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ORIGINAL ARTICLE

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Germination of *Dracophyllum sayeri* F.Muell. (Ericaceae), a vulnerable montane cloud forest endemic

Amelia V. Stevens[1] | **Bree-Ann Lautgier**[2] | **Gemma L. Hoyle**[1] | **Lydia K. Guja**[1,3] | **Stuart Worboys**[4] | **Darren M. Crayn**[4,5] | **Karen D. Sommerville**[6]

[1]National Seed Bank, Australian National Botanic Gardens, Acton, Australian Capital Territory, Australia

[2]Macquarie University, North Ryde, New South Wales, Australia

[3]Centre for Australian National Biodiversity Research (a joint venture between Parks Australia and CSIRO), CSIRO, Acton, Australian Capital Territory, Australia

[4]Australian Tropical Herbarium, James Cook University Nguma-Bada Campus, Smithfield, Queensland, Australia

[5]Centre for Tropical Environmental Sustainability Science, James Cook University Nguma-Bada Campus, Smithfield, Queensland, Australia

[6]The Australian PlantBank, Botanic Gardens of Sydney, Mount Annan, New South Wales, Australia

Correspondence
Amelia V. Stevens, National Seed Bank, Australian National Botanic Gardens, Clunies Ross Street, Acton, Australian Capital Territory, Australia.
Email: millie.stevens@dcceew.gov.au

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Abstract

Climate change in tropical montane cloud forest (TMCF) is predicted to impact species adapted to consistent, mild temperatures. We used a temperature gradient plate to investigate the effect of temperature on germination and early seedling survival of *Dracophyllum sayeri* (Ericaceae), a tree species endemic to TMCF in northeast Queensland, Australia. Despite a narrow distribution, results suggest that a wide range of temperatures is conducive to germination of *D. sayeri*, including up to 8°C higher than current temperatures. At higher temperatures, a day/night temperature amplitude of at least 5°C was required for optimal germination. In addition, germination was greater when seeds were exposed to natural diurnal light compared to constant darkness. Based on temperature, predictions under future climate conditions include a shift in peak germination from summer to winter/early spring. Results also suggest that *D. sayeri* has multiple strategies for maximizing germination in warm, alternating temperatures and light-filled gaps, and possesses more acclimation potential to persist under a future climate than previously assumed.

KEYWORDS

Dracophyllum, light, seed germination, temperature gradient plate, tropical montane cloud forest

1 | INTRODUCTION

Tropical montane (TM) regions of evergreen forest that experience persistent, frequent or seasonal low-level clouds give rise to "tropical montane cloud forests" (TMCFs). Compared to other TM forests, TMCFs are, on average, cooler (by 4.2°C), less seasonally variable, and at higher altitudes (Jarvis & Mulligan, 2010). Due to their steep environmental gradients and geographically restricted habitat niches, TM forests are highly threatened by even marginal increases in temperature under climate change (Costion et al., 2015; Helmer et al., 2019; Karger et al., 2021). Current global climate models predict enhanced warming of the tropical mid and upper

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troposphere and reductions in cloudiness leading to less reliable precipitation and more frequent extreme temperature events (see Hoyle, Sommerville, et al., 2023 for a review). In addition, tropical plants are considered more at risk from warming as they already exist close to their upper thermal limits (Sentinella et al., 2020). Impacts may include altitudinal shifts in species' ranges and extinction of species adapted to mild, non-variable temperatures (Elsen et al., 2021). For species that occur on mountain peaks, shifting to higher elevations is not an option and persisting under new environmental conditions will be necessary for species survival.

Plant regeneration via seeds is critical for species persistence under future climate scenarios (Walck et al., 2011). The ability of seed-bearing TMCF plants to persist in the future will depend on the ability of their seeds to germinate under new environmental conditions in their current location. However, our understanding of the regeneration and distribution of TM plant species (Baskin et al., 2020; Baskin & Baskin, 2014) and particularly TMCF species (Martin & Bellingham, 2016) is limited (Hoyle, Sommerville, et al., 2023). Temperature is one of the most influential climatic variables for seed germination since it synchronizes germination and emergence with environmental conditions optimal for subsequent seedling establishment. For many species, the difference between day and night temperatures (the daily temperature amplitude) is particularly important in signaling the growing season and promoting germination. For example, sedges, wetland species, and many alpine species will only germinate when there is a sizable daily temperature amplitude, and germination increases as this amplitude increases (Fernández-Pascual et al., 2015, 2020; Thompson & Grime, 1983). Changes in daily temperature amplitude can also signal that favorable seedling establishment environments, such as a canopy gap or a change in soil burial depth, have become available (Liu et al., 2013; Thompson & Grime, 1983). Knowledge of a species' optimum temperatures for germination, and the temperatures at which germination is limited, can provide an indication of vulnerability to climate change (Cochrane, 2016; Rosbakh & Poschlod, 2015; Sentinella et al., 2020). For example, climate warming is expected to lead to shifts in germination phenology among alpine mountain top plants (Mondoni et al., 2012).

In TMCF, where soil moisture under the canopy is high throughout the year and there is relatively little seasonal variation in temperature (Singh Ramesh et al., 2022), light may be a significant driver of germination. Canopy cover, leaf litter and disturbance events can all affect whether seeds are exposed to light or not (Reinhardt et al., 2010; Vázquez-Yanes et al., 1990; Zang et al., 2008). An absolute light requirement for germination, or a preference for high light quantity, has been reported for numerous TM species (Everham et al., 1996; Sady et al., 2010; Zang et al., 2008). Physical seed characteristics including seed size, anatomy and internal morphology can help predict critical events such as germination. For example, "smaller" seeded species (with seed mass <2 mg) from tropical habitats are more likely to require light for germination than "larger" seeded species (Aud & Ferraz, 2012; Hoyle, Stevens, et al., 2023; Jankowska-Blaszczuk & Daws, 2007; Milberg et al., 2000; Pearson et al., 2002; Tiansawat & Dalling, 2013).

The Wet Tropics World Heritage Area of northeast Queensland, Australia (within the Wet Tropics Bioregion) includes TMCF at or above 900 m elevation (Weber et al., 2021). Like other TM biodiversity hotspots around the world, this region is notable for high endemism and unique species assemblages with low median area of occupancy (Hoyle, Sommerville, et al., 2023; Martin & Bellingham, 2016). In Australian TMCF, substantial climate change impacts are expected before the end of the century (Costion et al., 2015; Williams et al., 2003). Plant distribution modeling has predicted a mean habitat loss of 63% for 37 Australian TMCF species, and complete habitat elimination for seven species by 2085 (Roeble, 2018). However, it is not known whether the current niche occupied by each species is essential for its survival because little is known about how environmental factors determine the distribution of TMCF species, particularly their capacity to regenerate from seed in the future.

Dracophyllum sayeri F.Muell (Ericaceae; Figure 1a) is a small tree endemic to Australian TMCF and listed as Vulnerable under the Queensland *Nature Conservation Act* 1992. Geographically isolated from related species of *Dracophyllum* (the genus has a predominantly southern temperate distribution), *D. sayeri* is restricted to a few mountain tops in the Bellenden Ker Range and west of Mossman in northeast Queensland (Wagstaff et al., 2010; Figure 1b), where it grows in stunted, windswept rainforest on exposed ridges, 1200–1500 m above sea level (Zich et al., 2018). The distribution of *D. sayeri* is narrow, and reliable records were too few for it to be included in the modeling of Costion et al. (2015) or Roeble (2018), raising urgent questions about its vulnerability under climate change. While there is limited germination literature available for *D. sayeri*, a single study (Hoyle, Stevens, et al., 2023) and seedling emergence data (Zich et al., 2018) indicate that seeds are non-dormant. Limited information on *Dracophyllum* species in other habitats suggests alternating temperatures and light may improve germination (Haase, 1986; Thomas et al., 2003).

Here, we employed a temperature gradient plate to investigate, for the first time, the thermal germination niche of *D. sayeri*, including early seedling survival. In addition, we investigated *D. sayeri* seed morphology and

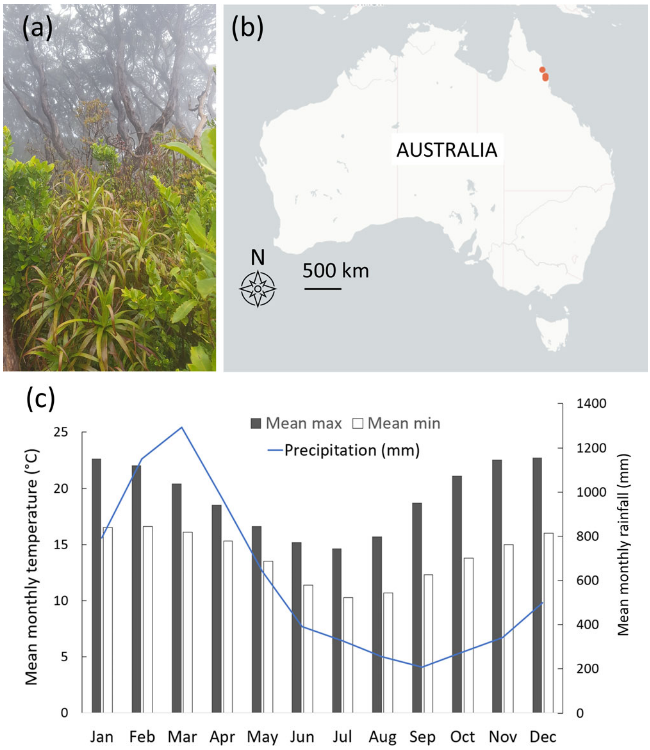

FIGURE 1 *Dracophyllum sayeri* (Ericaceae) (a) growing in situ, (b) distribution in northeast Queensland, Australia (Atlas of Living Australia, 2022), and (c) mean monthly air temperature and precipitation for the seed collection site (17°15′52″ S, 145°51′25″ E, altitude 1488 m a.s.l; data extracted from Xu et al., 2014a, 2014b, 2014c).

whether light is required for germination. We hypothesized that (i) germination would occur under a relatively narrow breadth of temperatures, (ii) a daily temperature amplitude may be required for germination, and (iii) seeds may require light for germination. Utilizing these data, we predicted germination phenology under a future, warmer climate.

2 | METHODS

2.1 | Seed collection and storage

Mature fruits (capsules) of *D. sayeri* (Figure 2a) were collected from Mt. Bellenden Ker (17°15′52 S, 145°51′25 E; 1488 m a.s.l.) on 11 June 2019. Over 2000 seeds were collected from fruiting branchlets from at least three individual plants. Each branchlet bore multiple fruits. Seeds from all fruits and individuals were mixed prior to storage. Appropriate post-harvest handling ensured that any viability loss prior to storage was kept to a minimum. Branchlets with intact fruits were transported in breathable calico bags to the air-conditioned laboratories of the Australian Tropical Herbarium and then by post to the Australian PlantBank. On arrival at PlantBank, the branchlets were held at ambient laboratory conditions for 2 weeks to facilitate release of seeds (Figure 2b,c). Seeds

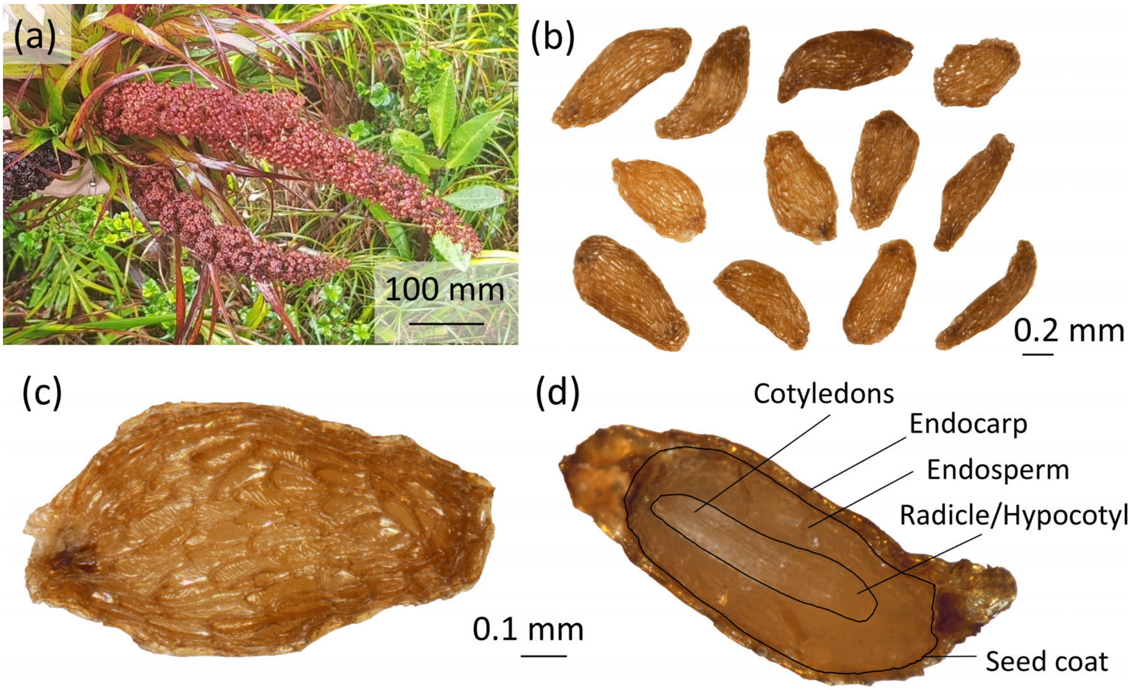

FIGURE 2 *Dracophyllum sayeri* (a) fruiting plant, (b) multiple seeds, showing variation in size and shape, (c) single seed morphology, showing seed coat texture, and (d) single seed anatomy in longitudinal cross section showing endosperm and embryo (large and small black outlines, respectively) within the seed coat.

were then dried for 6 weeks at ~15°C and 15% relative humidity (RH) before being vacuum-sealed in laminated foil packets. A proportion of the seeds were stored for conservation purposes (Accession No. P2019-0432), leaving the remaining seeds available for use in investigations of seed biology. Seeds used for experiments on the effect of temperature were stored for 3 months at 4°C prior to commencing the experiments. A proportion of this accession was transferred to the National Seed Bank, Australian National Botanic Gardens, on 13 August 2019 and held for 11 months at 4°C before experiments on germination in response to light commenced (Accession No. CANB 896369.3).

2.2 | Seed anatomy and internal morphology

Seed morphology was investigated using whole seeds and longitudinal sections of imbibed seeds, photographed under a Nikon SMZ25 microscope (Nikon, Rhodes), and measured from scaled images in ImageJ (www.imagej.nih.gov). Mean seed size was calculated by measuring the length and width of 12 seeds. Embryo:seed ratio (E:S) was calculated from measurements of sections of 11 seeds. Embryo type was classified following Baskin and Baskin (2007) and internal seed morphology described as per Ericaceae in Miller (2010). Seed shape and texture were defined using standard terms from the AusTraits database (Falster et al., 2021).

2.3 | In situ climate and microclimate

In the Wet Tropics Bioregion, most rain falls during the "wet" season. However, TMCF vegetation strips the clouds of moisture during the "dry" season, which reduces seasonality (McJannet et al., 2008). The mean maximum/minimum air temperatures for summer (Dec, Jan, Feb) and winter (Jun, Jul, Aug), based on interpolated data over the period 1983–2012, were 22/16°C and 15/11°C, respectively (Figure 1c; Xu et al., 2014a, 2014b). These data were used to guide the selection of experimental germination temperatures (see below). To confirm that the experimental temperatures were ecologically relevant, we compared the interpolated air temperature data to microclimate data that we collected in situ, close to where *D. sayeri* seeds were collected on Mt. Bellenden Ker (1538 m a.s.l.). TOMST TMS4 data loggers (www.tomst.com) were used to record temperatures 15 cm above the soil surface, at the soil surface, and 8 cm below the soil surface (in the location of seedlings, newly dispersed seeds, and the soil seed bank, respectively). Temperatures were recorded under closed canopy from December 2019 to November 2021 and under a canopy gap (exposed to full sun) from January 2021 to November 2022.

To provide an indication of light levels in cloud forest habitat, light quantity (total irradiance and photosynthetically active radiation (PAR)) was recorded on Mt. Fisher (1282 m), Mt. Lewis (1220 m), and Mt. Edith (1100 m), using a handheld SpectraPen (Photon Systems Instruments, www.psi.cz), between May 5 and May 10, 2021.

2.4 | Germination in response to drying and storage

To investigate whether seed germinability was affected by storage, germination tests were carried out on fresh seeds (within 2 weeks of seed release), after 6 weeks' drying at ~15°C and 15% RH, and after drying, packaging and storage for 5 months at 15 and −20°C. Germination tests used five replicates of 10 seeds sown into 9 cm diameter glass Petri dishes containing 0.8% plain water-agar. Petri dishes were sealed with Gladwrap to minimize agar desiccation before being placed in a walk-in incubator with constant 25°C, 12/12 h light/dark. Light was provided by 28 W cool white, fluorescent tubes generating 4 to 13 μmol m^{-2} s^{-1} PPFD at shelf level. Plates were placed on a single shelf and re-positioned weekly. Germination, defined as radicle emergence >2 mm, was scored every 7 days and germinated seeds were subsequently removed. Tests were terminated when there had been no further germination in any replicate for 4 weeks. All remaining intact seeds were dissected with a scalpel under a microscope and empty seeds were subtracted from the total when calculating final percentage germination.

2.5 | Germination response to temperature

Germination of *D. sayeri* in response to 21 constant and alternating temperature regimes, under a 12 h light/dark photoperiod, was investigated using a Grant 2-way temperature gradient plate (TGP, Grant Instruments, Cambridge). The programmed temperature range (5–35°C) encompassed interpolated air temperatures (Figure 1c), namely mean monthly maximum (range 14.6–22.7°C) and minimum (range 10.3–16.6°C) air temperatures for the seed collection location on Mt. Bellenden Ker, and a projected temperature increase of 5°C. The TGP was divided into a triangular grid of 21 square cells (125 mm^2), each representing a different nominal temperature combination. In each cell, we placed six replicates of five seeds, on 1% sterile water-agar, evenly distributed among six plastic sample tubes (ø 28 mm) arranged in a ring around a central tube containing agar only. A temperature logger (Thermocron, Castle Hill) on the agar surface of the central tube monitored temperature at seed level. Each set of six tubes was rotated twice weekly within the relevant cell so that every seed in the cell experienced, on average, the same temperatures. Germination data for all tubes within a cell were combined for analysis following Collette et al. (2022). Germination was monitored weekly, and seeds were considered to have germinated when the radicle reached at least 2 mm in length. Germination was monitored for 18 weeks (126 days) and there was no germination in any cell in week 18.

To monitor the effect of temperature on seedling survival, seedlings were left on the agar until the experiment was terminated, approximately 11 weeks after peak germination for any given cell (between week 17 and week 21). Upon termination, the number of healthy seedlings per cell was recorded. Seedlings were considered healthy if they had produced and maintained an upright, green shoot; seedlings with fallen, brown, or broken shoots were excluded. Seeds that failed to germinate were dissected with a scalpel under a microscope and final germination percentages were adjusted for viability by removing the number of empty seeds.

To predict the effects of future climate on germination we analyzed the final germination proportion in relation to TGP temperatures. Current temperature predictions were modeled with WorldClim 2.1 and downloaded from Worldclim (worldclim.org/data/worldclim21.html). Future climate predictions were based on predicted tmax and tmin produced from Coupled Model Intercomparison Project Phase 6 (CMIP6) models and were downloaded from Worldclim (https://worldclim.org/data/cmip6/cmip6_clim2.5m.html). We used climate scenario SSP5-8.5 representing "fossil-fuel development," leading to a global average temperature increase of approximately 5°C. We included all eight available CMIP6 SSP5-8.5 model variations from the Worldclim database for the years 2081–2100 at a 2.5 min (approx. 4.5 km^2) spatial resolution and averaged for each monthly data point.

2.6 | Germination response to light

Germination in response to constant dark and alternating light/dark was investigated in a polycarbonate propagation house (prop-house). Natural illumination was provided by the sun. Three replicates of 25 seeds per treatment were sown into 90 mm diameter plastic Petri dishes containing 1% sterile water-agar. Petri dishes were sealed using Parafilm to limit desiccation and placed into aluminum foil trays (325 × 270 × 95 mm). Dishes subjected to the constant dark treatment were double wrapped with aluminum foil to exclude light and all trays were covered with plastic wrap to prevent them filling with water from prop-house misters. Trays were arranged randomly on a 265 × 80 cm steel bench and temperatures in the prop-house were programmed to approximately 25/15°C, day/night. Temperature loggers (Hygrochron Humidity/Temperature Logger (DS1923, Thermochrom, Castle Hill, Australia)) were placed in trays along the length of the bench to record air temperature throughout the experiment. Light quantity (total irradiance and photosynthetically active radiation (PAR)) was recorded inside and outside the experimental propagation house in week 1 (July 2020) and week 12 (October 2020) using a handheld SpectraPen (Photon Systems Instruments, www.psi.cz). Germination, defined as radicle emergence of at least 2 mm, was scored 12 weeks after transfer to the prop-house. Any remaining ungerminated seeds from the dark treatment were then exposed to natural illumination and germination was scored again following a further 6 weeks. This treatment was termed "dark → light/dark." The experiment was terminated after a total of 18 weeks; seeds that failed to germinate were dissected with a scalpel under a microscope and final germination percentages were adjusted for viability by removing empty seeds.

2.7 | Data analysis

All analyses were performed using R statistical software (version 1.4.1103, R Core Team, 2021). To examine the effects of day and night temperatures, as well as the temperature amplitude (the difference between day and night temperatures) on final germination and early seedling survival, generalized additive models (GAMs) were developed using an R script and workflow developed by Collette et al. (2022).

Six GAMs were fitted using the binomial distribution on the final germination proportions using the "mgcv" package (version 1.9; Wood, 2017). These models incorporated smooth interaction terms (tensor product splines) for day and night temperature to capture nonlinear effects and their potential interaction. A combination of root mean squared prediction error (RMSE) and Pearson's correlation between actual versus predicted germination values was used to assess model performance.

Germination under current and future climate scenarios was then modeled using the chosen GAM (shown in Table 1) to predict monthly germination under current and future temperatures. Current maximum and minimum air temperatures for the collection location, and

TABLE 1 Generalized additive model (GAM) output and parameters tested to estimate final germination proportions for *Dracophyllum sayeri* using data generated from germination experiments on a temperature gradient plate.

Model	Mean error	Lower 95%	Upper 95%	RMSE	Correlation
prop_germ ~ s(day_temp, bs = "tp") + s(night_temp, bs = "tp")	0.086	0.04	0.161	0.067	0.937
prop_germ ~ te(day_temp, night_temp, bs = "ts", *k* = 4)	0.093	0.027	0.211	0.072	0.926
prop_germ ~ te(day_temp, night_temp, bs = "tp", *k* = 4)	0.099	0.026	0.207	0.062	0.945
prop_germ ~ s(day_temp, night_temp, bs = "tp", *k* = 4)	0.099	0.038	0.242	0.082	0.902
prop_germ ~ te(day_temp, night_temp, bs = "cr", *k* = 4)	**0.104**	**0.026**	**0.208**	**0.059**	**0.951**
prop_germ ~ ti(day_temp, night_temp, bs = "tp", *k* = 4)	0.11	0.038	0.188	0.087	0.889

Note: The chosen GAM model is in bold. Mean error is gained by hold-out samples via Monte Carlo resampling. Ninety per cent of the data were modeled and predicted into the held-out 10% for 100 iterations. Lower and upper 95% use the mean error to create confidence intervals (95-percentile of distribution). RMSE is the root mean squared error, a common measure of model error. Correlation is the Person's correlation between the modeled and observed data. The model in bold was that which was selected as the best fitting and was used to make subsequent predictions and plots. Prop_germ refers to the final germination expressed as a proportion. The letters before the model terms refer to the smoother that was used in the model. "te" and "ti" are tenser terms, while "s" is a smooth term. The letters after "bs" within the model refer to the type of smooth term used. "cr" refers to a cubic spline, "tp" refers to a thin plate smoother and "ts" is also a thin plate smoother, with a modification to the smoothing penalty, so null space is penalized. "K" refers to the number of knots used and is modified when there are smaller amounts of data.

future temperature predictions for the same location (based on an average global temperature increase of 5°C), were downloaded from Worldclim (https://worldclim.org/data/worldclim21.html and https://worldclim.org/data/cmip6/cmip6_clim2.5m.html, respectively; accessed July 2022).

Germination following 12 weeks in constant dark and light/dark was compared using a Pearson's chi-squared test. The light/dark results were also compared to the dark → light/dark results. The 95% confidence intervals for the difference in percentages were calculated using the prop.test function in the R base package.

3 | RESULTS

3.1 | Seed anatomy and internal morphology

Dracophyllum sayeri produces small seeds 0.47 ± 0.09 mm in width and 1.09 ± 0.14 mm in length ($n = 12$ seeds; Figure 2b,c). The seeds possess a linear, fully developed embryo (Baskin & Baskin, 2007; Figure 2d) with an E:S ratio of 0.58 ± 0.07 ($n = 11$ seeds), suggesting seeds do not have morphological dormancy. Seeds are categorized as comma-shaped to fusiform with a netted surface texture (Falster et al., 2021).

3.2 | In situ climate and microclimate data

Soil temperatures recorded in situ, in the understory (+15 cm, surface and −8 cm), fell well within the experimental temperature range used in this germination study (Figure 3a,c,e).

In the understory, mean maximum +15 cm, surface and −8 cm soil temperatures ranged from 21.3, 20.3 and 17.7°C, respectively, in December, to 13.3, 13.0 and 12.5°C, respectively, in July (Figure 3a,c,e). Mean maximum temperatures in the sun-exposed location were substantially higher throughout the year, with +15 cm, surface and −8 cm soil temperatures of 30.0, 27.8 and 22.0°C, respectively, in December and 21.2, 20.7 and 16.6°C, respectively, in July (Figure 3b,d,f). Mean minimum temperatures, however, varied by less than 2°C between understory and sun-exposed sites at all levels. Mean temperature amplitude at the soil surface ranged from 5.2°C in December to 2.3°C in June in the understory and 13.0–7.7°C in sun-exposed sites for the same months (Figure 3c,d). Soil surface temperature amplitudes differed little from +15 cm air temperature amplitudes, but −8 cm soil temperature amplitudes were considerably lower throughout the year (on average, 1.1°C in the understory and 4.3°C in sun-exposed sites). A heatwave in October 2021 led to maximum +15 cm temperatures in the sun-exposed location ranging from 35 to 43°C on 21 separate days.

Maximum interpolated air temperatures derived from Xu et al. (2014a) and WorldClim were, on average, 2.1 ± 0.9 and 3.4 ± 0.8°C higher, respectively, than +15 cm soil temperatures recorded in the understory, but were 6.5 ± 3.2°C and 5.3 ± 3.6°C *lower*, respectively, than +15 cm soil temperatures recorded in sun-exposed sites. The average difference between minimum interpolated air temperatures and in situ minimum +15 cm soil temperatures was ≤1°C for the understory and ≤1.3°C for sun-exposed sites.

Unsurprisingly, mean total irradiance and PAR were greatest at the edge of the forest canopy (298 and

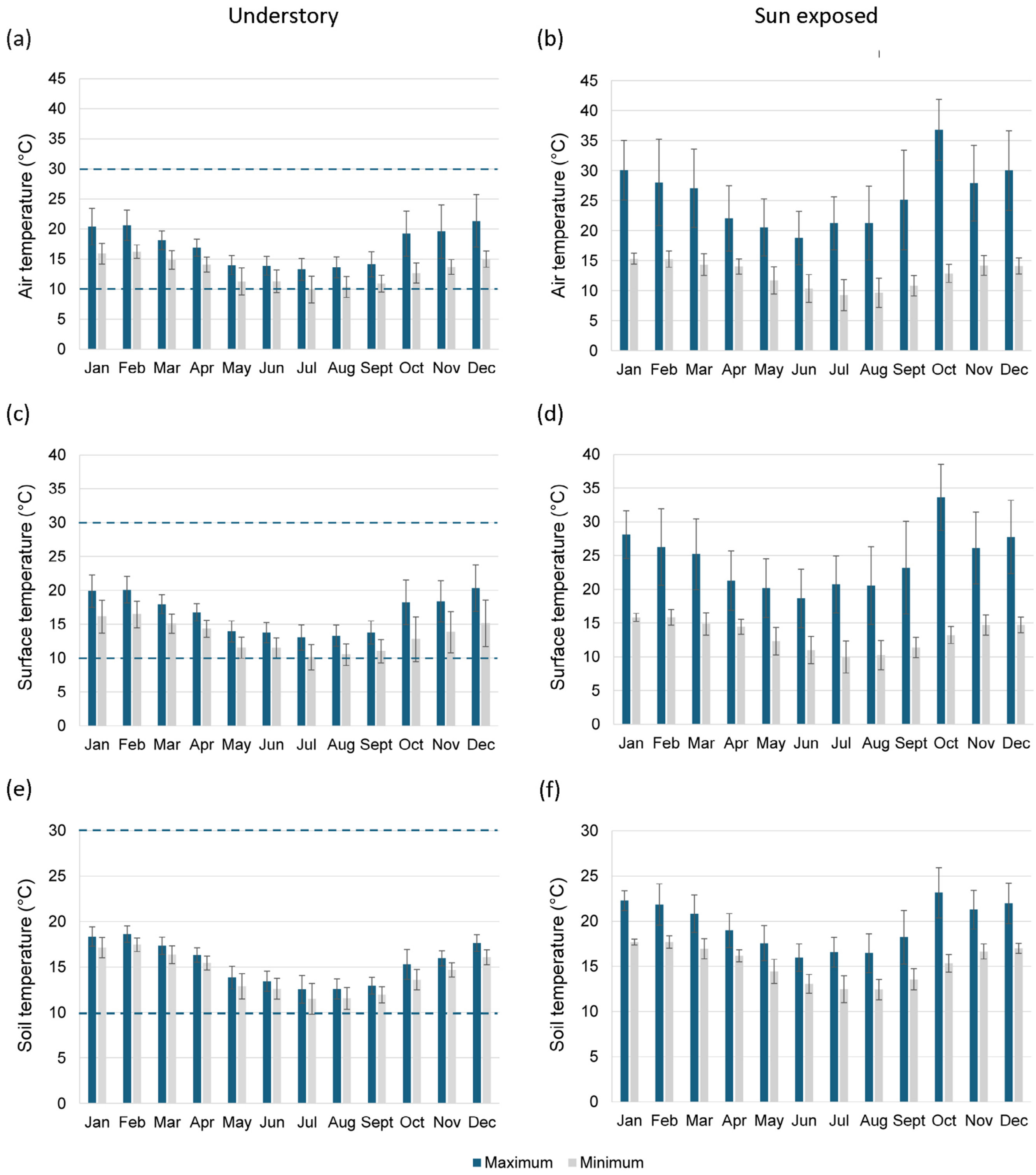

FIGURE 3 Soil temperatures recorded in situ on Mt. Bellenden Kerr (1538 m elevation), in northeast Queensland, Australia between December 2019 and November 2022. Mean maximum and minimum temperatures were recorded +15 cm above ground level (a and b); at the soil surface (c and d); and −8 cm below the surface (e and f), in both the understory and sun-exposed locations (Singh Ramesh et al., 2022). Dotted lines indicate the range of experimental temperatures in the temperature gradient plate.

211 μmol $m^{-2} s^{-1}$, respectively) compared to any other location (Table 2). Cloud cover reduced total irradiance and PAR below the canopy by only 3 and 1 μmol $m^{-2} s^{-1}$, respectively. Light quantity was lowest under leaf litter below the canopy. Light quantity in the light/dark experiment was comparable to that in situ at the edge of the canopy (Table 2).

TABLE 2 Light quantity (total irradiance and photosynthetically active radiation (PAR)) was recorded in tropical montane cloud forest (TMCF) in northeast Queensland (various locations above 1000 m elevation on Mt. Fisher, Mt. Edith and M. Lewis, May 5–10, 2021) and inside and outside the experimental propagation house in week 1 (July 2020) and week 12 (October 2020).

Location	Weather	Mean total irradiance (μmol m^{-2} s^{-1})	PAR (μmol m^{-2} s^{-1})
TMCF Edge of canopy Direct sunlight	Sunny	298 ± 3.1	211 ± 2.5
TMCF Below canopy Above leaf litter	Sunny	12 ± 3.1	7 ± 2.3
TMCF Below canopy Above leaf litter	Overcast	9 ± 1.3	6 ± 0.9
TMCF Below canopy Below leaf litter	Sunny	2 ± 0.4	0.9 ± 0.2
Experimental trays Beneath plastic wrap—Week 1	Sunny	194 ± 33	149 ± 24
Experimental trays Beneath plastic wrap—Week 12	Sunny	387 ± 29	290 ± 24

Note: Experimental light quantity increased as daylength increased. Indicative tropical montane cloud forest (TMCF) readings were taken in situ in various locations of differing canopy cover and leaf litter.

3.3 | Germination before and after drying and storage

To investigate whether seed germinability was affected by storage, germination tests were carried out before drying (within 2 weeks of seed release), after 6 weeks' drying at ~15°C and 15% RH, and after drying, packaging and storage for 5 months at 15 and −20°C. Seeds that were tested before drying commenced germination within 3 weeks and achieved 60 ± 7% germination within 5 weeks at 25°C. Dried and stored (15°C and −20°C) seeds also commenced germination within 3 weeks and germinated at day temperatures ranging from 19 to 30°C. At day 126 (the cut-off used in the TGP and light experiments), there was no significant difference in germination among treatments: before drying, 84 ± 4%; after drying, 71 ± 10%; after storage at 15°C, 67 ± 7%; and after storage at −20°C, 79 ± 5% (Kruskal–Wallis test, $p = 0.1376$). Final germination was 88 ± 6%, 80 ± 6%, 87 ± 8% and 91 ± 4%, respectively. These results suggest that the bulk of the seed collection was non-dormant throughout the TGP experiment.

3.4 | Germination response to temperature

Mean temperatures recorded at the agar surface in the center of each TGP cell ranged from 10.0 to 30.4°C, giving day/night temperatures for seeds at the three extremities of the grid of 12.0/10.5, 30.0/10.6 and 29.9/28.4°C. *Dracophyllum sayeri* seeds germinated to some extent under all temperature regimes but showed a trend toward greater germination at mid-range to high temperatures and temperature amplitude (Figure 4a). Germination >83% occurred only when day temperatures were between 22 and 27°C and night temperatures were 5–12°C lower. The highest germination (93%) occurred at alternating temperatures of 26.4/13.5°C; the second highest (90%) occurred at 26.8/20.9°C. Generalized additive modeling indicated that day and night temperatures had a significant effect on germination individually and in interaction ($p \leq 0.001$ in all cases). The final model chosen for climate modeling (incorporating day/night temperature interaction) had an adjusted R-sq of 0.846 and explained 87.9% of deviance. Overall, the maximum possible germination required cooler night-time temperatures. While the thermal tolerance limits for germination were not determined, both low (12°C) and high (30°C) day-time temperatures resulted in considerably less germination when compared to the optimum, particularly when the difference between day and night temperatures was ≤5°C. Early seedling survival showed a trend toward higher survival at higher temperatures (Figure 4b) with the highest seedling survival percentage (70%) occurring at day/night temperatures of 26.8/20.9°C.

Modeling of germination data against current interpolated air temperatures at the collection location (Figure 5a) indicated germination may occur throughout the year, with

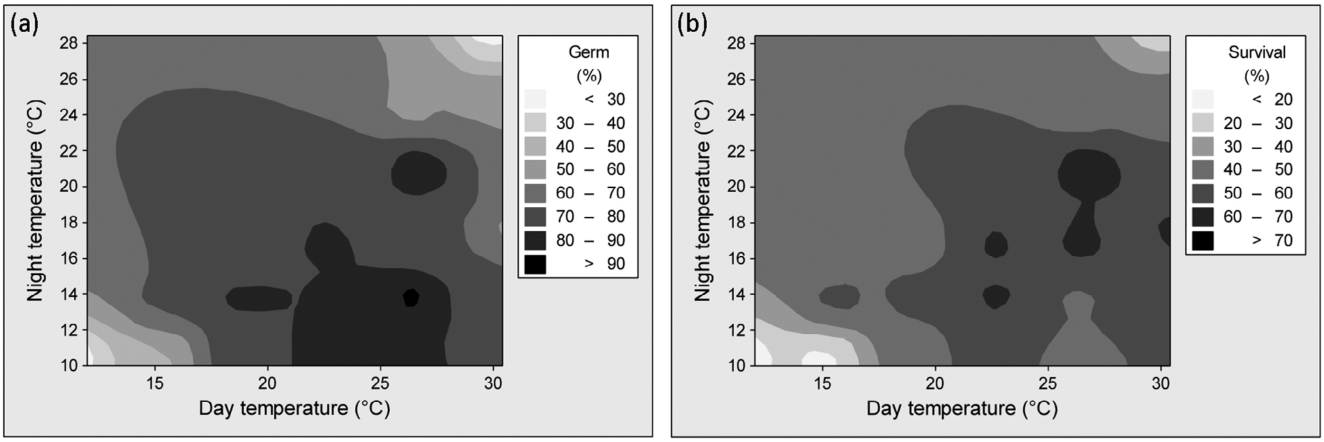

FIGURE 4 Contour plots showing day and night temperature effects on (a) final percentage germination and (b) early seedling survival for *Dracophyllum sayeri* seeds germinated on a temperature gradient plate.

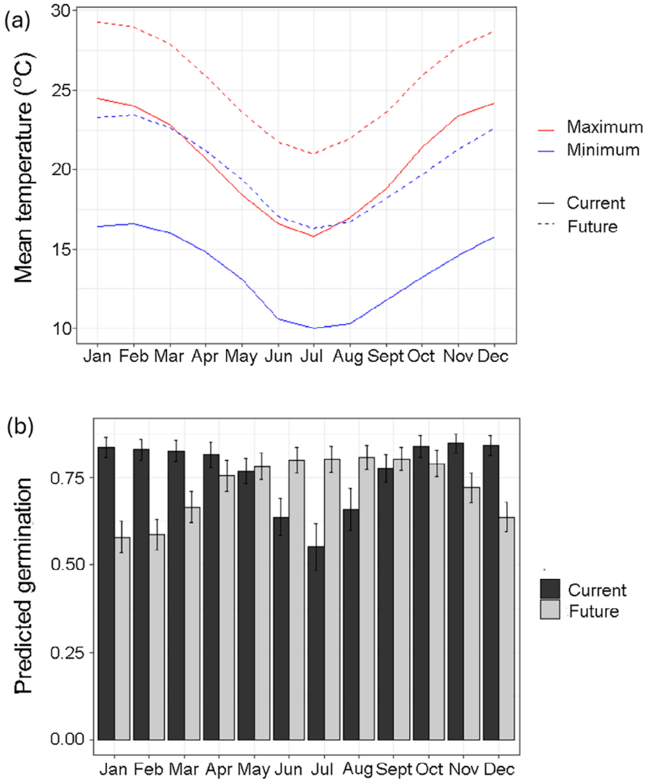

FIGURE 5 Germination of *Dracophyllum sayeri* under current and future climate models: (a) current and predicted monthly air temperatures in *D. sayeri* habitat based on interpolation of data from 1970 to 2000 downloaded from WorldClim, and an average global temperature increase of 5°C, respectively; (b) predicted germination of *D. sayeri* under current and future climates based on the response to multiple temperature regimes on a temperature gradient plate.

peak germination from late spring to early autumn (Figure 5b). Modeling against predicted future temperatures in that location (based on a global increase of approximately 5°C) suggested germination may still occur throughout the year, but peak germination will be slightly reduced and will shift to winter and early spring (Figure 5b).

3.5 | Germination response to light

Temperature in the trays in the prop-house averaged 24°C ± 0.03 during the day (13 h, 06:00–19:00) and 19°C ± 0.01 during the night (9 h, 20:00–05:00). Daylength (sunrise to sunset) ranged from 10 h 15 min at the start of the experiment to 14 h 21 min at the end. Light quantity inside the prop-house, beneath plastic wrap, increased with daylength. Mean total irradiance ranged from 194 ± 33 μmol m^{-2} s^{-1} in week 1 to 387 ± 29 μmol m^{-2} s^{-1} in week 12. PAR ranged from 149 ± 24 μmol m^{-2} s^{-1} in week 1 to 290 ± 24 μmol m^{-2} s^{-1} in week 12 (Table 2).

Mean final germination in alternating light/dark was significantly greater compared to constant darkness ($p < 0.05$; Figure 6). Final germination of dark → light/dark seeds did not differ from germination of seeds in alternating light/dark for 12 weeks—indicating that ungerminated seeds in constant darkness remained viable and required light to germinate ($p > 0.05$; Figure 6).

4 | DISCUSSION

This study investigated the effect of temperature and light on final germination, and the effect of temperature on early seedling survival, for *D. sayeri* to determine whether rising global temperatures could pose a threat to the survival of this TMCF endemic. The species had a greater thermal tolerance than expected, given its restricted range, and was capable of germinating at temperatures

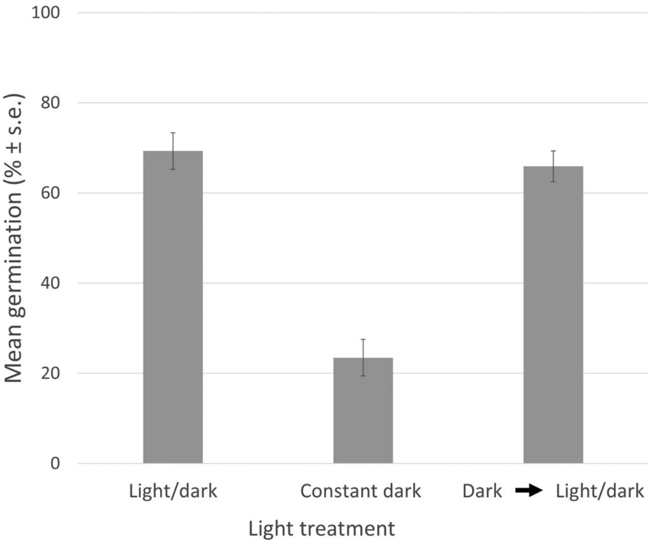

FIGURE 6 Final germination (mean ± s.e.) of *Dracophyllum sayeri* in a propagation house following 12 weeks in alternating light/dark conditions and 12 weeks in constant darkness followed by 6 weeks in alternating light/dark.

up to 8°C higher than the mean maximum summer soil surface temperatures recorded in situ in the understory (Figures 3a and 4a; Singh Ramesh et al., 2022). This result aligns with a recent study that found tropical plants do not have a narrow temperature tolerance (Sentinella et al., 2020) but contradicts a second finding from the same study that tropical plants are close to the upper limit of their thermal tolerance. This difference may reflect the montane distribution of *D. sayeri* and could potentially be a common feature of plants endemic to TMCF. However, more work is needed to understand the thermal tolerance of this and additional TMCF species as a priority.

At higher temperatures, however, germination >50% required a day/night temperature amplitude of at least 5°C; germination >83% only occurred when night temperatures were 6–12°C lower than day temperatures of 22–27°C. This result is consistent with one of the few germination studies of a related species which found germination improved with a daily temperature amplitude of 5°C in *Dracophyllum traversii* from New Zealand (Haase, 1986). Enhanced germination under fluctuating temperatures is a phenomenon common among smaller seeded species that germinate close to the soil surface (Liu et al., 2013). The small temperature amplitude recorded −8 cm below the soil surface, combined with the poor germination observed in the dark, suggests that buried *D. sayeri* seeds are unlikely to germinate. This may facilitate persistence in the soil seed bank until a disturbance event exposes seeds to light and fluctuating temperatures.

Microclimate data collected on Mt. Bellenden Ker indicated that conditions suitable for greatest germination chiefly occur in summer (also the wet season) in the understory, or autumn and spring in sun-exposed sites, when soil surface temperatures are 20–27°C and the temperature amplitude is >5°C (Figures 3c,d and 4a). Germination in summer or autumn would also ensure the warm temperatures and moisture required for optimum seedling survival (Figure 4b). Given that summer soil surface temperatures in the understory are presently 5–6°C lower than the temperature at which maximum germination occurred in this study (i.e., 26–27°C), a future rise in mean day-time temperatures of several degrees may lead to increased germination of this species in that habitat, providing the current amplitude between day and night temperatures is maintained or increases. If seed microclimate temperatures mirror air temperatures, amplitude is predicted to decrease in the future but remain in the range needed for optimal germination (Figures 4a and 5a). In contrast, a rise in soil surface temperatures in sun-exposed locations would be more likely to shift peak germination to winter, as suggested by our climate modeling (Figure 5b).

Local microclimate data can aid with interpretation of the ecological and phenological implications of climate change (Lembrechts et al., 2020), particularly for regeneration processes that occur close to the soil surface. Our microclimatic data indicated maximum germination is currently likely to occur in summer, and this matched well with modeling based on interpolated air temperatures which predicted highest germination from late spring to early autumn (Figure 5b). Due to the differences in interpolated and in situ temperatures, our model of current germination could be considered to represent germination under slightly warmer temperatures in the understory. Modeling of germination based on a global increase in air temperatures of 5°C (roughly equivalent to current surface temperatures in canopy gaps) indicated that germination would still be possible throughout the year, but peak germination in the understory could shift to winter and early spring. Phenological shifts in germination are an expected seed response to climate change (Fernández-Pascual et al., 2020) and have the potential to expose seedlings to unfavorable conditions for survival.

Optimum seedling survival in this experiment (70%) occurred at max/min temperatures of 26.8/20.9°C. When day-time temperatures reached 30°C, survival >50% occurred only when there was a day/night temperature difference ≥10°C. In alpine regions, upward migration of plants may not be a product of germination inhibition due to temperature increase, but rather of "precocious emergence" that exposes seedlings to conditions unfavorable for their survival (Mondoni et al., 2012). Under a warmer climate, germination of *D. sayeri* seeds in winter could expose seedlings to an environment too dry for establishment (Figure 1c), while germination in spring or early summer could expose seedlings to heatwave events such as those recorded in October 2021 where maximum +15 cm soil temperatures of >35°C were recorded in a sun-exposed location on 21 separate days (Singh Ramesh et al., 2022). Recent tropical montane climate models suggest greater rates of temperature rise at higher elevations compared to lower (Salinas et al., 2021), and changes in the reliability and quantity of precipitation in TMCF through reductions in cloudiness (Foster, 2001; Hu & Riveros-Iregui, 2016; Still et al., 1999). These factors increase the likelihood of longer drought periods and more frequent extreme temperatures, which are likely to significantly impact species adapted to consistent high-water availability and mild temperatures.

Clouds currently contribute around 21% of the soil moisture at Mt. Bellenden Ker per year through the phenomenon of cloud stripping (McJannet et al., 2006). The reduction in cloud cover predicted for TMCF in the future is likely to reduce water availability (Helmer et al., 2019) and alter light quality and quantity (Reinhardt et al., 2010). Given the broad temperature tolerances identified for *D. sayeri* germination and seedling survival, soil moisture and light (or these factors in combination with temperature) may be more important in limiting the distribution of *D. sayeri* than temperature alone. While *D. sayeri* did not have an absolute light requirement for germination, mean final germination was significantly greater in alternating light/dark compared to constant darkness. Seeds held in dry storage have been known to lose their requirement for light for germination (Baskin & Baskin, 2014), therefore this difference in germination may have been even greater if fresh seeds had been used in this study. In some tropical species, a fluctuating thermoperiod can substitute for light as a stimulus for germination (Vázquez-Yanes & Orozco-Segovia, 1982), which may also explain the *D. sayeri* germination in constant darkness. Recently, Hoyle, Stevens, et al. (2023) found that while germination of *D. sayeri* increased with increasing light quality (R:FR), it was not restricted to high-quality light, again suggesting acclimation potential for this species.

The small size of *D. sayeri* seeds and their greater germination under alternating light/dark conditions compared to constant darkness supports previous studies on the light requirement of small-seeded species (Aud & Ferraz, 2012; Hoyle, Stevens, et al., 2023; Jankowska-Blaszczuk & Daws, 2007; Milberg et al., 2000; Pearson et al., 2002; Tiansawat & Dalling, 2013). While *D. sayeri* seeds do contain endosperm, the small amount relative to larger rainforest seeds suggests the species may lack sufficient resources to survive germination in the absence of light. The publication of morphological and physiological seed traits for this and other TMCF species may help to increase the accuracy and applicability of species distribution models and allow us to rapidly identify climate vulnerable TM species and select those with climate-resilient regeneration traits for future-proof restoration (Hoyle, Sommerville, et al., 2023). Our results will enable the inclusion of *D. sayeri* in national and global seed trait databases in which there is currently poor representation of tropical species (Visscher et al., 2022).

Here, we were interested in the effect of temperature and light on germination of the rare and vulnerable TMCF tree species, *D. sayeri*. Germination occurred across a wide temperature gradient; the optimum temperature for germination was higher than current surface temperatures in the understory but equal to summer surface temperatures in sun-exposed sites/canopy gaps, and good germination required an amplitude of at least 6°C. In addition, *D. sayeri* preferred alternating light/dark for germination compared to constant darkness, suggesting that it takes advantage of gaps in the canopy and the subsequent increase in daytime soil temperature and light quantity. Thus, *D. sayeri* appears to have multiple strategies for limiting germination in cooler, darker environments and maximizing germination in warm, light-filled sites. Such conditions are expected to become more common under projected future climate conditions where we might expect to see the germination of *D. sayeri* increase relative to historic amounts. Overall, results of the current study indicate that this TMCF endemic possesses more potential to acclimate to a future, warmer climate than previously assumed. However, predicted phenological shifts in germination under a warmer climate could result in unfavorably timed germination, exposing seedlings to suboptimal environments for establishment and survival, and potentially limiting the long-term persistence of *D. sayeri*. In addition, without canopy cover, seeds and seedlings may be exposed to more extreme temperatures than were investigated here. Data collected in a sun-exposed site on Mount Bellenden Ker revealed air temperatures over 30°C, even in winter, and multiple days of temperatures reaching the high 30's and even >40°C in October (Singh Ramesh et al., 2022). Multifactorial experiments investigating the effect of a wider range of maximum temperatures, light and moisture gradients on germination response and seedling establishment of this and other species endemic to Australia's TMCF would provide more detailed predictions of climate response to support conservation.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ORCID

Amelia V. Stevens https://orcid.org/0000-0001-7935-0596

Gemma L. Hoyle https://orcid.org/0000-0002-5532-1157

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