RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

SER SOCIETY FOR ECOLOGICAL RESTORATION

ADVANCES IN MINING RESTORATION

RESEARCH ARTICLE

Understanding the interplay of temperature and moisture on the germination niche to improve management of threatened species impacted by mining

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The return of vegetation to mined lands often requires broadcast seeding of diverse native seed mixes. However, seeds are highly adapted to germination windows with specific hydrothermal thresholds that maximize the likelihood of seedling survival, and post-mining landscapes typically offer markedly different hydrothermal conditions than pre-disturbance ecosystems. According to niche theory, generalist species should exhibit broader hydrothermal performance niches than specialist taxa, which may influence the success of recruitment from seeds in post-mining ecological restoration. To test this assumption, the impact of hydrothermal stress (incubation temperature (10–30°C) and osmotic potential (−0.8 to 0 MPa)) on the time to 50% germination (t_{50}) and maximum germination (G_{max}) was compared between two narrow-range species of conservation concern (*Acacia woodmaniorum* and *A. karina*) restricted to mining-impacted Banded Ironstone Formations (BIF) and three broadly distributed congenerics (*A. assimilis*, *A. exocarpoides*, and *A. ramulosa*). The hydrothermal germination niches of the study species were broadly congruent with hydrothermal conditions of their habitats. The two range-restricted taxa were more tolerant of hydrothermal stress compared to the three widely distributed taxa, suggesting that tolerance of greater hydrothermal stress by both range-restricted *Acacia* species is likely to be adaptive to establishment in uncontested niche space. Complex interactions between thermal and water stress suggest these environmental gradients may shape the germination niche as well as patterns of plant diversity in BIF ecosystems. This study highlights the importance of quantifying interactions between niche dimensions and their implications for species performance, which will aid future restoration efforts for micro-endemic species impacted by mining.

Key words: drought stress, narrow-range endemic, performance model, seed biology, seed dormancy, threatened species conservation

Implications for Practice

- Knowledge of the germination niche (temperature and moisture stress), and highly resolved microclimatic data, can better indicate whether potential reintroduction to restoration sites is likely to be successful.
- Incorporation of mechanistic aspects of seed germination into the management of rare and range-restricted species, especially in the identification of prospective landscapes for translocation, may improve conservation and restoration outcomes.
- Range-restricted species are theoretically likely to have narrower hydrothermal germination niches compared to broadly distributed co-occurring congenerics, but higher levels of hydrothermal tolerance observed in seeds of some range-restricted species associated with mine sites indicate that greater levels of hydrothermal tolerance in seeds may enable range-restricted taxa to access uncontested niche space on harsher microclimates that are inaccessible to broadly distributed congenerics.

Introduction

The impact of mineral extraction on threatened and range-restricted species can be globally significant and has

Author contributions: all authors conceived the ideas and designed methodology; RPVGSWR collected the data; ST, RPVGSWR analyzed the data; all authors contributed to the interpretation of the results; RPVGSWR, ST led the writing and all authors contributed to writing; all authors contributed critically to the drafts.

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doi: 10.1111/rec.13708
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.13708/suppinfo

historically been compounded by poor regulatory oversight of mining activities and poor management decisions, often based on a lack of biological understanding (de Castro Pena et al. 2017; Sonter et al. 2018). Significant recent progress has driven policy and legislative development that aims to better conserve threatened species, including greater expectation of the mining industry to manage and mitigate ecological damage (Sonter et al. 2018). Specific terms and conditions are imposed upon industry proposing to impact threatened plant species in major mining jurisdictions, such as Western Australia (WA), and these conditions often require evidence that these species can be successfully returned to the post-mining landscape. For example, conditions relating to threatened species occurring on mining leases such as *Acacia woodmaniorum*, *Commersonia* sp. Mt Groper (syn. *Androcalva perlaria*), *Darwinia masonii*, *Lepidosperma gibsonii*, *Ricinocarpos brevis*, and *Tetratheca erubescens* (Government of Western Australia 2009, 2014, 2016, 2017, 2020) include expectations of research to improve their conservation and restoration, establish new populations to mitigate losses due to mining, and develop effective reintroduction and translocation techniques to move species to new locations as needed (Government of Western Australia 2009, 2014, 2016, 2017, 2020). Many threatened species occurring on mining leases are often locally or regionally endemic, because mining typically targets unique geological features such as Banded Ironstone Formations (BIFs; Gibson et al. 2010; Cross & Lambers 2017). The ecology and biology of these species is often poorly resolved, making post-mining translocation and management challenging, and greater understanding of their ecological requirements, including recruitment ecology is required to support long-term species persistence in restoration, reintroduction and translocation activities (Yates et al. 2007, 2011).

The fundamental niche of a species refers to the total set of conditions under which it can potentially survive and reproduce, whereas the occurrence niche, or the realized niche, refers to the conditions under which that species currently exists (Hutchinson 1978; Elith & Leathwick 2009). The realized niche is essentially a subset of the fundamental niche, filtered by biological processes, geography, and stochasticity. Although niche overlap along multiple environmental gradients is common in natural systems (Liu et al. 2018; Dehnhard et al. 2020), niche theory predicts that generalist species usually (but not always) have broader niches compared to specialist species (Carboni et al. 2016; Ainsworth & Drake 2020). There is often a good concordance between a species' occurrence niche and its physiological performance rates across various environmental gradients (Sánchez-Gómez et al. 2006; Martínez-Meyer et al. 2013). Generalist species are expected to perform moderately well in many conditions (the "jack of all trades" strategy; Huey & Hertz 1984). Specialist taxa, by comparison, typically outperform generalists in their uncontested niche space (Boulangeat et al. 2012; Peers et al. 2012). However, not all life stages contribute equally to overall population persistence (de Kroon et al. 1986; Pironon et al. 2018); species' niche structures are often determined by the performance of critical demographic stages such as germination and seedling emergence (Sánchez-Gómez et al. 2006; Fernández-Pascual et al. 2017).

Seeds are adapted to germinate optimally under conditions that are least risky for seedling recruitment (Giménez-Benavides et al. 2005; Luna et al. 2012). Temperature and water stress are critical environmental dimensions that determine the success of seed germination (Krichen et al. 2017; Zogas et al. 2020). Because seed germination is underpinned by metabolic processes that are mediated by enzymes (Huang, Ran, et al. 2020), the germination performance of seeds across a thermal gradient should resemble a unimodal asymmetric hump-shaped curve (Yan & Hunt 1999; Tomlinson et al. 2015). On a similar note, water stress in the external environment impedes the metabolic reactions of seed germination (Muscolo et al. 2014; Turner et al. 2018). Therefore, increasing water stress in the external environment of a seed should cause an exponential increase in time to reach 50% germination (t_{50}; Bradford 2002; Cochrane 2018) and a logistic decrease in maximum germination (Lewandrowski et al. 2017; Turner et al. 2018). The concept of "hydrothermal germination niche" is well-established in the literature (Hardegree et al. 2018; Onofri et al. 2018), but studies that have incorporated these mechanistic principles are scarce in the context of restoration (Huang et al. 2016; Turner et al. 2018).

Plant communities on rocky outcrops are often highly biodiverse and floristically distinct from surrounding deep-soil flora (Gibson et al. 2012; Porembski & Barthlott 2012), often hosting both range-restricted, edaphically specialized taxa and those that are widely distributed across different ecosystems (Gibson et al. 2010; Cross & Lambers 2021). For example, across southern WA, BIFs are a distinctive geological feature occurring as isolated ranges within a mosaic of alluvial clay soils and sandplains (Byrne et al. 2019). Many BIF outcrops harbor exceptionally high ß diversity, and are regional centers of plant diversification (Gibson et al. 2012; Byrne et al. 2019). Although the regional biodiversity values of these flora are well established with over 40 specialist BIF-centered species so far described (Jacobi & do Carmo 2008; Gibson et al. 2012), the ecological filters responsible for these distinctive patterns are yet to be fully investigated and explained (Tapper et al. 2014; Di Virgilio et al. 2018).

BIFs are found in different regions throughout the world and are particularly prevalent in WA, with many distributed across the mineral-rich arid to semiarid Yilgarn craton (Gibson et al. 2012). Many BIF outcrops contain commercial quantities of iron ore, and growing global demands have accelerated the mining of BIF ranges across WA with significant impacts on BIF restricted flora (Gibson et al. 2010, 2012; Yates et al. 2011). The exposed, skeletal soils of BIF outcrops (Yates et al. 2011) tend to be water-limited compared to those of neighboring deep-soil vegetation matrices (Elliott et al. 2019), but they are also highly spatially heterogeneous, where weathering has produced shaded slopes, crevices, and gullies that can retain rain water for differing periods of time (Yates et al. 2011; Di Virgilio et al. 2018). This diversity of microhabitats supports high species richness and endemism; many BIF specialist species are restricted to small numbers of ranges (or parts thereof), or even a single outcrop (Gibson et al. 2012). These outcrops function as refugia during periods of environmental

stochasticity for both BIF specialists and their widely distributed co-occurring congenerics (Byrne et al. 2019). However, there is a major shortage of research data on how the interactions of environmental variables, such as thermal and moisture stress affect the patterns of plant diversity in BIF habitats, which may assist future conservation and restoration efforts of BIF niche specialists impacted by mining (Yates et al. 2011; Di Virgilio et al. 2018).

The objective of this study was to compare the germination responses of seeds with physical dormancy from two range-restricted BIF specialist taxa (that are significantly impacted by mining) with those of three widely distributed co-occurring species to guide future restoration efforts. We expected that hydrothermal performance of seeds with physical dormancy would conform to established mechanistic principles, as shown for non-dormant seeds (Rajapakshe et al. 2020). However, we were unclear on the potential ecological and evolutionary implications of the hydrothermal germination response of BIF taxa in comparison with congeneric species, and sought to understand whether BIF specialist species would have the narrow germination niches predicted by niche theory.

Methods

Species Selection and Sourcing

Five Western Australian species of *Acacia* (Western Australian Herbarium 1998) were used for this study; all co-occurring in at least part of their distributional range, but with widely differing area of occupancy (AOO) and extent of occurrence (Table S1; Fig. 1). Seeds of two species restricted to mine-impacted BIF habitats were tested (*A. woodmaniorum* Maslin & Buscumb and *A. karina* Maslin & Buscumb), as well as three common broadly distributed congeneric species; *A. assimilis* S. Moore ssp. *assimilis* (hereafter *A. assimilis*), *A. exocarpoides* W. Fitzg, and *A. ramulosa* W. Fitzg var. *linophylla* Pedley (hereafter *A. ramulosa*). Seeds of the two range-restricted species were freshly harvested from wild populations in 2016 (*A. karina*) and 2017 (*A. woodmaniorum*), air dried, and then stored in an air-conditioned room until utilized in this study. Seeds of the three widely distributed taxa were purchased from a commercial seed supplier in 2018 (Nindethana Seed Company, King River, Western Australia). *Acacia woodmaniorum* and *A. karina* are gazetted as Declared Rare Flora and Priority 1 Flora, respectively, under Western Australian conservation legislation (Western Australian Herbarium 1998), so are of major conservation concern (Nevill et al. 2010; Millar et al. 2013). Populations of *A. woodmaniorum* are restricted to gullies, crevices, and BIF slopes in the Mungada/Mt Karara area of the arid to semiarid Yalgoo region (AOO approximately 12 km^2; Millar et al. 2013; Thackway & Cresswell 1997). *Acacia karina* is restricted to the Blue Hills Range of the Yalgoo region (AOO approximately 44 km^2), with scattered populations occurring on BIF slopes and adjacent flat plains of Mt Karara and Mt Jackson (Byrne 2019). The BIF where both species are found are variously impacted by mining for iron ore (Merino-Martín et al. 2017; Cross & Lambers 2021). Conversely, *A. assimilis*, *A. exocarpoides*, and *A. ramulosa* are common and structurally dominant trees or large shrubs that are broadly distributed throughout central and southwestern WA (Meissner & Caruso 2008). *Acacia ramulosa* also occurs in other Australian states (Western Australian Herbarium 1998). The AOO of all three common species ranges from 560 to greater than 1,000 km^2 (Table S1). *Acacia ramulosa* mostly occurs on dunes and sandplains (Ward et al. 2018), whereas *A. assimilis* occurs on granite outcrops, sandplains, and slopes of rocky hills, and *A. exocarpoides* inhabits a variety of rocky environments (Western Australian Herbarium 1998; Meissner & Caruso 2008). All three species can co-occur on the rocky slopes of BIF in the Blue Hills Range and Mungada/Mt Karara area (Cross & Lambers 2021).

In Situ Climatic Conditions

The climate of Morawa (the closest major regional town), which is approximately 60 km from where all five species co-occur in the Blue Hills range and Mungada/Mt Karara area, is semiarid with a mean annual rainfall of approximately 282 mm and mean annual evaporation of 2,781 mm (Fig. 1). Average monthly rainfall is highest (35–45 mm) during the cooler months (May to August), and very low (14–21 mm) during the summer months (Fig. 1). Summers are hot (mean daily maxima 35–37°C), whereas the winters are cool (mean daily maxima 6–20°C) with more frequent rainfall during this time (10–13 days; Fig. 1).

Seed Quality

Seeds were stored in a controlled environment of 15°C and 15% relative humidity for several weeks prior to experimentation, at the Biodiversity Conservation Centre, Kings Park, WA. Seeds were separated from chaff using a vacuum aspirator (SELECTA BV Gravity Seed Separator, the Netherlands). Percentage seed fill of each test species was quantified by x-ray analysis of 100 seeds (MX-20 digital x-ray cabinet, Faxitron, U.S.A.) following Erickson and Merritt (2016).

Hydrothermal Tolerance

Prior to experimentation, physical dormancy in all test species was alleviated by either exposure to hot water (approximately 95°C) or acid scarification, as described in Table S1. To quantify the germination response of seeds to hydrothermal stress, three to five replicates of 20 seeds per species (depending on seed availability) were exposed to 25 hydrothermal stress regimes (water stress levels of 0.0, −0.2, −0.4, −0.6, and −0.8 MPa at 10, 15, 20, 25, and 30°C). Seeds were placed on 84 mm germination paper (Advantec, Dublin, CA, U.S.A.) infused with either distilled water or different concentrations of polyethylene glycol 8000 (PEG) solution to generate the range of water potentials outlined above for each incubation temperature. Nine milliliters of distilled water or PEG solution was administered per 90 mm plastic Petri dish (Michel 1983).

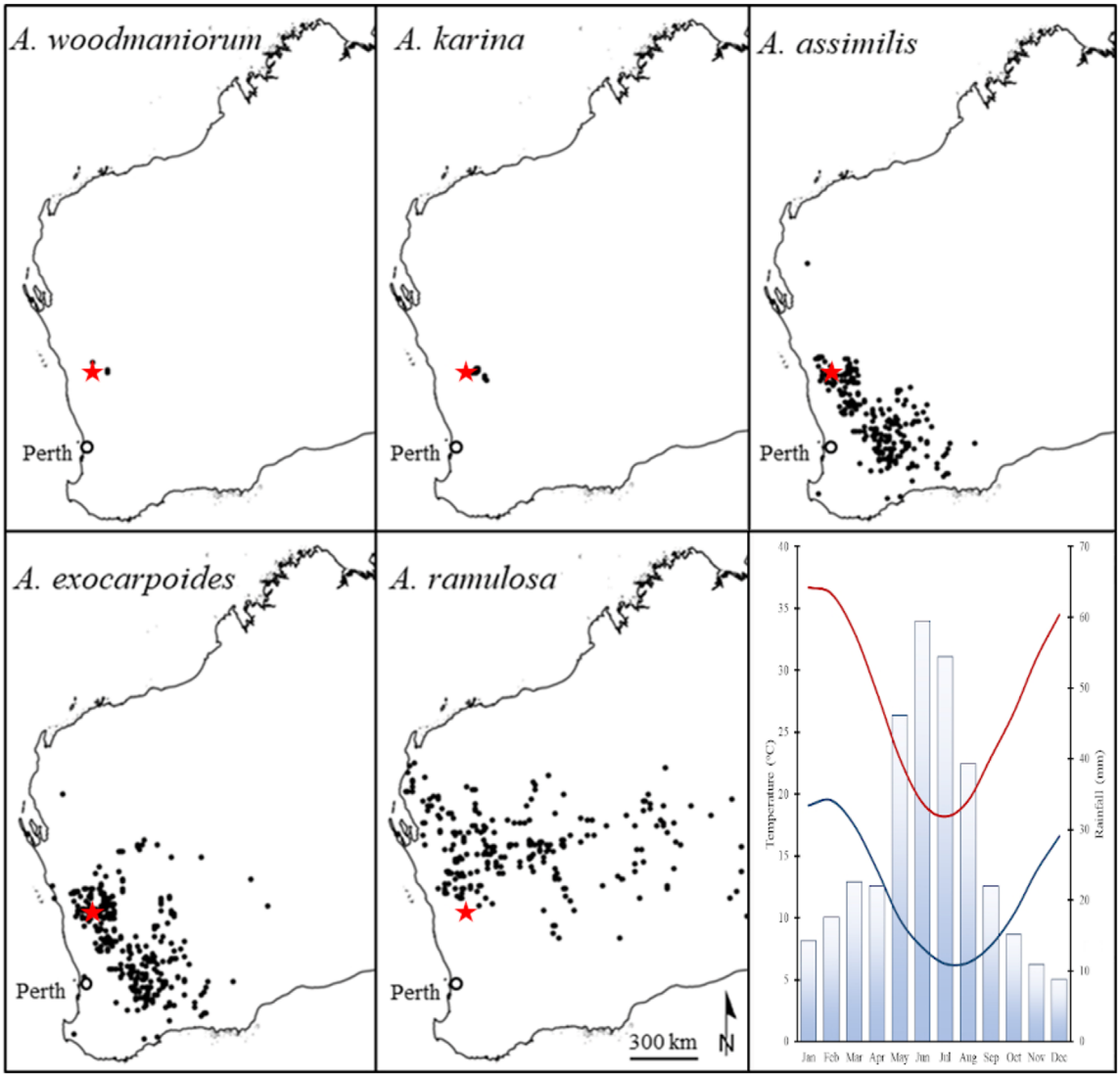


Figure 1. Distribution of the five study species (black dots) in Western Australia based on Atlas of Living Australia website (2020). The red star on each map indicates Morawa, where the nearest Bureau of Meteorology station is cited, the climatic data from which is presented in the sixth panel. The red line indicates the monthly average maximum temperature, the blue line indicates the monthly average minimum temperature, and the bars indicate the monthly average rainfall.

The temperature regimes used in this study encompass a wide range of the hydrothermal conditions reported for the locations of the test species across different seasons (Fig. 1). Prior to plating, seeds were surface sterilized using 2% (w/v) calcium hypochlorite ($Ca[Ocl]_2$) under vacuum (−70 kPa) for 30 minutes followed by rinsing thrice with sterile deionized water for several minutes per wash. Seed plating was conducted in a laminar flow cabinet under sterile conditions. Following the plating of seeds, Petri dishes were tightly sealed with plastic wrap to prevent desiccation during the incubation period. To accurately record the temperature that seeds were exposed to during incubation, iButton data loggers (Maxim Integrated, San Jose, CA, U.S.A.) were placed in the middle of each stack of six Petri dishes according to Table S2. Germination was scored as radicle emergence greater than 2 mm, and plates were scored 4 days per week for a duration of up to 28 days.

Statistical Analysis

Germination Modeling. A nonlinear regression approach was used to estimate the performance characteristics of each species, which minimizes overfitting and maintains the variance structure of the germination response data (Ritz & Streibig 2008). First, the relationship between time and germination response was investigated for each hydrothermal stress regime by fitting a nonlinear log-logistic function to the germination data (Tarszisz et al. 2017; Saatkamp et al. 2019). A three parameter log-logistic model was fitted to the data using the *drc* package

(Ritz & Streibig 2012) in the *R* statistical software environment (R Core Team 2013):

$$\text{Germination} = \frac{G_{\max}}{1 + \exp[b(\log(\text{time}) - \log(t_{50}))]} \quad (1)$$

where $G_{\max}$ is maximum germination, t_{50} is the time required for 50% of seeds (as a proportion of $G_{\max}$) to germinate, and b represents the slope of the equation at t_{50}. This equation assumes that the lower limit of germination is 0 (Lewandrowski et al. 2017). First, for each species, a common convergent curve was fitted to the proportion of incubated seeds that germinated for each hydrothermal regime. Next, the data were grouped by hydrothermal stress regime to produce multiple permutations of the primary model by fitting distinct values to the parameters of the equation. The log-logistic function categorized in unique stress categories was used to estimate t_{50} and $G_{\max}$ for each replicate of seeds exposed to each hydrothermal stress regime.

Hydrothermal Tolerance. To describe the thermal stress responses of seeds in terms of t_{50}, we applied an established thermal performance function (Yan & Hunt 1999; Rajapakshe et al. 2020):

$$r_{\max} = R_{\max}\left(\frac{T_{\max} - T}{T_{\max} - T_{\text{opt}}}\right)\left(\frac{T}{T_{\text{opt}}}\right)^{\frac{T_{\text{opt}}}{T_{\max} - T_{\text{opt}}}} \quad (2)$$

where $r_{\max}$ ($1/t_{50}$) is the maximum germination rate at a given temperature (T); T_{opt} is the optimum temperature for germination where germination is at its most rapid; $T_{\max}$ is the upper limit of thermal stress tolerance, at which germination ceases; and $R_{\max}$ is the upper limit of the germination response curve at T_{opt}.

In terms of $G_{\max}$, germination response to temperature should begin at the lowest temperature that is conducive to metabolic reactions of seed germination, increase with rising temperature up to a point, and decrease with escalating heat stress, until germination ceases at $T_{\max}$ due to thermal denaturation of enzymes (Rosental et al. 2014; Singh et al. 2019). Thus, a unimodal symmetrical quadratic function was selected to characterize the germination response of seeds in terms of ($G_{\max}$) to thermal stress:

$$G_{\max} = hT^2 + iT + j \quad (3)$$

where $G_{\max}$ represents maximum germination, T is any temperature, h and i are numerical coefficients, and j is the Y-intercept.

In the same way that thermal stress impedes germination, water stress is also detrimental to the seed germination process (Kaya et al. 2006; Muscolo et al. 2014). Increasing water stress in the external environment of a seed causes a logistic decrease in $G_{\max}$ (Mesgaran et al. 2017; Turner et al. 2018; Duncan et al. 2019).

On the basis of the mechanistic principles described above, we constructed a hydrothermal model that synchronously defines the two-dimensional hydrothermal germination niche of a given species, characterized by thermal stress and water stress (Fig. 2):

$$G_{\max} = \frac{p}{1 + e^{\{q \times [\log(w) - \log(t_{50})]\}}} \quad (4)$$

where $G_{\max}$ is the predicted maximum germination for a test species at any hydrothermal regime (Fig. 2C), p is final germination percentage at any hydrothermal regime as estimated by Equation 3 (by fitting Equation 3 to the final germination percentages of a species at a given water stress regime at different temperatures; Fig. 2A), q is a germination constant, w is the water stress level, and t_{50} is time required for 50% of the seeds to germinate at a specific hydrothermal regime as estimated by 1/Equation 2 in Figure S1A).

Unique Parametrization. The *nls* function was used to fit distinct values to the parameters of Equations 2 and 3 to parametrize unique $R_{\max}$, T_{opt}, $T_{\max}$, and $G_{\max}$ estimates across a wide range of temperatures at each different water stress regime (Ritz & Streibig 2008). To construct a hydrothermal germination niche for each test species, Equation 4 was fitted to all the observed final germination percentage values (p), and unique fits were permuted at each treatment level in the manner described above. The hydrothermal germination niche for each species was constructed in an *R* software environment using the packages *ggplot* and *Lattice* (Wickham & Wickham 2007; Sarkar 2008).

Results

Germination Modeling

In all test species, the response of $r_{\max}$ ($1/t_{50}$) to temperature at each water stress level was a unimodal asymmetric hump-shaped curve (Fig. S1A). In the absence of water stress, time to reach 50% germination (t_{50}) at T_{opt} was longest in *Acacia assimilis* (11 ± 2.2 days; Table 1), whereas the estimate for t_{50} at T_{opt} was shortest in *A. ramulosa* (2 ± 11.9 days). In *A. exocarpoides*, *A. karina*, and *A. woodmaniorum*, estimates for t_{50} at T_{opt} and 0 MPa were 5 ± 1.2, 3 ± 1.3, and 5 ± 0.5 days, respectively (Table 1). Increasing water stress decreased the breadth of the thermal performance niche of $r_{\max}$ in all taxa (Fig. S1A). In the absence of water stress, the T_{opt} estimates for all test species except *A. ramulosa* were between 15 and 24°C (Table 1; Fig. S1A). The T_{opt} estimate for *A. ramulosa* at 0 MPa was higher than that of any other species (39 ± 11.9°C; Table 1; Fig. S1A).

At 0 MPa, the estimated $T_{\max}$ of *A. ramulosa* was 56 ± 20.3°C indicating a higher level of thermal stress tolerance compared to the other four species (Table 1; Fig. S1A). In contrast, $T_{\max}$ at 0 MPa was the lowest in *A. woodmaniorum* (29 ± 1.0°C) whereas, in *A. assimilis*, *A. exocarpoides*, and *A. karina* $T_{\max}$ values at 0 MPa were between 29 and 44°C (Table 1; Fig. S1A). The thermal performance function (Equation 2) could not be fitted to the three widely distributed

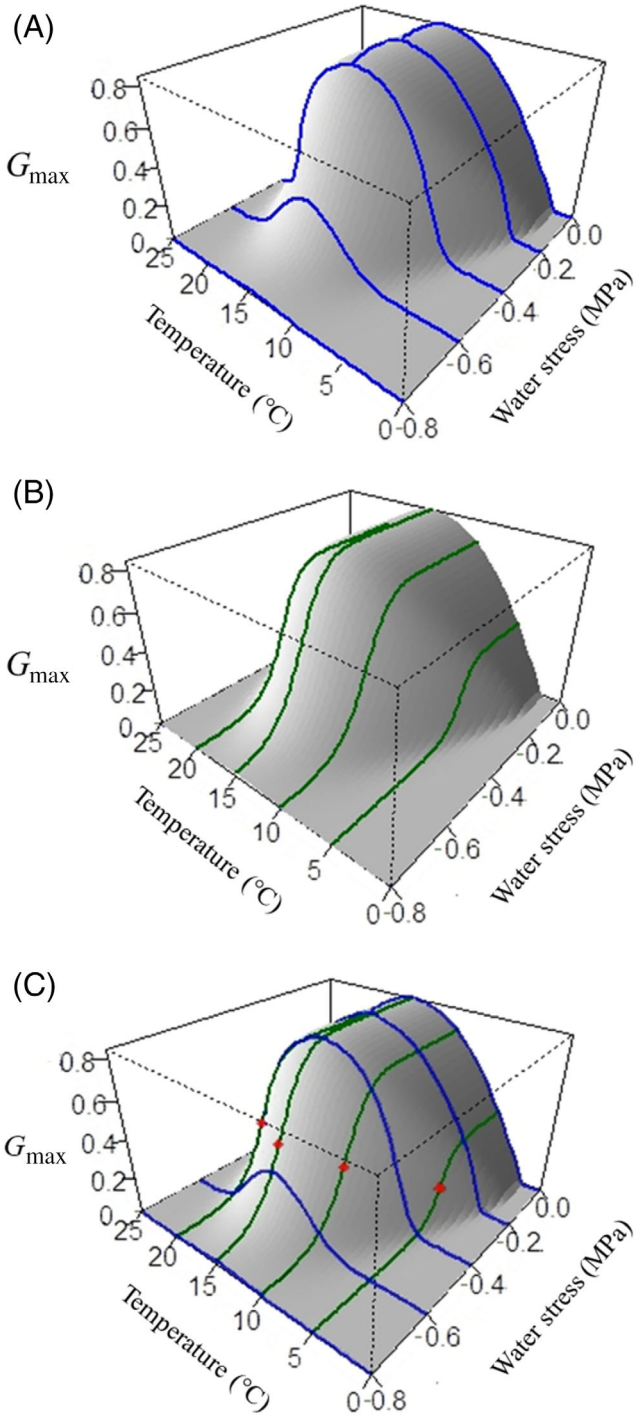


Figure 2. Schematic representation of the hydrothermal germination model described by Equation 4; (A) blue lines depict the parameter p of Equation 4; G_{max} estimates predicted by fitting a quadratic function (Equation 3) to the final germination percentages of a taxon at 0.0, −0.2, −0.4, −0.6, and −0.8 MPa across a thermal spectrum of 0–25°C. (B) Green lines depict the logistic function fitted to the final germination percentages of the taxon at 5, 10, 15, 20, and 25°C across a water stress spectrum of −0.8 to 0 MPa. (C) Red dots depict estimates for G_{max} as predicted by Equation 4 at 5, 10, 15, and 20°C, and −0.30, −0.50, −0.57, and −0.48 MPa, respectively.

Table 1. Coefficients for the thermal performance function (Equation 2) of effects of thermal stress on time to reach 50% germination (t_{50}), and quadratic function (Equation 3) of effects of thermal stress on maximum germination (G_{max}) in the absence of water stress (0 MPa) for the five study species, where T_{opt} is the optimum incubation temperature for germination, R_{max} is the upper limit of germination response curve (in terms of r_{max}) at T_{opt}, T_{max} is the highest temperature at which germination was observed, h and i are numerical coefficients, and j is the Y-intercept.

	Germination Speed, r_{max} ($1/t_{50}$)				*Maximum Germination, G_{max}*			
Species	T_{opt} (°C ± *SE*)	R_{max} ($1/t_{50}$ *at* T_{opt} ± *SE*)	t_{50} *at* T_{opt} (*Days*)	T_{max} (°C ± *SE*)	G_{max} *at* T_{opt}	h	i	j
Acacia woodmaniorum	18.6 ± 0.5	0.22 ± 0.01	4.6 ± 0.5	28.6 ± 1.0	0.9	−0.08 ± 0.03	2.48 ± 1.11	−0.04 ± 10.23
Acacia karina	22.6 ± 1.3	0.29 ± 0.05	3.4 ± 1.3	30.9 ± 1.5	0.8	−0.08 ± 0.01	25.97 ± 0.47	−11.24 ± 3.20
Acacia assimilis	17.2 ± 2.2	0.09 ± 0.01	10.6 ± 2.2	35.0 ± 8.8	0.8	−0.01 ± 0.02	0.11 ± 0.74	−15.08 ± 6.81
Acacia exocarpoides	21.6 ± 1.2	0.22 ± 0.02	4.5 ± 1.2	33.3 ± 1.8	1.0	−0.09 ± 0.01	3.35 ± 0.53	−11.33 ± 4.03
Acacia ramulosa	39.0 ± 11.9	0.57 ± 0.18	1.8 ± 11.9	56.1 ± 20.3	0.0	−0.07 ± 0.01	2.88 ± 0.37	−10.28 ± 2.79

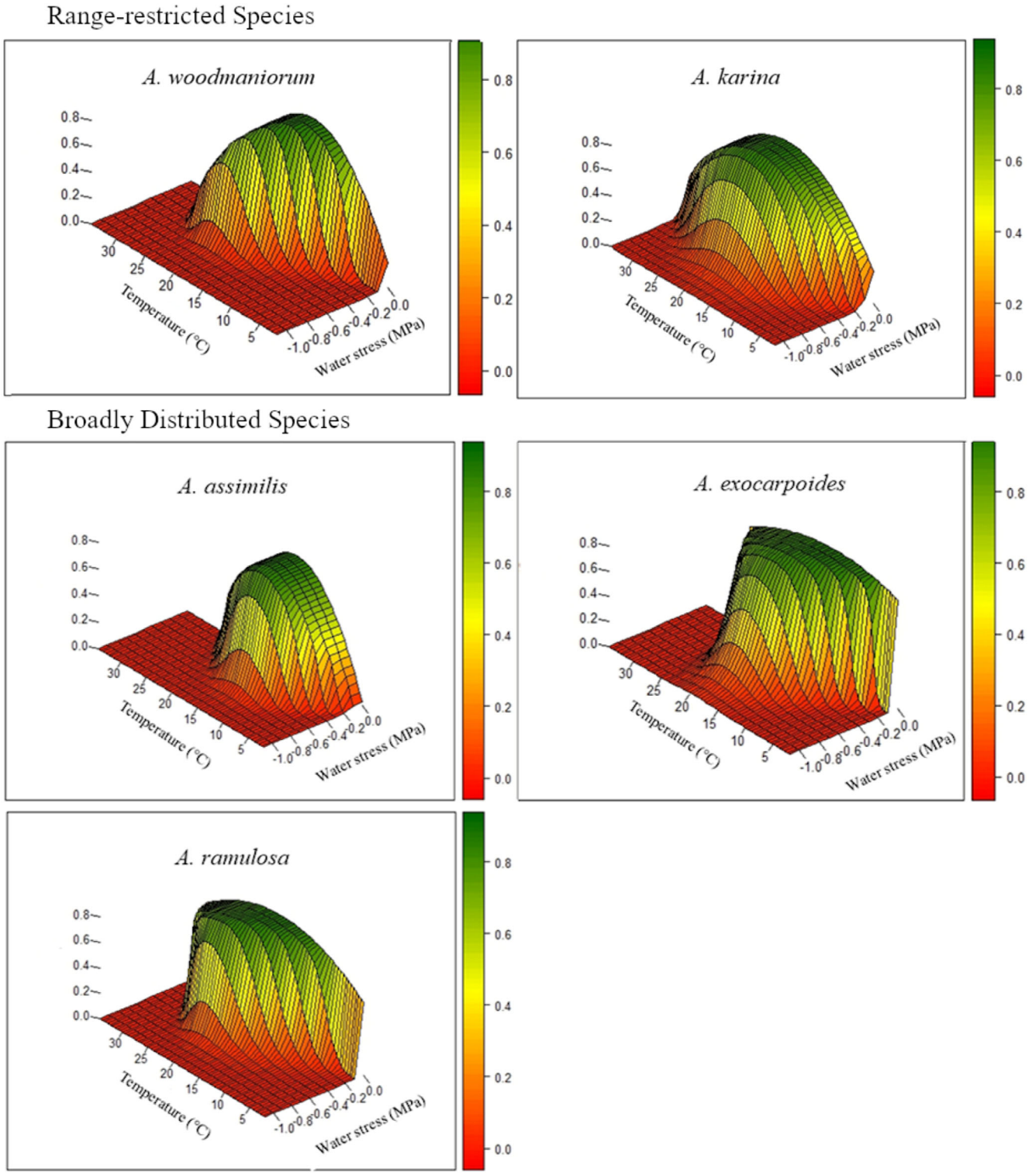


Figure 3. Hydrothermal germination niche for five Western Australian *Acacia* species in terms of maximum germination (G_{max}) estimated by a hydrothermal germination function following incubation of seeds in constant darkness at different hydrothermal regimes for 28 days. The two horizontal axes represent incubation temperature (°C) and water stress level (MPa). The vertical axis represents G_{max} (as a proportion) as estimated by Equation 4. Three to five replicates of 20 seeds were used for each treatment regime.

taxa at −0.6 MPa due to low germination percentages in those treatments (Fig. S1A).

The thermal performance of G_{max} followed a unimodal symmetrical hump-shaped curve in all species (Fig. S1B). Within favorable temperature ranges for germination, and in the absence of water stress, estimates of G_{max} were greater than 0.8 in all species after 28 days of incubation (Fig. S1B). Estimates of G_{max} in *A. woodmaniorum* were consistently greater than 0.8 throughout a broad range of water stress regimes (0–0.8 MPa) within favorable thermal conditions (approximately 10–16°C; Fig. S1B). Conversely, in all other test species, G_{max} at all thermal regimes declined to less than 0.5 at −0.8 MPa (Fig. S1B). Equation 3 could not be fitted to germination responses of *A. assimilis* at −0.8 MPa due to low final germination percentage values (Fig. S1B).

When seeds were not subjected to water stress, a temperature range of approximately 15–20°C was conducive to germination in all taxa (Fig. S1B). In the absence of water stress, *A. ramulosa* exhibited the broadest thermal tolerance range (approximately 4–40°C), whereas the narrowest thermal tolerance range was observed in *A. assimilis* (approximately 5–27°C; Fig. S1B).

Hydrothermal Tolerance

In terms of G_{max}, germination response to temperature at any water stress level was a unimodal symmetric and hump-shaped curve in all species (Fig. 3). At a given temperature, G_{max} decreased logistically with increasing water stress (Fig. 3). Under favorable thermal conditions and in the absence of water stress, germination probability of all taxa exceeded 0.8 (Fig. 3). In all species, increasing water stress decreased the breadth of the thermal performance niche (Fig. 3). Similarly, deviation from favorable thermal regimes constrained the breadth of the hydrological performance niche (Fig. 3). The hydrothermal germination niches of the two range-restricted taxa were broad and generally comparable to those of *A. exocarpoides* and *A. ramulosa* (Fig. 3). *Acacia assimilis* was less tolerant of hydrothermal stress than any other test species (Fig. 3). In all test species except *A. exocarpoides*, G_{max} declined to less than 0.5 at −0.6 MPa at all thermal regimes (Fig. 3). When exposed to low water stress conditions (0 to −0.4 MPa), the broadest thermal tolerance range was observed in *A. karina*, whereas under favorable thermal conditions *A. exocarpoides* was more tolerant of water stress than any other species (Fig. 3).

Discussion

Broadly speaking, the results of this study are consistent with previous reports of seed germination in response to univariate thermal or hydrological stressors (Cochrane 2018; Turner et al. 2018). Yet, despite the general support for the mechanistic hypotheses underpinning this series of experiments, the interaction between hydrological and thermal drivers of the germination niche are complex and do not conform to the initial expectations dependent upon niche theory. We expected that range-restricted species would be defined by a narrower hydrothermal germination niche than broadly distributed species, but this was not the case. In terms of t_{50} and G_{max}, the two range-restricted taxa were more tolerant of hydrothermal stress compared to the three widely distributed congenerics.

Germination Dynamics

Increasing water stress constrained the breadth of the thermal performance niche, and suboptimal thermal regimes constrained the breadth of the hydrological performance niche. These observations suggest that thermal stress and water stress are inter-dependent niche dimensions, interactively inhibiting germination in terms of both r_{max} and G_{max}, consistent with other recent work demonstrating the role of interacting niche axes in defining population dynamics (Huang, Zhou, et al. 2020).

The findings of this study lend further support to reports that the speed of germination; r_{max} ($1/t_{50}$) should follow a unimodal asymmetric hump-shaped curve similar to that of all enzyme mediated reactions (Rajapakshe et al. 2020). In addition, the results of this study support earlier reports that maximum germination response of seeds (G_{max}) to temperature can be characterized by a quadratic function (Singh et al. 2019). Furthermore, experimental data are in line with previous research that suggests that at a given temperature, estimates for G_{max} should decrease logistically with increasing water stress (Lewandrowski et al. 2017; Turner et al. 2018).

Ecological Correlates of the Germination Niche

In all test species except *Acacia ramulosa*, estimates for G_{max} were highest under test regimes that correspond to the hydrothermal conditions during autumn and winter, suggesting that all test species except *A. ramulosa* are adapted to synchronize germination across the austral autumn and winter, a strategy that is common among species native to this region (Bell et al. 1993; Bell et al. 1995). High soil moisture levels persist in deep-soil environments for an extended time during the cooler months of the year, ensuring successful establishment of seedlings (Yates et al. 2000; Merritt et al. 2007). Germination data support previous studies that suggest that flora native to Mediterranean climatic regions generally follow a strategy of summer germination avoidance due to the extreme establishment conditions that occur during this time (Luna et al. 2012; Clemente et al. 2017).

According to the estimates of G_{max}, *A. assimilis* was less tolerant of hydrothermal stress than the other four test species. This species inhabits the relatively deep skeletal soils in low-lying woodlands (Western Australian Herbarium 1998), rocky plains, and sand slopes extending from the more arid region in the north east of its range to relatively cooler, mesic environments along parts of the southern coast of WA (Meissner & Caruso 2008). Estimated t_{50}, r_{max}, and G_{max} for *A. assimilis* at 0 MPa are similar to those of other species native to southwest WA (Cochrane 2020; Rajapakshe et al. 2020). The hydrothermal germination niche suggests that this species, or at the very least the seed accession that we studied, is less arid-adapted than the other tested species.

In all test species except *A. assimilis*, rapid germination persisted across broad thermal tolerance ranges, and the

germination speed of these taxa (t_{50}) was higher at 0 MPa than those of many species native to southwest WA (Yates et al. 2000; Cochrane 2018, 2020). The two range-restricted taxa occur on shallow stony metamorphic soils of BIF habitats in the arid to semiarid Yalgoo region of midwest WA (Meissner & Caruso 2008). In contrast, the distribution range of *A. exocarpoides* and *A. ramulosa* extend from Yalgoo to the more arid regions of WA such as Murchison and Great Victoria Desert (Western Australian Herbarium 1998; Markey 2008). These arid regions are characterized by higher temperatures and annual evaporation rates that significantly exceed the irregular annual rainfall (Markey 2008; Markey & Dillon 2011). This results in a short, unpredictable window of opportunity for successful establishment of seedlings that may occur across a relatively broad range of temperatures. Relatively higher thermal performance in terms of G_{max} and r_{max} at low water stress regimes suggest that *A. exocarpoides*, *A. ramulosa*, and the two range-restricted taxa are adapted to maximize recruitment success within shorter periods of high soil moisture availability following sporadic rainfall events (Debat & David 2001). These observations are in line with previous studies that have reported species occurring in water-stressed habitats germinate rapidly whenever soil moisture availability is high, even if the thermal environment is suboptimal (Jurado & Westoby 1992; Rajapakshe et al. 2020).

The two range-restricted taxa were more tolerant of hydrothermal stress compared to *A. exocarpoides* and *A. ramulosa*. *Acacia woodmaniorum* generally inhabits the ridges of BIF outcrops (Byrne 2019), but has also been reported from disturbed overburden of mine sites (Western Australian Herbarium 1998). *Acacia karina* occurs on both BIFs and the surrounding relatively deep soil slopes and plains (Byrne 2019). BIF outcrops are regularly subjected to greater levels of hydrothermal stress compared to the surrounding deep-soil environments inhabited by *A. exocarpoides* and *A. ramulosa* (Hopper 2009). The higher levels of hydrothermal stress tolerance observed in *A. karina*, *A. woodmaniorum* strongly indicate adaptations to tolerate relatively harsh microclimates; a bet-hedging strategy by which these two species could potentially gain access to uncontested niche space on BIF outcrops (inaccessible to their congenerics inhabiting deeper-soil environments, due to comparatively lower levels of hydrothermal stress tolerance). The general concordance between the occurrence niches and the hydrothermal performance niche of seeds of the study species suggests that the germination niche plays an important role in shaping and filtering the overall niche structure of plants, in accordance with previous studies (Cochrane et al. 2014; Marques et al. 2014). The overall niche structure of a species is mostly determined by species performance rates that influence population growth to a large extent (Butterfield & Briggs 2011; Pironon et al. 2018). The link between the distribution range of the study species and hydrothermal performance of their seeds is broadly congruent with this, and further highlights the role of hydrothermal stress shaping the germination niche of taxa in Mediterranean ecosystems (Cochrane et al. 2014; Zogas et al. 2020). The breadth of the hydrothermal germination niche in the range-restricted species is, however, not consistent with niche theory, which generally predicts that such species should have specialist, narrow niches (Hutchinson 1978; Elith & Leathwick 2009). Instead, the hydrothermal stresses imposed by these habitats actually select for a broad tolerance, suggesting that there must be other filters post-germination that substantially narrow and define the niche of the range-restricted species. Quantifying the impact of various environmental dimensions on the vital performance rates of *A. karina* and *A. woodmaniorum* during other life stages may provide important insights into the niche shifts that may have caused these two species to become range-restricted (Pironon et al. 2018).

Future Research Directions

The method that we have applied predicts the hydrothermal germination niche of taxa only on the basis of final germination percentage (p) and time is not incorporated to the equation in the manner of hydrothermal time equations (Onofri et al. 2018). However, previous hydrothermal time models simplify the performance functions in ways that overlook important parameters such as T_{opt} (Bradford 2002; Onofri et al. 2018). Nevertheless, simpler models have facilitated the examination of patterns of ecology and evolution in wild species, whereas more complex models have mostly been applied to less phylogenetically variable domestic plant cultivars that are often highly inbred, leading to highly consistent and uniform germination (Onofri et al. 2018). Although we have gained some useful insights, we advocate that a broader phylogenetic perspective is required to understand how hydrothermal stress on germination response affects patterns of rarity and endemism (Byrne 2019).

This study demonstrates that thermal stress and water stress are inter-dependent environmental dimensions that interact to produce a negative effect on the germination niche of seeds in terms of both the time required to reach 50% germination (t_{50}) and maximum germination (G_{max}). The experimental data do not conform to a simple interpretation of niche theory where specialist taxa have a narrowly defined niche in which they outperform generalist species. Instead, the hydrothermal stresses of these specialized habitats select for a broad germination niche that facilitates rapid germination under a range of conditions, and it can be speculated that the two range-restricted species outperform more widespread species and gain access to uncontested niche space in their rocky environment. In other habitats, it can be speculated that the two range-restricted species must be outcompeted by other aspects of demographic filtering or niche partitioning, but this remains untested. Quantifying complex interactions between niche axes as well as their impact on species performance is essential to gain a comprehensive understanding of population dynamics which, coupled with high-resolution spatial modeling and the use of finely resolved microclimatic data, will aid future restoration efforts for micro-endemic species impacted by mining.

Acknowledgments

The authors acknowledge the Wadjuk people of the Noongar nation, traditional owners of the land on which this work was

undertaken and pay our respects to Elders past, present, and emerging. The authors are grateful to Dr. W. Lewandrowski (Department of Biodiversity, Conservation and Attractions Western Australia) for providing advice and guidance on statistical analyses and interpretation. We thank Kings Park Science for their support and providing access to their equipment and facilities. This research was funded under the Australian Research Council Industrial Transformation Training Centre for Mine Site Restoration (ICI150100041) and the 2021 Curtin University Publication Grant. Open access publishing facilitated by Curtin University, as part of the Wiley - Curtin University agreement via the Council of Australian University Librarians.

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Supporting Information

The following information may be found in the online version of this article:

Table S1: Distributional extent (Atlas of living Australia 2020) and seed traits of the Acacia species used in this study.

Table S2: Mean temperatures (± SE in parentheses) inside seed incubators for the duration of experiments.

Figure S1: Hydrothermal tolerance in five Western Australian *Acacia species* in terms of time to reach 50% germination (t_{50}) and maximum germination (G_{max}); **a)** Dots represent $1/t_{50}$ (r_{max}) estimates for each replicate of seeds following exposure to different hydrothermal regimes (as predicted by Equation 1), and the smooth lines depict the thermal performance function (Equation 2) fitted to the $1/t_{50}$ estimates (r_{max}) of each taxa. **b)** Dots represent G_{max} estimates for each replicate of seeds after exposure to different hydrothermal regimes (as predicted by Equation 1), and the smooth lines depict the quadratic model (Equation 3) fits for the G_{max} estimates of each species.

Coordinating Editor: Loralee Larios

Received: 9 November, 2021; First decision: 25 January, 2022; Revised: 3 March, 2022; Accepted: 19 April, 2022