RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

SER SOCIETY FOR ECOLOGICAL RESTORATION

THEMATIC SERIES Arid Lands

RE-AL THEMATIC SERIES

RESEARCH ARTICLE

Linking ex situ germination to in situ direct seeding for landscape scale restoration efforts in the semiarid Mallee region of Victoria, Australia

Joseph Stapleton[1,2], Shane R. Turner[3], David Warne[4], Singarayer Florentine[1,5]

Direct seeding has high potential for arid revegetation, but success is limited by decreased germination and seedling emergence. Direct seeding success may be improved through developing an understanding of the germination biology and requirements of species used for these projects. This study looked into the germination temperature and moisture requirements of four semiarid species from Victoria's Mallee ecosystems to understand how their germination biology may advise strategies for future plantings. Temperature's effect on germination was analyzed by incubating the seeds under three different regimes: 30/20, 25/15, and 17/7°C. Moisture requirements were determined by germinating seeds along a water potential gradient created using polyethylene glycol 8000 solutions. Results showed three different strategies employed by the study species: (1) *Acacia ligulata* has a generalist approach, germinating well in all temperatures with a reasonable tolerance to water stress; (2) *Eucalyptus calycongona* and *Melaleuca lanceolata* germinate rapidly under higher germination temperatures and have generally higher water stress tolerance; while (3) *Callitris gracilis* germinates poorly in hot or dry conditions restricting germination to cooler and wetter conditions. Based on our results, *A. ligulata* would be the most widely applicable species for direct seeding work based on generalist germination habits. *Callitris gracilis* appears to do well if planted in cool, wet conditions where the species prefers to germinate but would be intolerant to warm-weather planting. The ideal planting time for a mixed species planting based on germination requirements would be mid-autumn, as that is when temperature and moisture levels would be optimal for germination.

Key words: germination, Mallee, restoration, seed ecology, temperature effect, water potential

Implications for Practice

- Mid-autumn was identified as the optimal time for planting the selected species in the north-west Victorian Mallee region, based on germination temperature and water potential effects.
- Smaller seeded species, such as *Eucalyptus* and *Melaleuca*, may have more of a preference for warmer planting seasons than the larger-seeded species, such as *Acacia* and *Callitris*.
- *Acacia ligulata* was identified as the best candidate for large-scale restoration work due to its generalist germination habits, which included its ability to germinate over a wide range of temperatures.

Introduction

Arid and semiarid environments are Australia's largest habitat type, covering roughly 75% of the continent (Bowler 1976) and encompassing a wide range of vegetation types and endemic species (Byrne et al. 2008; Morton et al. 2011). In recent times, these environments have become increasingly degraded through human activities such as widespread land clearance (Allison et al. 1990), increased salinity brought on by removing native vegetation (George et al. 1997), introduction of exotic weeds (Clarke et al. 2005), and overgrazing by livestock and feral herbivores (Munro et al. 2009; Finlayson et al. 2021). In response to the problems caused by this degraded state, revegetation

Author contributions: JS conceived and developed the first draft; all authors made equal contributions to the material covered and the discussion of all topics in subsequent drafts.

[1]The Future Regions Research Centre, School of Science, Psychology and Sport, Federation University Australia, Mount Helen, Victoria 3350, Australia
[2]Address correspondence to J. Stapleton, email joseph.stapleton@federation.edu.au
[3]School of Molecular and Life Sciences, Curtin University, Bentley, Western Australia 6102, Australia
[4]Greening Australia, Level 3, 349 Collins Street, Melbourne, Victoria 3000, Australia
[5]Applied Chemistry and Environmental Science School of Science, STEM College, RMIT University, 124 La Trobe Street, Melbourne, Victoria 3000, Australia

© *2024 The Author(s).* Restoration Ecology *published by Wiley Periodicals LLC on behalf of Society for Ecological Restoration.*
This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
doi: 10.1111/rec.14220
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.14220/suppinfo

programs have been set up that aim to restore native vegetation to the landscape to improve ecosystem resilience (Mallee Catchment Management Authority 2008; Xu et al. 2023). One of the methods used to achieve this restoration outcome is direct seeding, in which seeds are mechanically sown into the soil and are left to germinate and grow without further treatment. This method is significantly cheaper and easier to apply over large areas than the transplanting of previously germinated seedlings (Pérez et al. 2019), which is an important consideration in arid areas due to the vast scales that often need to be revegetated (Kildisheva et al. 2016). However, this method suffers from the drawback of low and erratic emergence rates, higher mortality frequencies, and the subsequent economic loss of seeds and labor as a result of these failures (Azam et al. 2012; Pérez et al. 2019). In addition, direct seeding works are also more strongly dependent on rainfall during the project period (Figueiredo et al. 2021), making it necessary to estimate the right season for planting, having an optimum seeding window for favorable soil moisture and temperature conditions to promote germination. Thus, one way to improve restoration outcomes and get optimum benefit is to more clearly understand the germination biology of the species being used, which will allow the matching of their traits to the environmental conditions of the chosen planting season (Dalziell et al. 2022).

In this investigation, "germination biology" refers to a study of the attributes that govern the time and conditions for seeds to germinate, and despite this being an obviously important factor for understanding plant revegetation, it is an area often understudied in the field of restoration ecology (Jiménez-Alfaro et al. 2016). Arid and semiarid zone plants, in particular, have evolved a number of adaptations for germinating in water-stressed environments. For example, arid zone plants will often germinate during rare periods of rainfall, during which their desired germination environment will be closely related to the current climate conditions (Bell 1999). In order to wait for these rain events, many plants possess physical seed dormancy, which is a common strategy for species establishing in many arid ecosystems as it allows plants to survive harsh conditions and germinate when the environment is more favorable (Poschlod et al. 2013). Dormancy is often used in bet-hedging strategies, where seeds reduce the risk of mass germination failure in a single season by delaying germination in stages across multiple seasons (Tielbörger et al. 2012). Increased seed longevity is also commonly associated with these tactics, as it allows the seeds greater time to wait for germination conditions to improve, which may take months, if not years, to occur (Duncan et al. 2019).

Alternatively, among many of Australia's dominant woody taxa, seed dormancy is often replaced by rapid germination and high seed production. Instead of waiting out dry periods, some of these plants can produce high numbers of seeds at a relatively consistent rate, ensuring that there are always seeds in the soil that are ready to germinate once sufficient rainfall arrives (Commander et al. 2017; Duncan et al. 2019). These seeds are typically small and have a shorter viability duration in the soil when compared to larger-seeded species (Moles et al. 2003). They also often have wider temperature and water-stress tolerances than dormant species, allowing them to germinate in a wider range of conditions when moisture becomes temporarily available (Merino-Martín et al. 2017; Duncan et al. 2019*a*). While this strategy means that many of the seedlings die off after germinating, the high seed production offsets this impact and provides dominance for these species in Australia's woody arid areas. Indeed, this strategy may be the most preferred option in areas with unpredictable rainfall (Duncan et al. 2019, 2019).

This study investigated the seed germination biology of four different semiarid zone taxa and considered how these results may be applied to guiding future direct seeding work in the field. Given the high mortality rate of direct seeding, selecting the right conditions and species for direct seeding is of high priority (Araujo & Pérez 2023), and this study was designed to help determine these selection details. In particular, we examined how seeds respond to changes in temperature and water stress and how this could be related to planting times, noting whether any other assistance may be required to enhance seedling emergence and survival success. Seed response to light conditions was also used to determine whether tilling would be beneficial for these species. We hypothesized that the species' reaction to temperature and water stress would be determined by their morphology, with small-seeded species being quicker to germinate and more resistant to water stress than larger-seeded species or species with physical seed dormancy (Norden et al. 2009; Duncan et al. 2019).

Methods

Seed Selection

Seeds were provided by Greening Australia from their wide stock of arid zone species. All species selected for experimentation are native to the Mallee communities of north-west Victoria, which roughly correspond to the Lowan Mallee, Murray Mallee, and Wimmera regions. This area is characterized by a semiarid climate with hot summers and mild winters (Fig. 1), with rainfall conditions varying across the region from less than 250 to 450 mm per year (White 2006). Rainfall is generally highest during winter and spring (Fig. 1), though rainfall can be highly variable throughout the year.

The landforms in this region mostly comprise gently undulating sand plains, together with dune fields with relict streamlines. Soils are typically sandy loams to clay loams, which are nutrient poor. The Mallee vegetation canopy is usually dominated by low-growing, multi-stemmed *Eucalypt* species, although other tree or shrub species, including *Callitris* and *Melaleuca* species, may often dominate. Common canopy species include *Eucalyptus socialis*, *E. incrassata*, *E. dumosa*, and *Callitris gracilis*. The understory is typically composed of Heathy shrubs (e.g. *Leptospermum* spp.), Hummock or Tussock grasses (e.g. *Triodia* spp.), Chenopods (*Atriplex* spp.) or Broombush shrubs (e.g. *Melaleuca* spp.) (White 2006).

Species were selected for testing in this investigation based on the following criteria:

- If a relevant species (i.e. recorded from the north-west Mallee country) had low or no germination data recorded in the scientific literature, it was considered a high priority so that knowledge gaps on seed biology could be addressed.

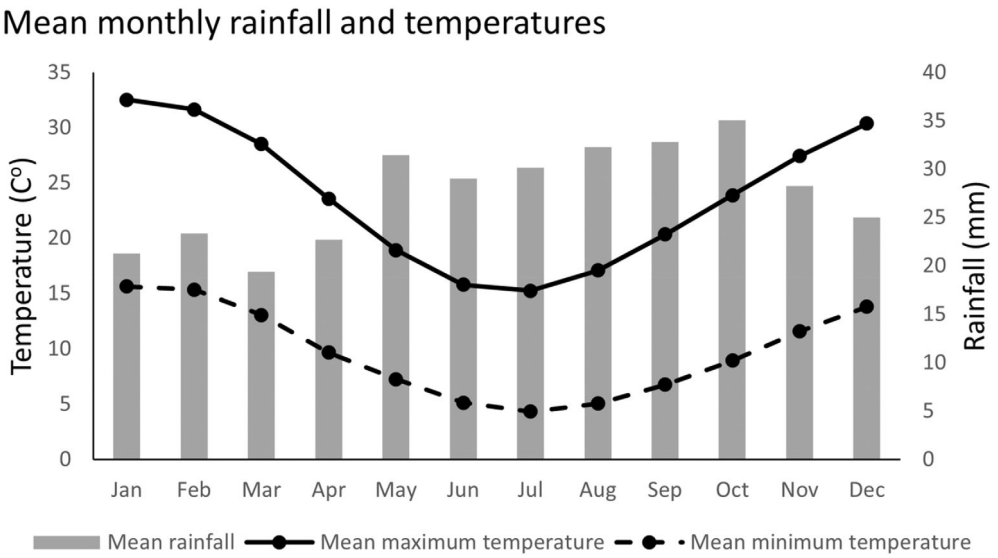


Figure 1. Mean monthly maximum and minimum temperatures from 1938 to 2022 and mean monthly rainfall from 1913 to 2022 for the Ouyen area. This area was chosen as representative of the seed collection locations. Climate data were obtained from the Ouyen (Post Office) Bureau of Meteorology (BOM) station number: 076047, Lat: −35.07°S and Lon: 142.31°E (Bureau of Meteorology 2023.

- If a species formed a dominant part of the vegetation structure, it was ranked higher as it was considered more desirable for revegetation.
- If a species was widely distributed, it was ranked higher as it could be used in a greater number of revegetation projects.
- Species that were difficult to establish in the field were also ranked higher, as information on the seed biology of these species would be useful for future revegetation work.
- Chosen species were taxonomically diverse (representing different genera), in order to provide a broader taxonomic pool.

Based on a full consideration of the above criteria, four species were selected for this study, which were *Eucalyptus calycogona* Turcz., *Melaleuca lanceolata* Otto, *Acacia ligulata* Benth. and *Callitris gracilis* R.Baker.

Seed Quality Check

Prior to testing, the quality of each seed batch was assessed using the methods outlined by Frischie et al. (2020). Firstly, a purity test was performed by separating the seeds from other inert material and determining the amount of seed as a percentage weight for each batch of seeds. Next, a viability assessment was undertaken, using a cut test to open up the seed with a scalpel in order to examine the endosperm/embryo under a binocular microscope. If the seed's endosperm and embryo were white, turgid, and solid, then the seed was considered intact and potentially viable. Due to *C. gracilis* batches being smaller than the other species, multiple *C. gracilis* batches were required over the course of the investigation, with each batch independently tested for seed quality.

Germination Response under Different Temperature Regimes

Prior to being plated, seeds were cleaned in a diluted hypochlorite solution for 3 minutes, then drained through a fine sieve and washed with distilled water. A 1% (v/v) hypochlorite solution was used for small seeds (*E. calycogona* and *M. lanceolata*), and a 4% solution was used for larger seeds (*A. ligulata* and *C. gracilis*). *Acacia ligulata* was the only species with seed dormancy and hence had their dormancy broken prior to plating by placing them in recently boiled (>90°C) water for 1 minute (Erickson et al. 2016).

Optimum germination temperature methodology was based on that used by Duncan et al. (2019), with four replicates of 25 seeds per temperature regime used for each species. An exception to this was *C. gracilis*, due to it having a lower number of seeds in the batch compared to the other species. In this latter case, only 15 seeds were used for each replicate. Seeds were placed in a 90 × 15.8 mm Westlab Petri dish on Whatman filter paper moistened with sterilized distilled water. A dark trial was also set up by following the same methodology but having the Petri dishes covered with aluminum foil to exclude all light. Dishes were placed in incubation cabinets with a 12/12-hour light/dark cycle, with the cabinets being set to temperature regimes of 30/20, 25/15, and 17/7°C. Seeds were checked every Monday, Wednesday, and Friday of each week for germination, and germination was recorded as the first emergence (>2 mm) of the seed radicle. Filter paper was also rehydrated at each check if necessary. Seeds which were growing mold were removed at each check, and the remaining seeds were replated onto a fresh Petri dish if necessary. Petri dishes that were part of the dark treatment were checked under a green light in line with the monitoring regime for the light-exposed seeds. Seeds were monitored for 30 days, and if they were still germinating within a week of the 30-day cut-off mark, they were monitored for a

further 15 days or until germination had ceased for a week. Once monitoring had concluded, a 1% (w/v) tetrazolium test was performed on ungerminated seeds to determine if any of them were still viable but had not germinated (Lakon 1949).

Germination Response Under Different Water Potentials

To test for the effect of water stress on germination, polyethylene glycol (PEG) 8000 solutions were constructed along a water potential gradient designated as 0, −0.2, −0.4, −0.6, −0.8, −1.0, and −1.5 MPa. The solutions were made by mixing different amounts of PEG (g/mL) with 100 mL of distilled water (Table 1), with the weights being used based on the calculations made by Michel (1983). The 0 MPa treatment consisted of pure distilled water.

Seeds were placed in a Petri dish on sterilized filter paper that had been moistened with 2.5 mL of the relevant PEG solution and then tightly sealed with cling film to reduce evaporation. Seeds were then placed in Thermoline Scientific model TRISLH-495-1-SD incubation cabinets using a light/dark regime. *Eucalyptus calycogona* and *M. lanceolata* seeds were placed in a 30/20°C cabinet, and *A. ligulata* and *C. gracilis* seeds were placed in a 25/15°C cabinet based on results from the first temperature experiment. As with the temperature regime experiment, seeds were checked every Monday, Wednesday, and Friday for germination. To avoid mold growth, each week the seeds were transferred onto a freshly sterilized Petri dish and sterilized filter paper soaked with the appropriate PEG solution. Seeds were monitored for 45 days. After this monitoring period, ungerminated seeds were placed on filter paper moistened with distilled water and monitored for a further 30 days, or until germination had stopped for a week, to determine which seeds were still viable. After the monitoring period, a 1% (w/v) Tetrazolium test (as previously described) was performed on any remaining seeds as a final viability check to check what proportion of the remaining seeds were viable.

Data Analysis

Response to Germination Temperature. All data analysis was conducted using R, version 4.2.3 (R Core Team 2023). For optimum germination analysis, the GerminaR package constructed by Lozano-Isla et al. (2019) was used to calculate the level of germinability (GRP) and the mean germination time (MGT) for each species across different temperatures and light regimes. In this investigation, the term GRP refers to the percentage of viable seeds that completed germination and was calculated using:

$$\mathrm{GRP} = \left(\frac{\sum_{i=1}^{k} n_1}{N} \right) \times 100$$

MGT refers to the number of seeds germinated at the time of evaluation, and was calculated using:

$$\mathrm{MGT} = \frac{\sum_{i=1}^{k} n_i t_i}{\sum_{i=1}^{k} n_1}$$

where n_i is the number of seeds germinated at the i-th time, k is the last day of evaluation, N is the total number of seeds in each replicate, and t_i is the time from the beginning of the experiment until the i-th observation (Lozano-Isla et al. 2019).

Once GRP and MGT are calculated, a Kruskal–Wallis test is used to assess significant differences between alternative light and temperature regimes. The Kruskal–Wallis test was chosen over a one-way analysis of variance due to its property of being able to handle non-normal data, since many of the GRP and MGT scores were non-normally distributed. The light regime was tested for significance, followed by the temperature regime. A Dunn test was then used to make pairwise comparisons between the different regimes. A cumulative analysis of germination was also performed by modeling the percentage of seeds germinated by day for each of the temperature regimes (Lozano-Isla et al. 2019).

Response to Water Potential. For water potential analysis, the R packages *drcte* and *drcSeedGerm*, developed by Onofri et al. (2022), were used. Hydro-time-to-event models were created to model the germination proportion of seeds at different water potentials. Multiple hydro-time-to-event models were created using different cumulative distribution functions. The distribution functions used were log-logistic (Onofri et al. 2018), Gaussian (Bradford 2002), logistic, Gumbel, and Weibull (Mesgaran et al. 2013). Full equations can be found in Supplement S1.

After each model was constructed, Akaike's information criterion was used to determine which model provided the best fit. The best fitting model was applied to the data, and results were inspected via graphical display and through the base water potential, which refers to the predicted lowest water potential at which a seed can germinate.

Table 1. Weights of polyethylene glycol used to form the water potential gradient.

	17/7°C	*25/15°C*	*30/20°C*
MPa	*g PEG/100 mL*	*g PEG/100 mL*	*g PEG/100 mL*
−0.2	11.17	11.60	11.89
−0.4	16.39	17.05	17.50
−0.6	20.40	21.24	21.81
−0.8	23.79	24.77	25.46
−1.0	26.78	27.89	28.66
−1.5	33.14	34.53	35.50

Results

Seed Quality

Eucalyptus calycogona, *Melaleuca lanceolata*, and *Acacia ligulata* showed high levels of viability of about 90% within their

batches (Table 2). *Callitris gracilis* viability was much lower than that of the other species, and this observation, combined with the smaller size of the batches in which *C. gracilis* were delivered, forced multiple batches to be used throughout the experiment. Batches 1 and 2, with an average of 32.5% viability, were used for the germination temperature experiment, while batches 3 and 4, with an average of 33.3% viability, were used for the water potential experiment. Overall, the batches of *C. gracilis* averaged 32.9% viability.

GRP Response to Light and Temperature Regime

There was no significant effect of the light regime on the GRP among any of the species tested (Table S1; Fig. 2), and there was also no significant effect observed for the incubation temperature on the GRP for *E. calycogona* and *A. ligulata*. However, there were significant effects for *M. lanceolata* and *C. gracilis* (Table S2). There was no germination of *C. gracilis* seeds exposed to the 30/20°C regime, and among the remaining regimes, there was no significant difference between the 25/15 and 17/7°C regime, although 25/15°C did, overall, produce a higher proportion of germinating seeds. *Melaleuca lanceolata* seeds showed a significant difference in GRP between 30/20 and 17/7°C, with the latter producing a lower number of germinating seeds. There was no significant difference between 25/15 and 17/7°C or between 30/20 and 25/15°C, although there was a trend for 30/20°C to have a higher overall GRP and for 17/7°C to have a lower GRP. While there was no significant difference between regimes for *E. calycogona* and *A. ligulata*, there was a trend for the seeds under the 17/7°C regime to have lower germination for *E. calycogona* and for *A. ligulata* seeds in the 25/15°C regime to have a slightly higher GRP than the other two regimes. The 30/20°C range had the most variable GRP values.

The median for most species was lower than the original seed viability value, with the exception of *E. calycogona* and the light and 25/15°C treatments of *C. gracilis*. *Melaleuca lanceolata* was also notable for often having a median value that was much lower than the original viability of 89% (Table 2), this being most pronounced in the 17/7°C treatment (Fig. 2H), where the median is around 50%.

MGT Response to Light and Temperature Regime

There was no significant effect of light regime on the MGT of *E. calycogona*, *M. lanceolata*, and *A. ligulata*, although there was a near significant effect ($p = 0.0735$) on the *M. lanceolata* seeds, with seeds being slightly faster germinating in the light regime. There was another near-significant effect ($p = 0.0848$) in *A. ligulata*, with dark being slightly faster (Table S3; Fig. 3). The effect of the light regime was most notable in *C. gracilis*, with seeds being significantly faster at germinating under light conditions.

Among the different temperature regimes, there was no significant effect on MGT for *A. ligulata* and *C. gracilis* other than a lack of *C. gracilis* seeds germinating in the 30/20°C regime (Table S4; Fig. 3). There was a near significant effect ($p = 0.0518$) for *A. ligulata* between 30/20 and 25/15°C, with 30/20°C being the slowest germinating regime. The effect of temperature was more pronounced in *E. calycogona*, with the MGT being different between all the temperature regimes. Germination was quickest in the 30/20°C regime and the slowest in the 17/7°C regime. *Melaleuca lanceolata* seeds in the 17/7°C range were significantly slower germinators than in the other two regimes, although there was no significant difference in MGT between 30/20 and 25/15°C.

Table 2. Viability assessment of seed batches using a cut test followed by a tetrazolium test.

Species/batch	*Proportion of viable seeds (%)*
Acacia ligulata	93.0
Callitris gracilis (batch 1)	33.3
C. gracilis (batch 2)	31.7
C. gracilis (batch 3)	26.7
C. gracilis (batch 4)	40.0
Eucalyptus calycogona	92.0
Melaleuca lanceolata	89.0

Germination Response to Different Water Potentials

Results showed a significant effect of water potential on germination for all species (Tables 3 & S5–S8) All species declined in germination percentage and rate as the water potential lowered, although all species other than *C. gracilis* had a few seedlings in the lowest (1.5 MPa) water potential (Fig. S1). Overall, germination percentage decreased in line with lowering water potential.

Although all species showed a trend toward decreasing germination with decreasing water potential, the species showed a difference in individual levels of resistance. *Melaleuca lanceolata* showed the highest base water potential values (Table 3) with around 15% germination still being recorded in some Petri dishes under −1.5 MPa. This indicated that the species, overall, may be most resistant to germination under moisture limited conditions. *Callitris gracilis* showed the lowest base water potential value, with no germination recorded at −1 and −1.5 MPa. *Eucalyptus calycogona* and *M. lanceolata* had overall higher germination percentage and rates compared to *A. ligulata* and *C. gracilis*.

Discussion

The study found variable effects of the different germination conditions on the plant species studied, though some general trends were found. Light regime was found to have no effect on the germination percentage and rate of most species; similar results were also reported by Beveridge et al. (2024), who found that light conditions had no effect on the germination of sub-tropical Australian plant species. An exception to this was the germination speed of *Callitris gracilis*, which germinated more rapidly under light conditions. This may indicate that the species prefers not to be buried when germinating, though follow-up seed burial studies (J. Stapleton unpublished results) indicate that seeds exposed to the topsoil germinate poorly compared to seeds placed within the soil, likely due to being more

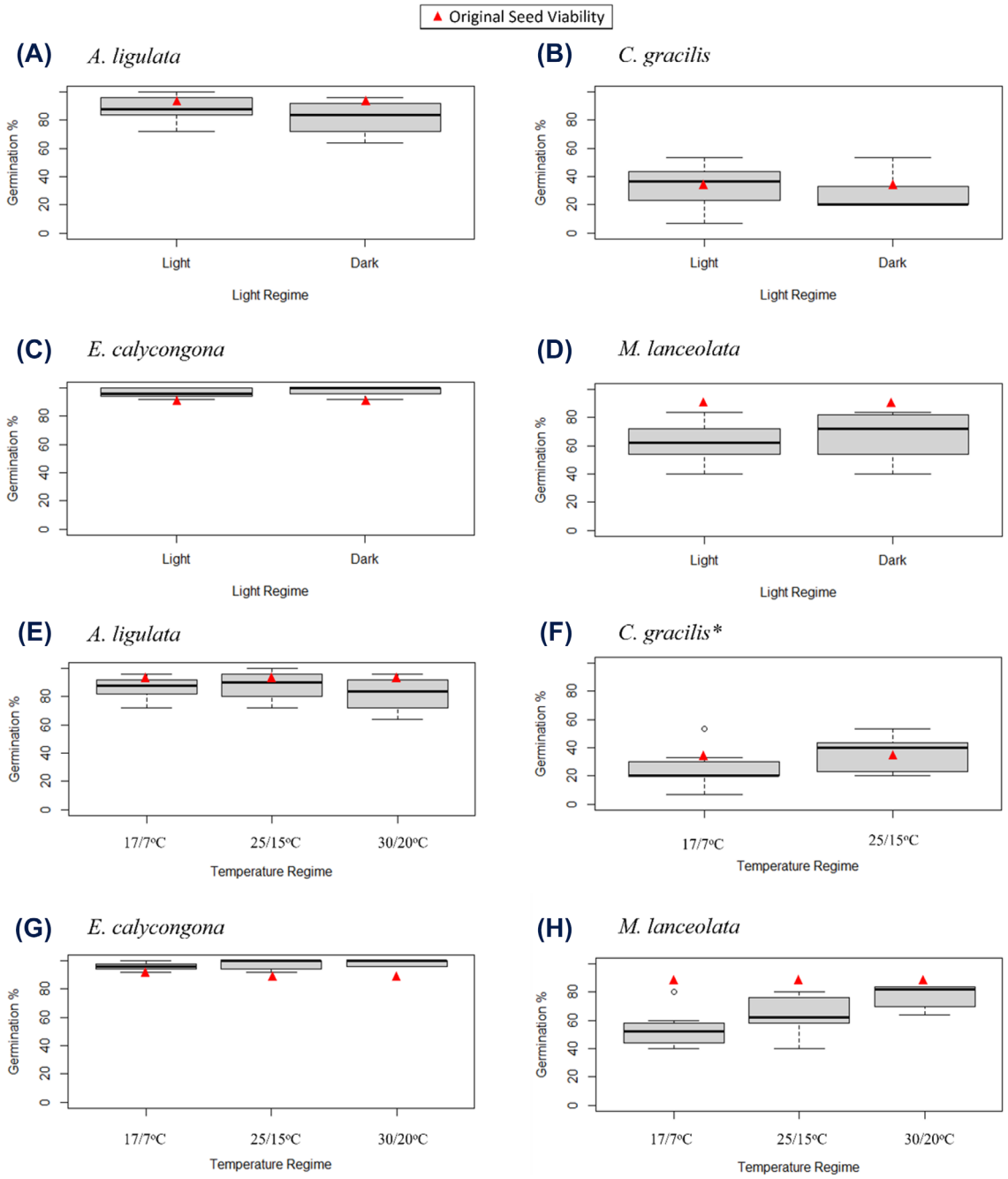


Figure 2. Seed GRP (mean ± SE) for *Acacia ligulata*, *Callitris gracilis*, *Eucalyptus calycongona*, and *Melaleuca lanceolata* across different light (A–D) and temperature (E–H) regimes with original seed viability % shown (red triangle represents that there was no germination under the 30/20°C regime, so this was not included in the analysis).

exposed to temperature change and desiccation (Turner et al. 2006). The reasons for these conflicting results may be due to Petri dishes having tightly controlled environmental conditions, while work involving soil introduces other factors that influence germination, such as interactions with soil microbes (El-Keblawy et al. 2018).

While the effect of temperature on germination varied between species, overall, it was found that the 25/15°C regime produced the best results for germination percentage and rate across all the species. In general, it was found that the smaller seeded species responded better to the warmer temperature regimes. Likewise, the smaller seeds also seemed to respond most negatively to the lowest temperature regime, particularly with regard to rate of germination.

Overall, *Melaleuca lanceolata* was the most resilient to dry conditions in the study, while *C. gracilis* was the least tolerant.

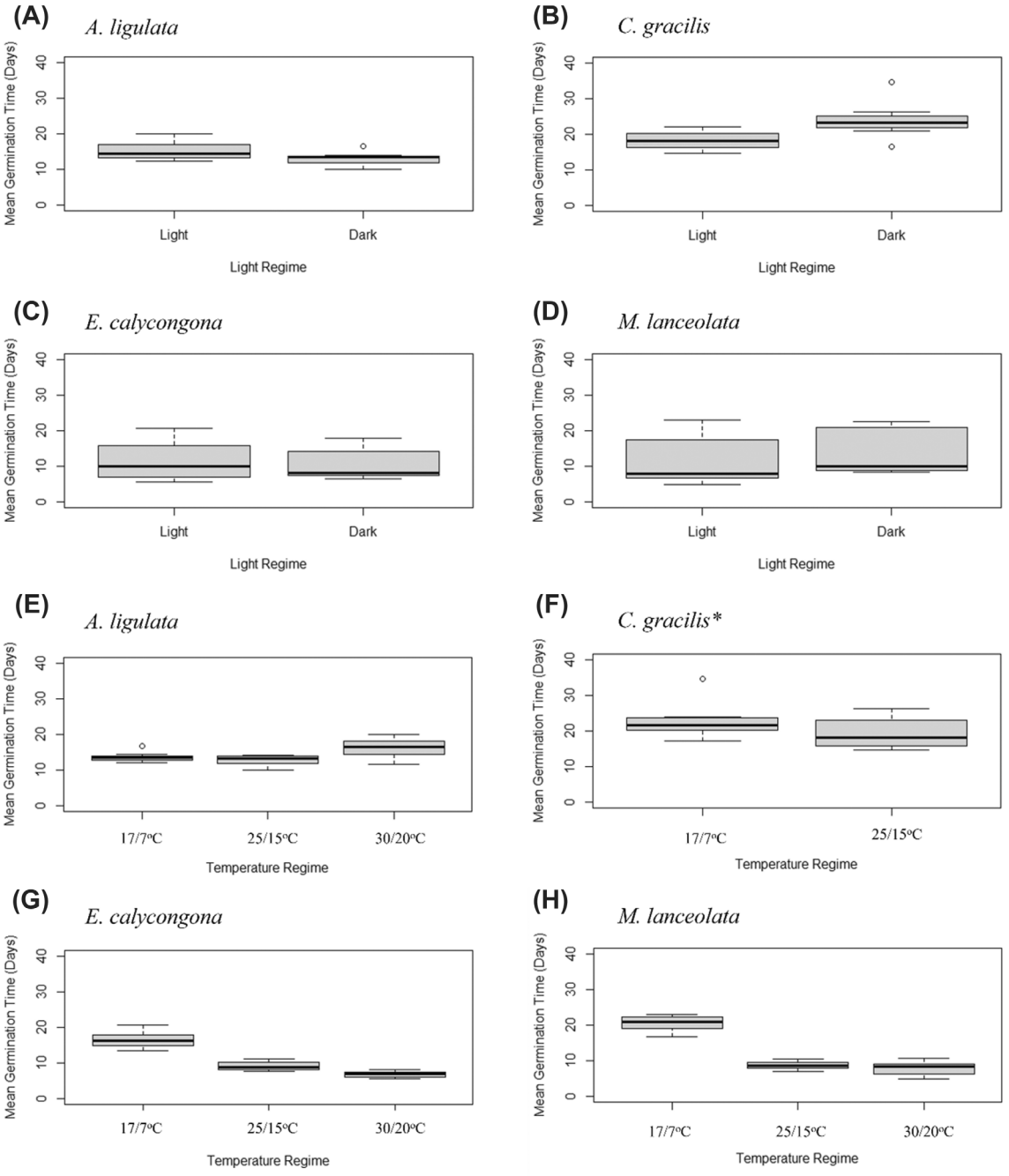


Figure 3. Seed MGT (mean ± SE) for *Acacia ligulata*, *Callitris gracilis*, *Eucalyptus calycogona*, and *Melaleuca lanceolata* across different light (A–D) and temperature (E–H) regimes (red triangle represents that there was no germination under the 30/20°C regime, so this was not included in the analysis).

Table 3. Mean or median base water potential values for each species depending on the distribution selected either the mean or median value was used for determining water potentials.

Species (mean or median)	*Base water potential value*	*SE*	t *value*	*Pr(*>t*)*
Acacia ligulata (mean)	−0.70	0.0038	−182.54	<2e−16
Callitris gracilis (median)	−0.64	0.0460	−13.97	<2e−16
Eucalyptus calycogona (median)	−0.88	0.0240	−36.76	<2.2e−16
Melaleuca lanceolata (median)	−1.19	0.0079	−151.07	<2e−16

Nonetheless, the fact that all species, other than *C. gracilis*, were able to germinate even at −1.5 MPa suggests that these species have a surprisingly high tolerance to dry conditions. As with temperature, the smaller seeded species (*Eucalyptus calycogona* and *M. lanceolata*) appeared to be overall more resistant to dry conditions than the larger seeds, which coincides with a similar result found by (Beveridge et al. 2024), who found that smaller seeded species were more tolerant to water stress. A study by Merino-Martín et al. (2017), which also tested species from a semiarid climate, found somewhat similar results between seed sizes under water stress, both in terms of overall germination percentage and germination rate, with the smaller seeds germinating faster. However, an exception to this was with the *Melaleuca* species *M. nematophylla*, which was found to perform poorly under water stress. It is unknown why the two species, *M. nematophylla* and *M. lanceolata*, differ in water tolerance since *M. nematophylla* occupies a similar climate and habit to *M. lanceolata* with both occurring in semiarid sandy habitats, suggesting environmental effects can be ruled out. It is possible that these two species have different levels of natural tolerance to water stress.

Variation of Seed Germination Strategies Across Species

The results of this study highlight the different germination strategies that semiarid species may employ. Among the four species tested, three germination strategies can be identified. These are: (1) quick germination under high temperature and high rainfall conditions for the small-seeded Myrtaceae species (*E. calycogona* and *M. lanceolata*); (2) the ability to tolerate and germinate in a wide array of conditions (*Acacia ligulata*); and (3) delaying of germination until wetter and cooler conditions arise (*C. gracilis*).

Acacia ligulata seeds are notable for being the only seeds in the study to have seed dormancy. The dormancy-breaking conditions for *A. ligulata* are varied, and include ingestion by birds and scarification by fire, which allows the plants to bet-hedge their germination across different conditions (Letnic et al. 2000). Being able to germinate under a wide variety of temperature and moisture levels once dormancy is broken is likely to assist the plants in this generalist approach by allowing them to take advantage of dormancy-breaking events as they occur under variable environmental conditions. Other features of *A. ligulata* ecology, such as being dispersed over long distances by animals (Letnic et al. 2000; Whitney 2002), its ability to colonize recently disturbed environments (Onans & Parsons 1980), its persistent seedbank allowing it to germinate at any time of year over several years after dispersal (Auld 1995*b*), and its wide distribution across Australia's arid areas, may also be facilitated by its ability to establish under a range of variable temperatures.

The two small-seeded Myrtaceae species, *E. calycogona* and *M. lanceolata*, showed a preference for germinating quickly under high temperatures. In *M. lanceolata*, this was also combined with a higher germination percentage at warmer temperatures. This suggests that these plants may prefer to germinate during the warmer months after rainfall events, during which they can quickly become established. Rapid germination is most likely a response to sporadic rainfall conditions, which is a feature of much of Australia's arid areas, allowing the plants to take advantage of these transient events when they occur (Duncan et al. 2019). The ability to still germinate under low water potentials may also help with this tactic, as evaporation rates would be higher at these times of the year, making the soil dry out much quicker than in cooler months (Dalziell et al. 2022). Notably, the *E. calycogona* germination rate, although slower at lower temperatures, had a similar germination percentage across all temperature regimes, indicating it may possess more of a generalist germination ecology, similar to *A. ligulata*. These germination strategies can be risky, as high temperatures and low moisture, which are more prevalent in warmer months, are common causes of plant death in arid areas (Houston 2006; Huang et al. 2019). However, this can be partly offset by producing higher quantities of seed than with larger-seeded species. Related *Eucalyptus* and *Melaleuca* species have been found to produce large numbers of small seeds, which are usually released steadily at low levels throughout the year, with marked periods of mass release after events such as fires (Rayachhetry et al. 1998; Booth 2017); it is assumed that the study species show similar seed-production strategies. These small-seeded species put significantly less energy into producing each seed, and hence there is less investment loss from germination failure, which makes allowance for involving risky strategies (Moles et al. 2003; Duncan et al. 2019). It is noted, however, that not all small-seeded species will be tolerant of dry conditions, even within the same genera, with other *Melaleuca* species being found to be less tolerant to water stress (Merino-Martín et al. 2017). It is, therefore, important to consider each species' water stress tolerance on a case-by-case basis. Another point of note was that *M. lanceolata* seeds tended to germinate at much lower percentages than their original seed viability test. It was observed that these seeds had a greater tendency to lose viability through rot or mold during the experiment, with the effect being most obvious at the lower temperatures. This may suggest that *M. lanceolata* seeds are more vulnerable to disease and other environmental factors than other species. Previous studies have found that other *Melaleuca* species are only viable in the environment for a short amount of time and, overall, experience poor viability (Rayachhetry et al. 1998; Robinson et al. 2006). As previously suggested, this may be offset again by their high seed production rates.

Compared to the other species, *C. gracilis* had a narrower temperature range for germination, with no seeds germinating in the hottest temperature regime. In addition, this species also seemed less tolerant of low water potentials. *Callitris gracilis* is also slower germinating than the other species with at least 10 days passing before germination commenced. These features are indicative of a risk-adverse or bet-hedging strategy, with this species likely delaying germination until desired periods of cool, wet weather, which are more beneficial for early seedling survival (Duncan et al. 2019). The preference for low temperatures has also been found by Carr et al. (2007), which found that the species did best when sown in autumn or winter. Another report by Adams (1999) on two closely related *Callitris* species also

found similar results in that the seeds were intolerant of low water potentials and germinated best at cool temperatures of 16–20°C with germination inhibited above 20°C. The author also suggests an autumn planting time for these species.

Application to Revegetation Works

Acacia ligulata showed no strong preference for germination temperature and was relatively resistant to high water stress. The species can therefore be planted during most times of the year and, as long as conditions are not extremely dry and the seeds have been pre-treated to break dormancy, the seeds will be able to germinate at an acceptable rate once sufficient soil moisture is present. This high tolerance to different environmental conditions and its natural tendency to grow in disturbed environments (Onans & Parsons 1980), makes *A. ligulata* ideal for early revegetation efforts in cleared areas where temperature and moisture are not moderated by surrounding vegetation. *Eucalyptus calycogona* similarly shows no strong preference for temperature in regard to overall germination proportion, although it is significantly slower at germinating at lower temperatures. Avoiding winter plantings with this species may be preferable, as eucalypt seed viability can decline quickly in soil (Florentine & Fox 2002), and it is therefore best to choose conditions where these seeds will germinate rapidly, such as immediately prior to the wet season. *Melaleuca lanceolata* also shows an intolerance to low temperatures, with both germination proportion and speed declining with a lower temperature. As with eucalypts, the seeds of the *Melaleuca* species are only viable in the environment for a short period of time (Robinson et al. 2006), making the choice of sowing times where germination will likely be rapid, a priority. It is recommended that winter sowing avoids the use of *M. lanceolata* seeds, with this species instead being seeded during warmer periods and preferably during periods of high soil moisture. *Callitris gracilis*, on the other hand, is completely intolerant of high temperatures and more sensitive to low moisture levels than the other species. It is therefore highly recommended that this species not be sown during the later months when temperatures are increasing, as the heat would suppress seed germination. The species is naturally slow germinating so periods where moisture is likely to stay higher in the soil for an extended time would be preferable, as the seeds may sit in the soil for a period before emerging. Unlike *E. calycogona* and *M. lanceolata*, *C. gracilis* seeds are large and covered in a protective seed coat, thus mortality in the soil bank is likely to be initially lower (Moles et al. 2003).

Given *C. gracilis'* apparent sensitivity to water stress, projects using this species may want to involve water-retaining methods to increase moisture levels and germination. One of the simplest methods is ensuring that direct-seeding projects position the seeds within the furrows where the microclimate is cooler and moister (Hernández & Pérez 2023). Other possible methods include the use of materials that may improve soil water retention, such as hydrogels (Wei et al. 2016) or soil microbial inoculants (Azizi et al. 2022). These materials should be able to be added using the same direct seeding machinery used to place seeds. It is likely that the practicality of this approach will depend on project budgets, and future studies will be needed to see whether the materials are beneficial to direct seeding work. While irrigation is another possibility to supply water directly to seedlings, the high cost of installing irrigation and the significant distances from water sources of many planting sites may rule this out as a possibility in most projects, except for niche situations such as small sites near existing infrastructure or when working with threatened plant species (Josa et al. 2012).

Based on this analysis, temperatures of around 25–15°C would produce the best overall results for all species used in the study. These temperatures roughly correspond to mid-autumn (April) and late spring (October to November) in the study area. Late spring, in particular, also coincides with the highest average rainfall for the region. However, given that evaporation rates will likely be higher at this time of year and that the following summer period has the lowest average rainfall and highest temperatures, it would be preferable to plant during mid-autumn, since late autumn and winter are wetter than summer. Given that all species showed preference for germinating at higher water potentials, choosing the wetter times of year for planting is essential. It should also be noted that some woody Mallee species, such as *Acacia* and *Eucalyptus*, have seed release and/or germination triggered by fires (Wellington & Noble 1985; Letnic et al. 2000), which commonly occur during the warm dry summer months. This may mean that germination in natural settings is more constrained to the summer and autumn months following summer fires. Since many of the plants differ in their optimum germination conditions, it might be worth planting different species at different times to maximize success rates. In this respect, *E. calycogona* and *M. lanceolata* prefer to be planted during warmer times, such as March or November, where they can germinate rapidly, while *C. gracilis* would do better in cooler and wetter times, such as May or August to October, where they can germinate slowly while the soil remains cool and relatively moist. Although this is the ideal situation, it is recognized that this may not be possible given the budget constraints to which many revegetation projects are subject (Ewing et al. 2013; Copeland et al. 2018). Another possible option is to delay the germination of seeds through the application of synthetic seed coats so that seeds begin germination during the desired temperature regime (Madsen et al. 2016). This approach would add further costs to planting; thus, the technique requires further study before its suitability can be unequivocally determined (Pedrini et al. 2020).

Overall, *A. ligulata* appears to be the preferred choice of species to be used in direct seeding projects due to its wide temperature and water stress tolerance, meaning that, as long as seed dormancy is broken before planting, this species should be able to germinate in a variety of situations at a relatively high rate. *Eucalyptus calycogona* is also highly recommended for similar reasons but should be planted around warmer times of the year to allow for quicker seed germination. *Melaleuca lanceolata* may also be a good choice for warm season plantings, but its low seed viability and high seed vulnerability may impact its performance negatively. This species may be more successful

if initially germinated in a plant nursery for the production of greenstock, then subsequently transplanted into the field. *Callitris gracilis* has the potential to establish itself in field settings so long as it is seeded during cooler times of the year and, preferably, during years forecasted to have higher rainfall. Outside of these times, the species may be better off being first grown in a nursery as greenstock before being transplanted into the field or alternatively sown in situ with some water-retaining techniques.

Limitations of Research

The results of these studies are clearly limited to the species analyzed, and thus caution should be used when applying these findings directly to other species. There will likely be some similar germination habits among closely related species, it was noted that the results did confirm some trends found among species of the same genus and seeds of similar morphology. Therefore, it may be possible to extract information from the biology of the studied species and apply them to similar species, such as the preference of *Callitris gracilis* for cooler temperatures (Carr et al. 2007). However, it is recommended that information on individual species should be determined before extensive planting.

While this study solely looked into the effects of temperature and soil moisture on germination, in the field there will be a number of other factors at play that will also influence whether seedlings are able to germinate. Examples include soil type (Hallett et al. 2014), competition from other plants, particularly weeds (Clarke et al. 2005), and the individual microclimates of the soil in which seeds are planted (Lozano et al. 2017), which can also have a large influence on germination and emergence. It is also worth noting that Australia tends to have highly erratic rainfall patterns over much of the continent (Morton et al. 2011), so planting in a particular season, based on annual averages, still may not produce the desired soil moisture as rainfall conditions can change greatly from year to year and from season to season.

The experiments performed were exclusively laboratory-based, using Petri dishes and seed incubators under highly controlled conditions. Although these studies can be useful as an indicator of what may happen in the field, it is not an infallible comparison, as the range of aforementioned unexpected conditions in the field may interact with seed biology to produce a range of different results (Ronnenberg et al. 2008). Further field testing will be required to determine whether the results found in this study translate into performance in the field.

Although germination is an important factor in revegetation efforts, it should be kept in mind that once a seed germinates, it will not necessarily survive. Emergence of a seed post-germination and survival of an emerged seedling are also important bottlenecks in arid revegetation (James et al. 2011; Hallett et al. 2014) and other strategies may be needed to overcome these separate issues. Emergence from the soil post-germination, for example, can be restricted by factors such as high temperatures and a lack of adequate soil moisture (Muñoz-Rojas et al. 2016; Lewandrowski et al. 2021). Once they emerge, factors such as follow-up rainfall and grazing pressure will have a significant impact on seedling survival. For example, previous studies have found *A. ligulata* to be particularly sensitive to grazing pressure and desiccation (Auld 1995*a*; Denham & Auld 2004), which may impact its performance in the field post-emergence.

Acknowledgments

This work was supported by Greening Australia and the Federation University Australia through funding aspart of the PhD project of Joseph Stapleton. Sarah Bates from Greening Australia also helped in editing the final report. Open access publishing facilitated by Federation University Australia, as part of the Wiley - Federation University Australia agreement via the Council of Australian University Librarians.

LITERATURE CITED

Adams R (1999) Germination of Callitris seeds in relation to temperature, water stress, priming, and hydration-dehydration cycles. Journal of Arid Environments 43:437–448. https://doi.org/10.1006/jare.1999.0567

Allison GB, Cook PG, Barnett SR, Walker GR, Jolly ID, Hughes MW (1990) Land clearance and river salinisation in the western Murray Basin, Australia. Journal of Hydrology 119:1–20. https://doi.org/10.1016/0022-1694(90)90030-2

Araujo MER, Pérez DR (2023) From seed germination to established seedlings: a comparative evaluation in five shrub species and implications for seed-based restoration in arid lands. Restoration Ecology 31:e13862. https://doi.org/10.1111/rec.13862

Auld TD (1995*a*) The impact of herbivores on regeneration in four trees from arid Australia. The Rangeland Journal 17:213–227. https://doi.org/10.1071/RJ9950213

Auld TD (1995*b*) Soil seedbank patterns of four trees and shrubs from arid Australia. Journal of Arid Environments 29:33–45. https://doi.org/10.1016/S0140-1963(95)80062-X

Azam G, Grant CD, Nuberg IK, Murray RS, Misra RK (2012) Establishing woody perennials on hostile soils in arid and semi-arid regions – a review. Plant and Soil 360:55–76. https://doi.org/10.1007/s11104-012-1215-6

Azizi S, Tabari M, Abad ARFN, Ammer C, Guidi L, Bader MKF (2022) Soil inoculation with beneficial microbes buffers negative drought effects on biomass, nutrients, and water relations of common Myrtle. Frontiers in Plant Science 13:892826. https://doi.org/10.3389/fpls.2022.892826

Bell DT (1999) Turner review no. 1: the process of germination in Australian species. Australian Journal of Botany 47:475–517. https://doi.org/10.1071/BT98007

Beveridge FC, Williams A, Cave R, Kalaipandian S, Dayananda B, Adkins SW (2024) Interactions between seed functional traits and environmental factors and their influence on germination performance of Australian native species. Seed Science Research 1–16. https://doi.org/10.1017/S0960258523000235

Booth TH (2017) Going nowhere fast: a review of seed dispersal in eucalypts. Australian Journal of Botany 65:401–410. https://doi.org/10.1071/BT17019

Bowler JM (1976) Aridity in Australia: age, origins and expression in aeolian landforms and sediments. Earth Science Reviews 12:279–310. https://doi.org/10.1016/0012-8252(76)90008-8

Bradford KJ (2002) Applications of hydrothermal time to quantifying and modeling seed germination and dormancy. Weed Science 50:248–260. https://doi.org/10.1614/0043-1745(2002)050[0248:AOHTTQ]2.0.CO;2

Bureau of Meteorology (2023) Climate Data Online. http://www.bom.gov.au/climate/data/ (accessed 23 Nov 2023)

Byrne M, Yeates DK, Joseph L, Kearney M, Bowler J, MaJ W, et al. (2008) Birth of a biome: insights into the assembly and maintenance of the Australian

arid zone biota. Molecular Ecology 17:4398–4417. https://doi.org/10.1111/j.1365-294X.2008.03899.x

Carr D, Bonney N, Millsom D (2007) The effect of sowing season on the reliability of direct seeding. Rural Industries Research and Development Corporation, Canberra, Australian Capital Territory, Australia

Clarke PJ, Latz PK, Albrecht DE (2005) Long-term changes in semi-arid vegetation: invasion of an exotic perennial grass has larger effects than rainfall variability. Journal of Vegetation Science 16:237–248. https://doi.org/10.1111/j.1654-1103.2005.tb02361.x

Commander LE, Golos PJ, Miller BP, Merritt DJ (2017) Seed germination traits of desert perennials. Plant Ecology 218:1077–1091. https://doi.org/10.1007/s11258-017-0753-7

Copeland SM, Munson SM, Pilliod DS, Welty JL, Bradford JB, Butterfield BJ (2018) Long-term trends in restoration and associated land treatments in the southwestern United States. Restoration Ecology 26:311–322. https://doi.org/10.1111/rec.12574

Dalziell EL, Lewandrowski W, Commander LE, Elliott CP, Erickson TE, Tudor EP, Turner SR, Merritt DJ (2022) Seed traits inform the germination niche for biodiverse ecological restoration. Seed Science and Technology 50:103–124. https://doi.org/10.15258/sst.2022.50.1.s.06

Denham AJ, Auld TD (2004) Survival and recruitment of seedlings and suckers of trees and shrubs of the Australian arid zone following habitat management and the outbreak of Rabbit Calicivirus Disease (RCD). Austral Ecology 29:585–599. https://doi.org/10.1111/j.1442-9993.2004.01393.x

Duncan C, Schultz NL, Good MK, Lewandrowski W, Cook S (2019*a*) The risk-takers and -avoiders: germination sensitivity to water stress in an arid zone with unpredictable rainfall. AoB Plants 11. https://doi.org/10.1093/aobpla/plz066

Duncan C, Schultz N, Lewandrowski W, Good MK, Cook S (2019*b*) Lower dormancy with rapid germination is an important strategy for seeds in an arid zone with unpredictable rainfall. PLoS One 14:e0218421. https://doi.org/10.1371/journal.pone.0218421

El-Keblawy A, Gairola S, Elsheikh EA, Hussain MI, Abhilash P (2018) Variability in seed germination behaviour of six grasses under laboratory and natural field conditions: implications for restoration of degraded lands in subtropical arid deserts. Tropical Ecology 59:715–726

Erickson TE, Merritt DJ, Turner SR (2016) Overcoming physical seed dormancy in priority native species for use in arid-zone restoration programs. Australian Journal of Botany 64:401–416. https://doi.org/10.1071/BT16059

Ewing CP, Catterall CP, Tomerini DM (2013) Outcomes from engaging urban community groups in publicly funded vegetation restoration. Ecological Management and Restoration 14:194–201. https://doi.org/10.1111/emr.12054

Figueiredo MA, Teixeira Braga Messias MC, Praça Leite MG, Kozovits AR (2021) Seed covering and dry periods in the rainy season interfere with direct seeding success in the restoration of post-mined grasslands. Ecologia Austral 31:444–455. https://doi.org/10.25260/EA.21.31.3.0.1446

Finlayson G, Taggart P, Cooke B (2021) Recovering Australia's arid-zone ecosystems: learning from continental-scale rabbit control experiments. Restoration Ecology 30:e13552. https://doi.org/10.1111/rec.13552

Florentine SK, Fox JED (2002) Seed longevity of *Eucalyptus victrix* in grassland in the floodplain of the Fortescue River, Pilbara, Western Australia. Biologia Plantarum 45:477–479. https://doi.org/10.1023/A:1016250608248

Frischie S, Miller AL, Pedrini S, Kildisheva OA (2020) Ensuring seed quality in ecological restoration: native seed cleaning and testing. Restoration Ecology 28:S239–S248. https://doi.org/10.1111/rec.13217

George R, Mcfarlane D, Nulsen B (1997) Salinity threatens the viability of agriculture and ecosystems in Western Australia. Hydrogeology Journal 5:6–21. https://doi.org/10.1007/s100400050103

Hallett LM, Standish RJ, Jonson J, Hobbs RJ (2014) Seedling emergence and summer survival after direct seeding for woodland restoration on old fields in south-western Australia. Ecological Management and Restoration 15:140–146. https://doi.org/10.1111/emr.12110

Hernández JA, Pérez DR (2023) Performance of five arid land shrub species in direct seeding: implications for seed-based restoration. Restoration Ecology 32:e14022. https://doi.org/10.1111/rec.14022

Houston J (2006) Evaporation in the Atacama Desert: an empirical study of spatio-temporal variations and their causes. Journal of Hydrology 330:402–412. https://doi.org/10.1016/j.jhydrol.2006.03.036

Huang L, Wang D, Yao L, Li X, Wang D, Du Q, Zhang Y, Hou X, Guo Y (2019) Primary limitation on vegetation productivity shifts from precipitation in dry years to nitrogen in wet years in a degraded arid steppe of Inner Mongolia, northern China. Journal of Soils and Sediments 19:544–556. https://doi.org/10.1007/s11368-018-2070-8

James JJ, Svejcar TJ, Rinella MJ (2011) Demographic processes limiting seedling recruitment in arid grassland restoration. Journal of Applied Ecology 48:961–969. https://doi.org/10.1111/j.1365-2664.2011.02009.x

Jiménez-Alfaro B, Silveira FAO, Fidelis A, Poschlod P, Commander LE (2016) Seed germination traits can contribute better to plant community ecology. Journal of Vegetation Science 27:637–645. https://doi.org/10.1111/jvs.12375

Josa R, Jorba M, Vallejo VR (2012) Opencast mine restoration in a Mediterranean semi-arid environment: failure of some common practices. Ecological Engineering 42:183–191. https://doi.org/10.1016/j.ecoleng.2012.02.020

Kildisheva OA, Erickson TE, Merritt DJ, Dixon KW (2016) Setting the scene for dryland recovery: an overview and key findings from a workshop targeting seed-based restoration. Restoration Ecology 24:S36–S42. https://doi.org/10.1111/rec.12392

Lakon G (1949) The topographical tetrazolium method for determining the germinating capacity of seeds. Plant Physiology 24:389–394. https://doi.org/10.1104/pp.24.3.389

Letnic M, Dickman CR, Mcnaught G (2000) Bet-hedging and germination in the Australian arid zone shrub *Acacia ligulata*. Austral Ecology 25:368–374. https://doi.org/10.1046/j.1442-9993.2000.01047.x

Lewandrowski W, Stevens JC, Webber BL, Dalziell EL, Trudgen MS, Bateman AM, Erickson TE (2021) Global change impacts on arid zone ecosystems: seedling establishment processes are threatened by temperature and water stress. Ecology and Evolution 11:8071–8084. https://doi.org/10.1002/ece3.7638

Lozano YM, Armas C, Hortal S, Casanoves F, Pugnaire FI (2017) Disentangling above- and below-ground facilitation drivers in arid environments: the role of soil microorganisms, soil properties and microhabitat. New Phytologist 216:1236–1246. https://doi.org/10.1111/nph.14499

Lozano-Isla F, Benites-Alfaro OE, Pompelli MF (2019) GerminaR: an R package for germination analysis with the interactive web application "Germinaquant for R". Ecological Research 34:339–346. https://doi.org/10.1111/1440-1703.1275

Madsen MD, Davies KW, Boyd CS, Kerby JD, Svejcar TJ (2016) Emerging seed enhancement technologies for overcoming barriers to restoration. Restoration Ecology 24:S77–S84. https://doi.org/10.1111/rec.12332

Mallee Catchment Management Authority (2008) Mallee native vegetation plan. Mallee Catchment Management Authority, Mildura, Victoria, Australia

Merino-Martín L, Courtauld C, Commander L, Turner S, Lewandrowski W, Stevens J (2017) Interactions between seed functional traits and burial depth regulate germination and seedling emergence under water stress in species from semi-arid environments. Journal of Arid Environments 147:25–33. https://doi.org/10.1016/j.jaridenv.2017.07.018

Mesgaran MB, Mashhadi HR, Alizadeh H, Hunt J, Young KR, Cousens RD (2013) Importance of distribution function selection for hydrothermal time models of seed germination. Weed Research 53:89–101. https://doi.org/10.1111/wre.12008

Michel BE (1983) Evaluation of the water potentials of solutions of polyethylene glycol 8000 both in the absence and presence of other solutes. Plant Physiology 72:66–70. https://doi.org/10.1104/pp.72.1.66

Moles AT, Warton DI, Westoby M (2003) Seed size and survival in the soil in arid Australia. Austral Ecology 28:575–585. https://doi.org/10.1046/j.1442-9993.2003.01314.x

Morton SR, Stafford Smith DM, Dickman CR, Dunkerley DL, Friedel MH, Mcallister RRJ, et al. (2011) A fresh framework for the ecology of arid Australia. Journal of Arid Environments 75:313–329. https://doi.org/10.1016/j.jaridenv.2010.11.001

Muñoz-Rojas M, Erickson TE, Martini DC, Dixon KW, Merritt DJ (2016) Climate and soil factors influencing seedling recruitment of plant species used for dryland restoration. The Soil 2:287–298. https://doi.org/10.5194/soil-2-287-2016

Munro NT, Moseby KE, Read JL (2009) The effects of browsing by feral and reintroduced native herbivores on seedling survivorship in the Australian rangelands. Rangeland Journal 31:417–426. https://doi.org/10.1071/RJ08027

Norden N, Daws MI, Antoine C, Gonzalez MA, Garwood NC, Chave J (2009) The relationship between seed mass and mean time to germination for 1037 tree species across five tropical forests. Functional Ecology 23:203–210. https://doi.org/10.1111/j.1365-2435.2008.01477.x

Onans J, Parsons RF (1980) Regeneration of native plants on abandoned mallee farmland in south-eastern Australia. Australian Journal of Botany 28: 479–493. https://doi.org/10.1071/BT9800479

Onofri A, Benincasa P, Mesgaran MB, Ritz C (2018) Hydrothermal-time-to-event models for seed germination. European Journal of Agronomy 101: 129–139. https://doi.org/10.1016/j.eja.2018.08.011

Onofri A, Mesgaran MB, Ritz C (2022) A unified framework for the analysis of germination, emergence, and other time-to-event data in weed science. Weed Science 70:259–271. https://doi.org/10.1017/wsc.2022.8

Pedrini S, Balestrazzi A, Madsen MD, Bhalsing K, Hardegree SP, Dixon KW, Kildisheva OA (2020) Seed enhancement: getting seeds restoration-ready. Restoration Ecology 28:S266–S275. https://doi.org/10.1111/rec.13184

Pérez DR, González F, Ceballos C, Oneto ME, Aronson J (2019) Direct seeding and outplantings in drylands of Argentinean Patagonia: estimated costs, and prospects for large-scale restoration and rehabilitation. Restoration Ecology 27:1105–1116. https://doi.org/10.1111/rec.12961

Poschlod P, Abedi M, Bartelheimer M, Drobnik J, Rosbakh S, Saatkamp A (2013) Seed ecology and assembly rules in plant communities. Pages 164–202. In: Vegetation ecology. John Wiley & Sons. https://doi.org/10.1002/9781118452592.ch6

R Core Team (2023) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Rayachhetry MB, Van TK, Center TD (1998) Regeneration potential of the canopy-held seeds of *Melaleuca quinquenervia* in south Florida. International Journal of Plant Sciences 159:648–654. https://doi.org/10.1086/297583

Robinson RW, Boon PI, Bailey P (2006) Germination characteristics of *Melaleuca ericifolia* Sm. (swamp paperbark) and their implications for the rehabilitation of coastal wetlands. Marine and Freshwater Research 57:703–711. https://doi.org/10.1071/MF06006

Ronnenberg K, Wesche K, Hensen I (2008) Germination ecology of central Asian *Stipa* spp: differences among species, seed provenances, and the importance of field studies. Plant Ecology 196:269–280. https://doi.org/10.1007/s11258-007-9351-4

Tielbörger K, Petruů M, Lampei C (2012) Bet-hedging germination in annual plants: a sound empirical test of the theoretical foundations. Oikos 121: 1860–1868. https://doi.org/10.1111/j.1600-0706.2011.20236.x

Turner SR, Pearce B, Rokich DP, Dunn RR, Merritt DJ, Majer JD, Dixon KW (2006) Influence of polymer seed coatings, soil raking, and time of sowing on seedling performance in post-mining restoration. Restoration Ecology 14:267–277. https://doi.org/10.1111/j.1526-100X.2006.00129.x

Wei J, Yang H, Cao H, Tan T (2016) Using polyaspartic acid hydro-gel as water retaining agent and its effect on plants under drought stress. Saudi Journal of Biological Sciences 23:654–659. https://doi.org/10.1016/j.sjbs.2015.08.016

Wellington AB, Noble IR (1985) Post-fire recruitment and mortality in a population of the mallee *Eucalyptus incrassata* in semi-arid south-eastern Australia. Journal of Ecology 73:645–656. https://doi.org/10.2307/2260501

White MD (2006) The Mallee vegetation of North Western Victoria. Proceedings of the Royal Society of Victoria 118:229–243

Whitney KD (2002) Dispersal for distance? *Acacia ligulata* seeds and meat ants *Iridomyrmex viridiaeneus*. Austral Ecology 27:589–595. https://doi.org/10.1046/j.1442-9993.2002.01216.x

Xu H, Xu F, Lin T, Xu Q, Yu P, Wang C, et al. (2023) A systematic review and comprehensive analysis on ecological restoration of mining areas in the arid region of China: challenge, capability and reconsideration. Ecological Indicators 154:110630. https://doi.org/10.1016/j.ecolind.2023.110630

Supporting Information

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

Supplement S1. Full equations.
Table S1. Pairwise comparison for GRP under different light regimes.
Table S2. Pairwise comparison for GRP under different temperature regimes.
Table S3. Pairwise comparison for MGT under different light regimes.
Table S4. Pairwise comparison for MGT under different temperature regimes.
Table S5. Hydro-time model parameters for *A. ligulata* using a Weibull type II distribution.
Table S6. Hydro-time model parameters for *C. gracilis* using a log-logistic distribution.
Table S7. Hydro-time model parameters for *E. calycongona* using a logistic distribution.
Table S8. Hydro-time model parameters for *M. lanceolata* using a log-logistic distribution.
Figure S1. The effect of different water potentials (0, −0.2, −0.4, −0.6, −0.8, −1.0, −1.5 MPa) on the cumulative germination of *A. ligulata*, *C. gracilis*, *E. calycogona*, and *M. lanceolata*.

Coordinating Editor: Ali El-Keblawy

Received: 23 January, 2024; First decision: 19 April, 2024; Revised: 12 June, 2024; Accepted: 12 June, 2024