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Germination dynamics of *Nothofagus glauca* seeds: provenance-specific responses to temperature variation

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Abstract

Background: The influence of temperature on seed germination is crucial, and climate change effects on plant distribution are significant. To grasp climate change's impact on terrestrial ecosystems, understanding plant adaptation to temperature shifts is vital. *Nothofagus glauca*, a vulnerable species endemic to Chile's Mediterranean region, is the most representative species of South American Mediterranean forests.

Methods: Seeds of *N. glauca* were collected from two Andean provenances during mast years (2017, 2022) and processed according to the standards of the International Seed Testing Association (ISTA). Germination experiments were conducted under controlled laboratory conditions in the absence of light, testing four temperature levels (18°C, 22°C, 26°C, and 30°C) and two provenances (El Colorado, located further north, and San Fabian, located further south). Seeds were pretreated with gibberellic acid to break physiological dormancy, and germination parameters were assessed over a 40-day period.

Results: Temperature had a significant impact on germination process, although the effect varied by provenance. The optimal germination capacity temperature was 22°C for the northern origin and 26°C for the southern origin. In both provenances, germination capacity remained relatively high at temperatures of 18°C and 30°C, suggesting that these temperatures did not approach the minimum or base and maximum or ceiling temperature thresholds. Furthermore, no clear trend was observed in the germination start day for either provenance. Significant differences were observed in average germination speed and germination vigour between the two provenances. Considering all variables, the optimal temperature differs between them (22°C for El Colorado and 26°C for San Fabian).

Conclusions: Temperature's pivotal role in germination and diverse provenance responses highlight potential impacts on genetic distribution and conservation. Understanding provenance-specific adaptation to changing climates is essential for comprehending climate change's effects on terrestrial ecosystems. Tailoring conservation approaches to distinct provenances, like *N. glauca*, is crucial. This approach can effectively tackle climate change challenges and protect vulnerable species.

Keywords: Hualo; seeds; Mediterranean plants; seed provenance.

Introduction

Nothofagus glauca (Phil. Krasser) (Hualo) is a vulnerable tree species that is endemic to the Mediterranean region of Chile (Barstow et al. 2017), being the most representative species in terms of abundance in the Mediterranean forests of South America (Santelices-Moya et al. 2022). The deciduous forests of *N. glauca* have adapted to the prolonged summer dry periods and play important roles in water and soil organic conservation, biogeochemical carbon cycling, and offer a wide variety of ecological conditions and resources for flora, fauna and associated microbiota (Arroyo et al. 1996).

However, *N. glauca* forests have been strongly impacted by anthropogenic factors, leading to high deforestation rates (Altamirano & Lara 2010). It has been reported that in almost half a century, more than 80% of *N. glauca* forests have been lost (Urzúa 1975; Santelices-Moya et al. 2022).

In the context of the global climate crisis, it is necessary to understand how climate change can affect the germination of *N. glauca* and, therefore, its survival and distribution. Germination is a crucial process for the natural regeneration of forests, and temperature is a key factor influencing this process. Germination of *N. glauca* seeds has been studied extensively due to its importance for forest conservation and restoration (Fajardo & Alaback 2005; Santelices et al. 2013; Cabello et al. 2019; Navarro-Cerrillo et al. 2020; Santelices-Moya et al. 2020). However, the effect of temperature on *N. glauca* germination has only been investigated for five coastal provenances (Santelices-Moya et al. 2022). Additionally, temperature is a crucial factor in seed germination (Baskin & Baskin 2014), affecting enzymatic activity, periodicity of seed germination, and species distribution (Belmehdi et al. 2018). The results obtained by Santelices-Moya et al. (2022) showed that for 5 coastal provenances of *N. glauca*, germination rate and energy increased linearly with temperature until reaching an optimum value (e.g., 22°C), above which they decreased severely. The base temperature was around 18°C, and the maximum was above 30°C, which may be close to inhibition of germination.

To further comprehend the impact of temperature on *N. glauca* germination, it is crucial to broaden the research towards the complete geographical distribution of the species and consider several climatic conditions. Given that *N. glauca* displays masting behaviour and that 71% of its natural distribution is in the Andean region (Santelices-Moya et al. 2020), this study aims to evaluate the temperature effect on seed germination of *N. glauca* from two Andean provenances in Chile. This research will help us to understand how climate change and local weather patterns may affect *N. glauca* germination and it will enable us to develop better conservation and restoration strategies for this vulnerable tree species.

Methods

Seed material

The seeds of *Nothofagus glauca* utilised in the experimentation were collected from two distinct forest provenances situated in the Andean distribution range of the species (Figure 1).

Given the masting behaviour of *N. glauca*, seeds were only available for collection during March 2017 from El Colorado in the Maule Region of Chile and in March 2022 from San Fabian in the Ñuble Region, coinciding with mast years for the species (Table 1). Following collection, seeds were transported to the laboratory, where they were manually separated from other plant material, with damaged seeds discarded. Subsequently, seeds were weighed, dried, and stored in glass containers under controlled conditions of 4°C in darkness, adhering to the standards outlined by the International Seed Testing Association (ISTA) for their characterisation (ISTA 2006). Seed weight was expressed as the average weight of 1000 seeds, calculated from 100 seeds weighed in eight replicates. Additionally, dimensions of dimer seeds (length and width) and trimers (length, width, and thickness) were measured (Table 2). Dormancy of the seeds was broken by soaking them in a 200 mg L^{-1} gibberellic acid solution (Giberplus® Tablets, ANASAC Chile S.A., Santiago, Chile) for 24 hours, prior to commencing germination tests, as described by Cabello et al. (2019).

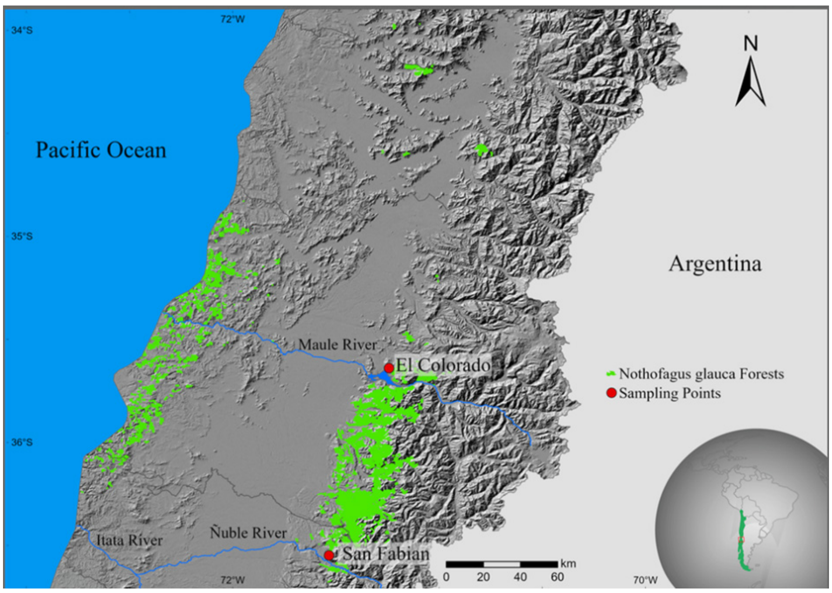

FIGURE 1: Geographical distribution of natural *Nothofagus glauca* forests and locations of seed collection.

TABLE 1: Geographical coordinates and climatic data of the provenances from which *Nothofagus glauca* seeds were collected.

Provenance	Latitude	Longitude	Elevation (m a.s.l.)	M.A.T[1] (°C)	M.A.R[2] (mm year^{-1})
El Colorado	35°38’01” S	71°12’49” W	805	10.4	946
San Fabian	36°32’54” S	71°31’59” W	667	9.6	1,240

[1]M.A.T.: mean annual temperature; [2]M.A.R.: mean annual rainfall.The mean annual precipitation and temperature were obtained from WorldClim (version 2) at a spatial resolution of 30 s (~1 km^2) by interpolation of the records of the meteorological stations from 1970 to 2000 (Fick & Hijmans 2017).

Experimental trial

The experimentation was conducted within a laboratory at Universidad Católica del Maule, Talca, Chile (35°26′10″ S, 71°37′13″ W, 131 m a.s.l.), during January and February 2020, following the methodology proposed by Santelices-Moya et al. (2022). Seeds were soaked in a 200 mg L^{-1} gibberellic acid (GA_3) solution for 24 hours using distilled water, and non-floating seeds were considered viable. To assess the impact of temperature on *N. glauca* seed germination from the Andean provenance, four temperature levels were tested: 18°C, 22°C, 26°C, and 30°C. Cultivation was conducted in germination chambers devoid of light, with temperatures maintained according to treatment requirements, utilising filter paper as the substrate. Ambient laboratory temperature was kept below 16°C to prevent interference with treatments. Irrigation was performed manually, ensuring constant moisture around the seeds. Germination progress was monitored daily until cessation over a 40-day period. Seeds were deemed germinated when radicles exceeded 2 mm in length. Germination parameters were calculated as following several authors (Czabator 1962; Hernández-Herrera et al. 2014; Kamran et al. 2021):

– Germination capacity (GC): is the quotient between the total number of germinated seeds (GS) and the seeds sown (SS), expressed as a percentage:

$$GC = (GS/SS) * 100$$

– Germination Start Day (GSD): the time elapsed from the sowing of the seeds to the germination of 5% of the sown seeds.
– Germination Energy (GE): accumulated percentage of germination on the day when the maximum value occurs (maximum value is the maximum quotient obtained by dividing successive cumulative germination values by the relevant incubation time).
– Average Germination Speed (AGS): corresponds to the average number of germinated seeds per day, calculated by the expression:

$$\sum_{1}^{k} \frac{ni}{ti}$$

– Germination vigour (GV): reflects in a single value the changes in the germination peak, the total germination, and the germination speed, calculated as the product between the maximum value and the average germination speed.

The trial involved the testing of two factors: temperature and provenance, with temperature examined at four levels and provenance at two levels. These factors were combined in a factorial design, resulting in eight treatments (4 × 2), each replicated five times in a split-plot design. Fixed effects were randomly assigned within subplots, with temperature applied to whole plots and provenance to subplots. Each factorial combination was tested with 25 viable seeds, totalling 125 seeds per treatment. ANOVAs and mean comparisons were conducted using the general linear model (GLM) procedure within the SPSS statistical software for Windows (SPSS, Chicago, IL, USA). Significant mean differences were assessed using the Tukey test at a 5% significance level.

Results

Temperature had a significant effect on the germination of *Nothofagus glauca* seeds from the two studied provenances (Table 3, Figures 2 and 3). Germination capacity fluctuated based on temperature and provenance. Specifically, 22°C was identified as the optimal temperature for germination in El Colorado, while San Fabian’s optimum temperatures were 22°C and 26°C. Seeds from El Colorado took longer to germinate than those from San Fabian, and germination rate was faster at higher temperatures in both provenances.

TABLE 2: Weight and morphometric characterisation of seeds from two provenances of *Nothofagus glauca* (mean ± Standard Error).

Provenance	Weight of 1000 seeds (g)	Number of seeds per kilogram	Dimerous Seeds		Trimerous Seeds		
			Length (mm)	Width (mm)	Length (mm)	Width (mm)	Thickness (mm)
El Colorado	445.9 ± 0.4	2,244 ± 14.6	17.9 ± 1.4	12.0 ± 1.3	16.7 ± 0.2	11.6 ± 0.1	9.5 ± 0.1
San Fabian	461.8 ± 0.3	2,165 ± 14.6	18.2 ± 0.1	10.2 ± 0.1	17.6 ± 0.2	9.3 ± 0.1	5.9 ± 0.1

TABLE 3: Effect of temperature on different germination parameters of *Nothofagus glauca* (mean ± SE). Different letters indicate significant differences by Tukey's multiple comparison test (P < 0.05).

Provenance	Temperature (° C)	Germination capacity (%)	Germination energy (%)	Germination start day	Average germination speed (seed/day)	Germination vigour
El Colorado	18	18.7 ± 0.4 [d]	16.6± 0.5 [c]	24 ± 0.3 [b]	0.9 ± 0.0 [d]	0.5 ± 0.0 [d]
	22	70.7 ± 0.4 [a]	54.0± 1.7 [b]	11 ± 0.2 [a]	7.1 ± 0.3 [a]	24.0 ± 0.3 [a]
	26	60.7 ± 0.4 [b]	58.8 ± 1.9 [a]	11 ± 0.2 [a]	4.8 ± 0.3 [b]	9.0 ± 0.3 [b]
	30	23.3 ± 0.4 [c]	16.7± 0.5 [c]	11 ± 0.4 [a]	2.3 ± 0.3 [c]	2.3 ± 0.3 [c]
San Fabian	18	62.2 ± 4.2 [bc]	60.5± 4.2 [a]	25 ± 0.5 [c]	0.5 ± 0.0 [b]	0.9 ± 0.1 [b]
	22	86.4 ± 4.8 [a]	67.3 ± 10.1 [a]	14 ± 0.4 [b]	0.9 ± 0.1 [b]	2.8 ± 0.6 [b]
	26	79.9 ± 7.5 [ab]	61.6 ± 11.2 [a]	8 ± 0.4 [a]	1.5 ± 0.2 [a]	7.2 ± 1.5 [a]
	30	54.8 ± 2.2 [c]	41.7 ± 9.7 [b]	24 ± 0.4 [c]	0.4 ± 0.0 [b]	0.8 ± 0.1 [b]

Furthermore, Germination Energy was higher with warmer temperatures, and optimal temperature varied by seed provenance. For instance, in El Colorado, the highest germination energy was 54% at 22°C, while in San Fabian, it was 67% at 22°C. Additionally, Average Germination Speed was also higher at warmer temperatures and varied based on provenance. In El Colorado, the highest average germination speed was 7.1 seeds per day at 22°C, while in San Fabian, it was 1.5 seeds per day at 26°C. Lastly, significant differences in germination vigour were observed in both provenances, with El Colorado showing much higher vigour than San Fabian. Optimal temperatures for obtaining the highest germination vigour were different for each provenance (22°C and 24°C, respectively).

Discussion

Seed germination is a complex process influenced by multiple factors. Two crucial growth regulators, gibberellic acid and abscisic acid, play distinct roles in promoting or inhibiting germination (Baskin & Baskin 2014). In seeds with internal dormancy, like *Nothofagus glauca*, achieving a proper balance between these regulators is vital. Cold stratification or gibberellic acid soaking becomes necessary to initiate germination (Cabello et al. 2019). Temperature, among other factors, significantly impacts germination by affecting metabolic activity and germination speed (Baskin & Baskin 2014). Temperatures exceeding the optimum range cause delayed seed germination due to elevated levels of abscisic acid in the embryo and endosperm. Additionally, at these temperatures, the synthesis of gibberellic acid is suppressed in these tissues (Toh et al. 2008; Izydorczyk et al. 2018). Our research showed a significant reduction in germination for El Colorado provenance seeds when exposed to temperatures of 30°C, consistent with that reported by Santelices-Moya et al. (2022) for other provenances of the same species. It is likely that at temperatures above this threshold, *N. glauca* seeds from El Colorado experience thermal inhibition, hindering the biosynthesis of gibberellins. While germination of San Fabian seeds also decreases at 30°C, they may not be as susceptible to this inhibition. Therefore, further investigation is warranted to evaluate the effects of temperatures above 30°C and determine the maximum

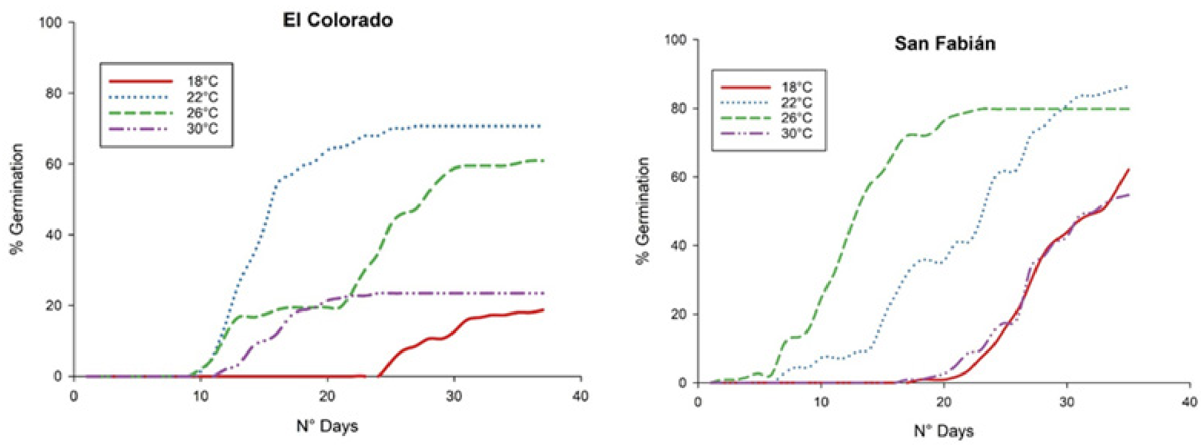

FIGURE 2: Cumulative germination percentage during 40 days for two *Nothofagus glauca* provenances treated at different temperatures in the absence of light.

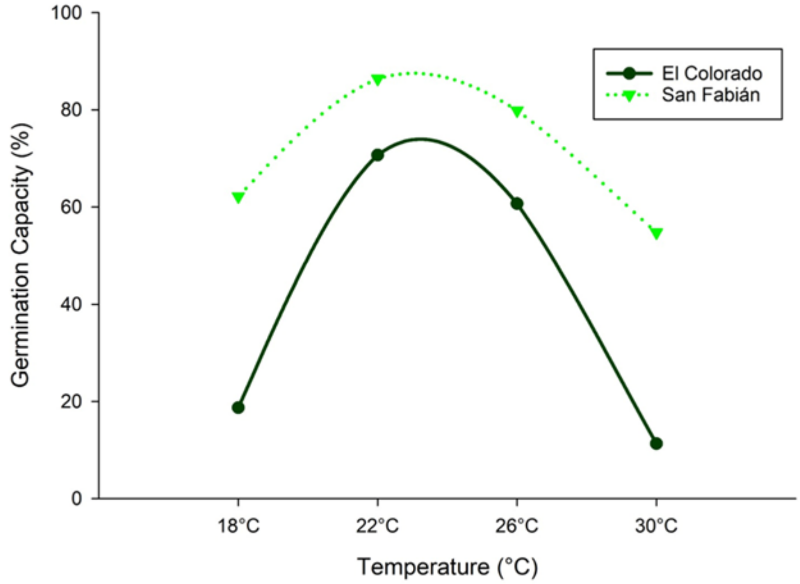

FIGURE 3: Final germination percentage of two provenances of *Nothofagus glauca* seeds treated at different temperatures in the absence of light.

tolerable temperature, differentiating the phenomena of thermo-inhibition and thermo-dormancy described by Wei et al. (2024).

The cardinal temperatures for germination are related to the environmental range of adaptation of a specific species. Their purpose is to ensure that germination time coincides with environmental optimal conditions for the subsequent seedling growth and development (Bewley et al. 2013). Germination rate will increase within the range of minimum to optimum temperatures, while temperatures exceeding the optimum and approaching the maximum will result in a decrease in this germination attribute (Bradford 2002; Wei et al. 2024). In this context, our research findings showed that germination rates in the two studied provenances increased as temperatures rose from 18°C, reaching a peak at 22°C, and subsequently declined. Consequently, the optimal germination temperature for *N. glauca* appears to be around 22°C, while the minimum or base temperature could be below 18°C, and the maximum or ceiling temperature exceeds 30°C. While it is known that the optimal germination temperature may vary among seed lots of the same species due to distinct environmental and genetic conditions (Belmehdi et al. 2018), this was not the case for the two provenances of *N. glauca*, where the optimal temperature remained around 22°C. It is noteworthy that with all the tested temperatures, germination percentage was consistently higher in San Fabian, which reinforces the idea that it could be two genetically distinct populations (Vergara et al. 2014). However, the longer storage time of the El Colorado seeds compared to those of San Fabian (3 years for El Colorado and 1 year for San Fabian) could also be a factor influencing the germination rate. Undoubtedly, from an experimental point of view, it would have been desirable for the seeds from both origins to have the same age and storage time. However, this was not possible because the species under study does not produce seeds every year (i.e., it exhibits masting behaviour), and given this natural condition that cannot be controlled, the research was adjusted accordingly. Therefore, it would be necessary to study the effect of seed storage on *N. glauca* germination.

After imbibition, which is when the seed has been rehydrated, and under appropriate temperature conditions, physiological processes are triggered, allowing the germination process (Baskin and Baskin, 2014). While germination occurred in both studied provenances with all tested temperatures, it is clear that not all temperatures are suitable for germination. The best results were obtained above 18°C and below 30°C. According to Baskin and Baskin (2014), the optimal temperature range for seed germination of *N. glauca* from the Andes is between 22°C and 26°C, which aligns with observations from coastal origins of the same species (Santelices-Moya et al. 2022). The described trend is evident in the germination onset time of the seeds. In El Colorado, at the highest temperature tested (30°C), 5% of the seeds began to germinate concurrently with those exposed to 22°C and 26°C. However, most of the seeds at 30°C initiated germination after 14 days (Table 3 and Figure 2). Additionally, the total germination percentage was only 23.3%. In contrast, in the San Fabian provenance, seeds treated at 26°C took 8 days to start germinating. These seeds not only differed significantly from the other treatments but also exhibited more explosive germination (a steeper slope was observed in the cumulative germination curve), with most of the batch germinating in approximately 10 days (Figure 2).

When comparing the morphometric characteristics of seeds from both origins, a general similarity can be observed (Table 2). However, it is worth noting that seeds from San Fabian have a greater weight compared to those from El Colorado, suggesting a higher mass and greater content of nutrient reserves for the germination process. This relationship between size and germinative capacity has also been observed in other species of *Nothofagus*, where larger and heavier seeds tend to have greater germinative capacity compared to smaller and lighter ones (Donoso 1987). Therefore, this difference in seed weight could explain, at least in part, the higher germinative capacity observed in the seeds from San Fabian in all tested treatments (Figure 3). However, seed vigour was higher from El Colorado when germinated at 22°C, reinforcing the idea of the possible existence of two genetically distinct populations (Vergara et al. 2014).

According to Santelices-Moya et al. (2022), the optimal germination temperature for coastal origins of *N. glauca* is estimated to be around 22°C, with a minimum temperature of 18°C and a maximum temperature close to 30°C. On the other hand, Buamscha et al. (2012) have mentioned that the temperature range for *N. glauca* germination would be between 10°C and 30°C. However, based on our research, the germination percentage achieved under extreme temperatures indicates that the minimum temperature should be below 18°C, while the maximum temperature should be above 30°C, particularly in the San Fabian provenance. These findings do not fully align with the statements by Santelices-Moya et al. (2022) and Buamscha et al. (2012), at least regarding the maximum temperature. Testing provenance-specific responses from only two provenances, which are not so far away from each other, is the minimum in terms of sampling from different locations. The coastal provenances of *N. glauca* studied by Santelices-Moya et al. (2022) are distributed at altitudes ranging from 129 to 403 m a.s.l., whereas the provenances analysed in our study are situated at elevations of 667 and 805 m a.s.l. Moreover, the coastal provenances had higher mean annual temperatures and lower precipitation levels compared to the Andean provenances. These climatic and altitudinal differences may partially account for the variations observed in our study relative to those reported by Santelices (2022). Therefore, it is suggested to expand the range of considered temperatures for these and other Andean origins of the species to determine the suitable temperature ranges for seed germination amongst different populations.

In the context of climate change, where an increase in temperature, prolonged periods of drought, and extreme heat events are observed, especially in Mediterranean regions where *N. glauca* naturally occurs, physiological processes of the species are being affected. The current climate crisis is undeniably impacting the reproductive cycle of species, leading to periods of up to 8 years with almost no seed production in an *N. glauca* forest (unpublished data). Since temperature plays a crucial role in the germination process (Baskin & Baskin 2014), it is recommended to study the adaptive capacity of this species and others to the new conditions of higher temperatures and reduced moisture availability during germination. This becomes highly significant considering the current scenario of climate change and the challenges it poses for the survival and reproduction of species.

Conclusions

Based on the results of this investigation in two Andean origins of *N. glauca*, it can be concluded that temperature has a significant impact on germination, although in a differential manner depending on the provenance. Under dark conditions, optimal germination temperature was determined to be around 22°C for the northern origin and around 26°C for the south origin. By maintaining the seeds at a constant temperature of 18°C during germination, germination can be induced. However, this temperature did not approach the minimum temperature, especially for seeds from the southern origin. The same trend was observed when germinating seeds at 30°C, where germination percentage was also relatively high. Moreover, if seeds are exposed to 30°C, there is no risk of inhibiting the germination process. In summary, temperature plays a crucial role in the germination of *N. glauca*, exhibiting differences among the studied origins. The optimal temperature varies according to provenance, while both minimum and maximum germination temperatures also differ. These findings emphasise the importance of understanding the specific temperature requirements of each origin to promote successful germination.

Competing interests

The authors declare that they have no competing interests regarding the publication of this paper.

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Authors' contributions

Conceptualisation, R.S.-M.; methodology, R.S.-M., A.M.C.-A.; software, R.S.-M. and A.M.C.-A.; validation, R.S.-M. and A.M.C.-A.; formal analysis, R.S.-M.; investigation, R.S.-M., C.B.-B. and A.M.C.-A.; resources, R.S.-M.; data curation, R.S-M., R.M.N.-C. and A.C.M.-A.; writing—original draft preparation, R.S.-M.; writing—review and editing, A.M.C.-A., M.P.-A., P.R., C.B.-B. and R.M.N.-C.; visualisation, R.S.-M. and A.M.C-A.; supervision, R.S.-M.; project administration, R.S.-M.; funding acquisition, R.S.-M. All authors have read and agreed to the published version of the manuscript.

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