the two seed collection sites.

Materials and methods

Study area and species information

Seeds were collected from populations located in the Mosquito Range of the Colorado Rocky Mountains. These populations have shown an increase in an average maximum temperature of 1.5-2°C for June to August since 1986 (Fig. 1).

Two endemic, rare alpine forb species were selected for this study: *Physaria alpina* Rollins (Brassicaceae; G2/S2) and *Townsendia rothrockii* A. Gray ex Rothrock (Asteraceae; G3/S3). Seeds of *P. alpina* were collected from Weston Pass in 2019 and seeds from *T. rothrockii* were collected from Boreas Pass in 2021. Vouchers were deposited in the Kathryn Kalmbach Herbarium at Denver Botanic Gardens. Seeds from *P. alpina* were stored in standard *ex situ* seed bank conditions (−20°C and 20% RH) for about 2 years prior to the start of the study, while seeds of *T. rothrockii* were stored at room temperature for about 6 months prior to the start of the experiment. Previous testing of these species found that stratification is necessary to break dormancy and that temperatures of at least 20/10°C (day/night) are required for high germination percentage (Seglias, 2022; unpublished data).

Germination experiment

Seeds were placed in sterile plastic Petri boxes containing 1.5% agar. Each box consisted of 25 seeds, with four replicates per treatment. Seeds were stratified (4°C) for 4 weeks (*P. alpina*) and 8 weeks (*T. rothrockii*). Following stratification, seeds were placed in climate-controlled incubators with three separate treatments: 20/10°C with an alternating 12 h light/12 h dark regime (control treatment); 22/12°C (+2 treatment as shown in figures) and 24/14°C (+4 treatment as shown in figures). The conditions of stratification and the control treatment were determined based on previous germination studies with these species (Seglias, 2022; unpublished data), while the conditions of the warming treatments are based on projected future emission scenarios for the area (Saunders et al., 2021). Seeds remained in incubation conditions for 4 weeks and germination was evaluated weekly during this period. Seeds with radicle emergence were considered to have germinated, and those that did not germinate by the end of the treatment were subjected to a 'cut test,' and factored into a viability-adjusted germination (VAG) percentage.

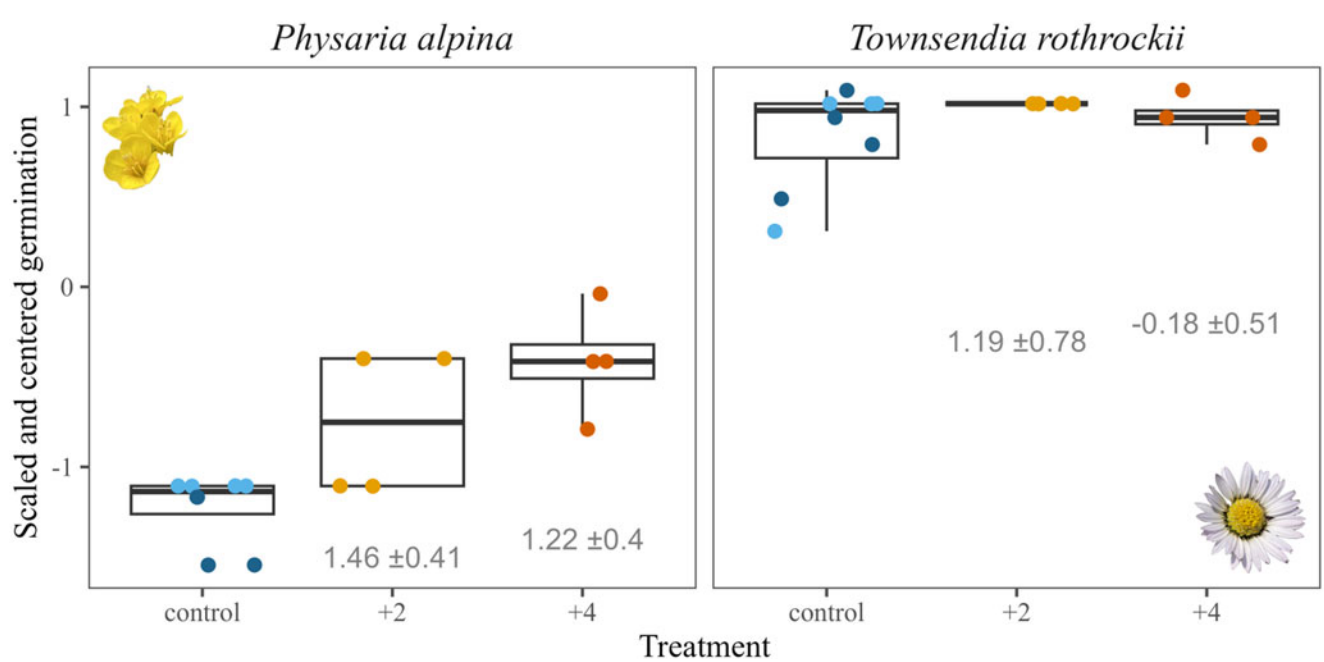

Figure. 2. Scaled and centred germination across treatments. Values shown include offset from the control and the standard error. If the standard error is larger than the offset, there is no significant difference between the control and treatment. +2 is the 22/12°C treatment and +4 is the 24/14°C treatment.

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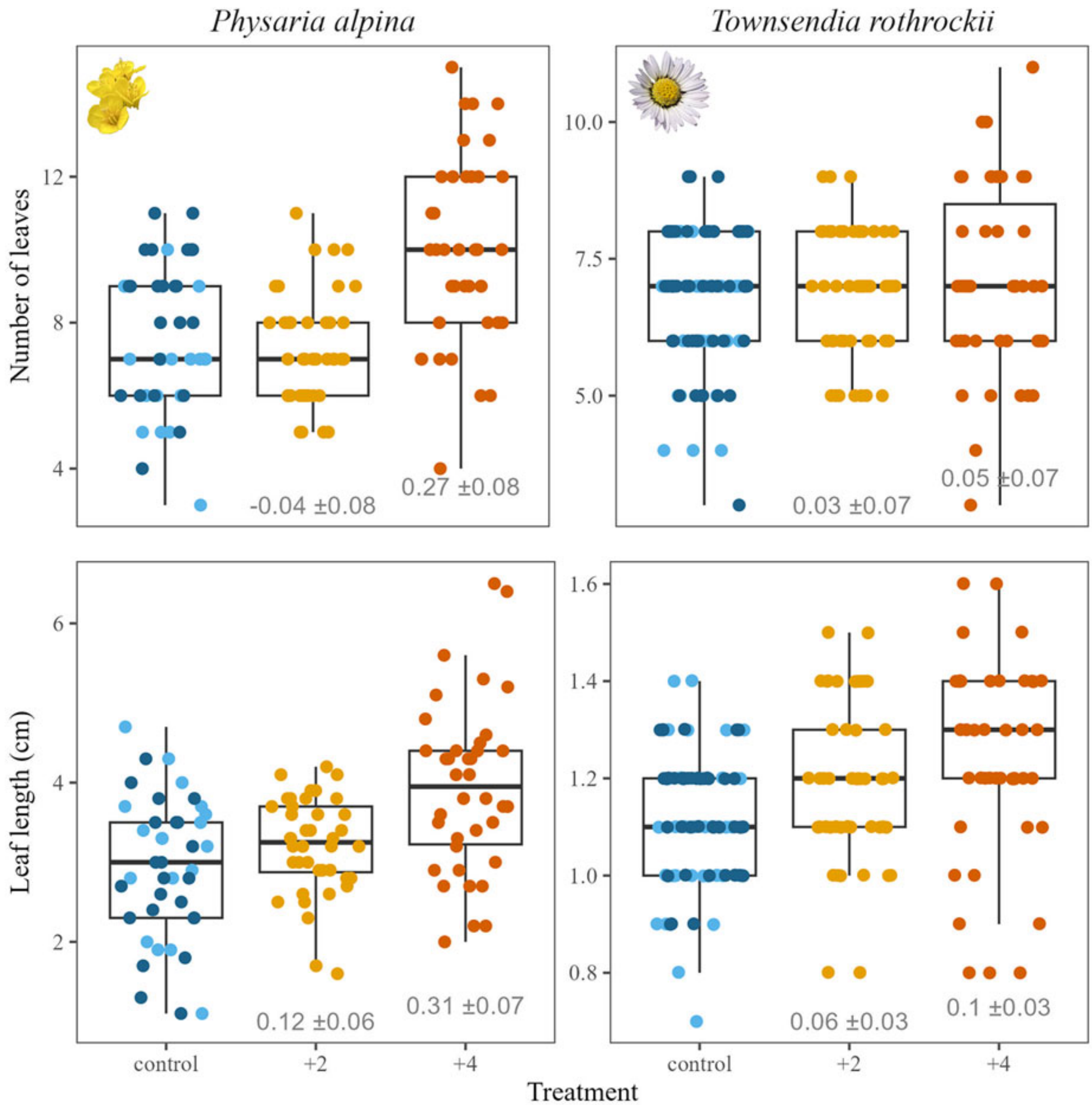

Figure. 3. Final measurements of the number of leaves and the length of the longest leaf (cm) among treatments. Values shown include offset from the control and the standard error. If the standard error is larger than the offset, there is no significant difference between the control and treatment. The two control treatments (20/10°C) are combined. +2 is the 22/12°C treatment and +4 is the 24/14°C treatment.

Seedling experiment

Once the germinants produced their first true leaves, 50 individuals were transplanted to 5-inch-deep trays with a mix of 2 parts Lambert LM-HP soil, 2 parts perlite and 1 part turface. The trays were placed into the incubators at the same temperature and light conditions that the seeds experienced and were watered weekly. Measurements were taken every 2 weeks for 2 months on the number of leaves and the length of the longest leaf.

Statistical analysis

All germination analyses were performed on VAG (number of germinated seeds/number of viable seeds) using the R environment for statistical computing (R Core Team, 2023). To account for variable conditions between trials due to a refrigerator malfunction (increase in the temperature of ~10–12°C) during the stratification period of *P. alpina* in the second round of treatments (20/10 (2) and 24/14), the VAG of replicates in all treatments were centred and scaled. Once the mean was subtracted from the results and divided by their standard deviation, the control treatments were combined. The effects of treatment on germination and leaf length were analyzed using a Gaussian linear model, and the effects on the number of leaves were analyzed using a generalized linear model with Poisson error distribution. Binomial generalized linear models were used to measure the effect of treatment on survival.

Results

Germination of *P. alpina* increased by about 5% between the control treatment and the +2°C treatment, and by about 25% between

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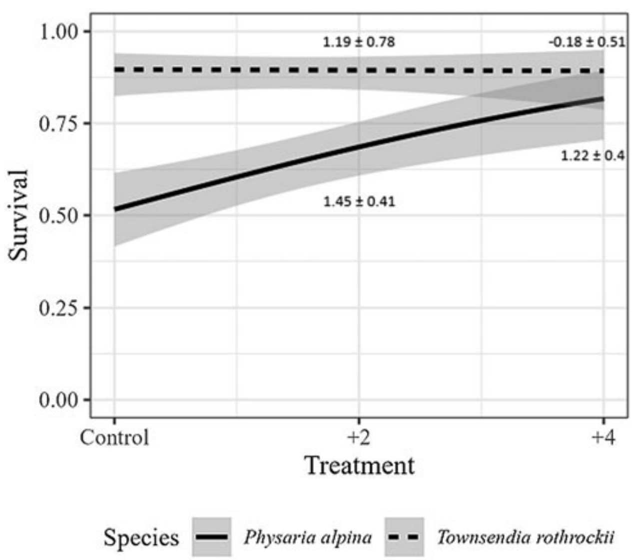

Figure. 4. Survival curves by treatment for the two species. Results are from the final data collection of the seedling growth period. Values shown include offset from the control and the standard error. If the standard error is larger than the offset, there is no significant difference between the control and treatment. The two control treatments (20/10°C) are combined. +2 is the 22/12°C treatment and +4 is the 24/14°C treatment.

the control and +4°C treatment (Fig. 2). There were no significant differences among treatments for *T. rothrockii,* with germination close to 100% across all conditions.

At the seedling stage, *P. alpina* showed significant differences in the number of leaves in the warmest treatment (+4°C) and the length of the longest leaf in the +2°C treatment (Fig. 3). There were no significant differences in the number of leaves among treatments for *T. rothrockii*, but there was a significant difference in the length of the longest leaf between the control and the +2°C treatment (Fig. 3).

There was a significant increase in the survival of seedlings for *P. alpina* as the temperature conditions warmed, with the highest survival in the +4°C treatment (Fig. 4). Survival increased by over 25% between the control treatment and the warmest treatment. There were no significant differences in survival among the treatments for *T. rothrockii*.

Discussion

Effects on germination

Higher temperatures increased germination success for *P. alpina* and did not impact the germination of *T. rothrockii*. The germination proportion of *T. rothrockii* was consistently high, suggesting that increased temperatures will not be detrimental. For *P. alpina* on the other hand, there was a substantial increase in the germination proportion as temperatures increased. These results parallel others that have found that warmer temperatures increase germination in alpine species (e.g., Mondoni et al., 2022). However, there could be negative impacts on germination if temperatures continue to increase beyond predictions for the next two decades.

Effects on seedling growth and survival

In general, warming had a neutral to positive effect on seedling vigour for both species. Leaf length increased for both species as temperatures warmed, and the number of leaves increased for *P. alpina* but remained constant across treatments for *T. rothrockii*. The number and size of leaves on a seedling influence the relative growth rate of plants (Fenner and Thompson, 2005), suggesting that some warming could be beneficial to the establishment and survival of alpine plants. Furthermore, if alpine plants grow larger with increased warming, there may be a competitive advantage as low-elevation species move up and compete for resources (Grime, 1979; Keddy et al., 2002).

Moderate warming increased the survival of *P. alpina* seedlings, while survival was constant for *T. rothrockii* across treatments. Since survival was high across all treatments, *T. rothrockii* is likely to have a wide niche breadth in response to variable environmental conditions. These results contradict studies that show warming has a negative effect on seedling survival (Wang et al., 2018; Vázquez-Ramírez and Venn, 2021). However, results varied by species, suggesting an inconsistent response of seedling survival to warming.

Implications of increased temperatures

Despite the sensitivity of rare alpine species to climate change, the results of this study showed that increased temperatures did not have a negative effect on the germination and seedling growth of *P. alpina* or *T. rothrockii*. However, increased temperatures also alter season length, precipitation patterns and snowpack, which could all affect alpine plants. Additionally, there may exist a temperature threshold by which there are no longer beneficial, but rather detrimental effects to early life stages, or there may be negative effects at later life stages due to any one or a combination of these factors.

The understanding of the impacts of climate change on seed and seedling dynamics comes from a relatively small number of studies ($N = 45$; Mondoni et al., 2022), which show varying effects based on the environmental factors, life stage, and habitat location. Therefore, our knowledge of how early life stages of alpine plants will respond is still limited. Despite evidence to suggest that early life stages of alpine plants may be able to survive certain impacts of climate change, rare alpine species are still at risk of extinction. Rare species typically already have a restricted range and require specific conditions for growth and survival, with little room to migrate or adapt (Vincent et al., 2020). Reducing the uncertainty of the effects of environmental change on rare alpine populations is needed to implement conservation measures to prevent extinction.

Acknowledgements. The authors would like to thank the Research and Conservation Department at Denver Botanic Gardens for helping with seed collection and providing feedback on this manuscript. This research received no specific grant from any funding agency, commercial or not-for-profit sectors.

Competing interest. The authors declare none.

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