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Seed germination traits of desert perennials

Lucy E. Commander · Peter J. Golos · Ben P. Miller · David J. Merritt

Abstract While understanding that seed germination is crucial for ecological restoration activities, the seed traits of desert perennials are understudied. We experimentally determined germination traits of 43 species from 14 families from Hummock grasslands in the Great Sandy Desert, Australia. We defined morphological and physiological seed traits of framework species required for restoration and investigated the effects of fire and temperature on seed germination. We classified dormancy and explored the effect of Karrikinolide, a fire cue derived from smoke, on germination. Seeds of 38 (88%) out of 43 species were dormant: 13 (30%) with physical and 25 (58%) with physiological dormancy. Karrikinolide promoted seed germination of 9 (21%) species across all life-forms except trees, and widened the range of germination temperatures and increased germination rate of one species. Although high germination percentages were obtained over a wide temperature range, germination rate was affected by temperature. Non-dormant seeds and seeds pre-treated to overcome physical dormancy germinated quickly, with times to 50% germination of 1–5 days. Dormancy class differed between life-forms and families. Fast germination of non-dormant seeds is a trait that allows seeds to germinate during short periods of moisture availability. An absence of under-developed embryos is consistent with the global trends for hot deserts. A response to Karrikinolide shows that seed germination is related to a fire cue. These results will inform land managers of effective seed pre-treatments prior to seed broadcasting for restoration, and information on seed germination temperatures and rates will improve the understanding of when and where seeds could germinate in restored sites.

Keywords Community assembly · Dormancy · Environmental filter · Karrikinolide · Plant trait · Restoration

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Introduction

Seeds are central to the regenerative success of plants. Seeds influence the ability of plants to disperse across the landscape, persist through periods of adverse environmental conditions, and germinate at a time when the chances of seedling survival and growth are most favourable (Saatkamp et al. 2011). Seed traits that control germination timing in particular, strongly

influence the success or failure of seedling recruitment—arguably the most critical stage of a plant's lifecycle. In arid regions, the majority of plants produce seeds that possess some type of dormancy—an adaptive trait that regulates seed germination and that can confer an establishment advantage in environmentally variable or harsh climatic regions (Cohen 1966; Volis and Bohrer 2013). Dormancy has been especially well studied in desert annuals, among which there is commonly a significant variation in the degree of seed dormancy that contributes to risk-spreading against regenerative failure in these unpredictable environments (Venable 2007). However, dormancy is also known to be a predominant trait in seeds of all major plant life-forms in arid regions (Jurado and Flores 2005).

In the deserts of Australia, physiological and physical dormancy appear to be the most common types of seed dormancy (Erickson et al. 2016), as in other arid regions (Baskin and Baskin 2014). Although drylands make up more than 70% of Australia, studies are still limited to a relatively small number of species (Erickson et al. 2016). Conservation of these unique ecosystems is increasingly a concern as land degradation increases due to broad-acre pastoral activities and intensive mining (Environmental Protection Authority 2014). The management of dryland ecosystems calls for ecological restoration on an enormous scale (Kildisheva et al. 2016) and seeds form a core component of landscape-scale restoration programs (Merritt and Dixon 2011). Seed dormancy can be a constraint to restoration, hampering efforts to reinstate biodiverse plant communities through direct seeding, or limiting opportunities to produce nursery-grown plants (Merritt et al. 2007). Resolving seed dormancy types—through the classification system of Baskin and Baskin (2004), for example—provides for the efficient design of seed pre-treatments to ensure that seeds are in a physiological state that allows for germination.

However, dormancy is not the only factor determining recruitment: environmental conditions must still be suitable for germination of non-dormant seed (Ooi et al. 2007). Different environments filter for different seed traits, and characterising the germination traits of seeds is necessary to describe the regeneration niche (Marques et al. 2014). Non-dormant seeds respond to a host of abiotic factors to control germination timing, including soil moisture

and temperature, and, in certain environments, disturbance-related cues such as smoke (Merritt et al. 2007). While seeds of any particular species will have a range of temperatures over which germination is possible (Baskin and Baskin 2014), in arid or seasonally arid climate zones, optimal temperatures for germination generally coincide with those during periods of rainfall (Bell 1999). Seeds of some arid zone species germinate over a wide range of temperatures (e.g. *Solanum orbiculatum* has $\geq$90% germination when treated with Karrikinolide (KAR_1) and incubated at 10–30 °C (Commander et al. 2008)), whereas others have a narrow range (e.g. *Lycium bosciifolium* has highest germination at 22/15 °C (Kos and Poschlod 2007)). In fire-prone regions, fire-related regeneration cues can filter community membership as plants must have traits that enable them to either be able to survive fire and resprout or recruit from seed (reviewed in Keith 2012). Fire cues, such as heat, and smoke-derived chemicals KAR_1 and glyceronitrile (Flematti et al. 2004, 2011) are key germination triggers in fire-prone ecosystems (Nelson et al. 2012) and may act singly, or in combination, to promote seed germination (Tieu et al. 2001a).

Germination speed is also an important functional trait that may confer competitive advantage (Jiménez-Alfaro et al. 2016) and varies across habitats. Seeds of desert plants often exhibit rapid germination (Jurado and Westoby 1992) due to the limited rainfall that often occurs as localised, pulse events, meaning moisture is available only in the shallow layers of the soil and for only brief periods (Chesson et al. 2004). Rapidly germinating seeds, while naturally conferring a competitive advantage in regions of transient soil moisture, may require careful management in the context of ecological restoration. Sowing seeds first pre-treated to render them non-dormant may consign the entire population to a germination event upon the first instance of rainfall. This synchronous germination may give the population little against those rainfall events that are insufficient for subsequent seedling establishment.

Seed regeneration traits are yet to be fully incorporated into functional ecology, despite their importance to the distribution, persistence, and dynamics of plant species and communities (Jiménez-Alfaro et al. 2016; Larson and Funk 2016). The relative frequency of certain seed traits may differ between plant communities and environments. For example, the

proportion of dormant seeds increases with decreasing temperature and rainfall in tropical and subtropical zones (Baskin and Baskin 2014). Seed functional traits, including morphological (e.g. seed mass) and physiological traits (e.g. dormancy), strongly influence plant community assembly from local to landscape scales (Leyer and Pross 2009; Myers and Harms 2010). In fact, germination traits, such as initial temperature of seed germination, are generally correlated with environmental conditions (e.g. temperature, light and moisture) of the adult plants' habitat, thereby influencing species distribution (Marques et al. 2014; Rosbakh and Poschlod 2014), but not always (Cochrane et al. 2015). Studies of seed regeneration traits also contribute to practical horticultural or conservation goals, including the development of methods for propagation of plants in nursery settings, through to landscape-scale, ecological restoration and land management (Peishi et al. 1999).

The desert chosen for this study was the Great Sandy Desert in Australia, which is Australia's second largest desert, at 267,250 km^2 (Geoscience Australia 2015). The vegetation is a mosaic of sparse low tree-steppe and sparse shrub-steppe (*Acacia* and *Grevillea* spp.) with hummock grasses (*Triodia* spp.). This grassland steppe is the largest vegetation type in Western Australia, covering 27.7 million hectares (Beard et al. 2013; Western Australian Herbarium 1998). There are several mines in the region, notably one, Telfer Gold Mine, has been extracting ore since 1977 (Golos 2013). The mine has a large open cut pit, and a number of waste rock dumps that require rehabilitation. While topsoil can be used as a source of seeds for rehabilitation, there is likely to be a shortage of topsoil to cover the extensive waste rock dumps, hence seed will be required for broadcasting. Information on seed biology is crucial to restoration activities such as seed broadcasting (Commander et al. 2009b). A strategic approach to obtaining this information by classifying dormancy and identifying seed pretreatments to enable germination may increase seed germination and consequently seedling establishment of plants in restored areas. There is a paucity of information on the seed biology of Australian desert species, particularly in the Great Sandy Desert, whereas information is available for species in the Southern Kalahari (Kos et al. 2012), and annual species in the Negev (Gutterman 2000) and Sonoran

Deserts (Adondakis and Venable 2004). Understanding traits involved in plant regeneration strategies, such as seed germination, is the key to understanding how ecosystems function in these variable environments, which have temporal fluctuations in temperature and moisture.

This study considers the key regeneration traits of seed dormancy and germination of plant species from Australia's Great Sandy Desert that vary in life-form and that are representative of dominant elements of the vegetation in regions where ecological restoration is required. Seed morphological and physiological traits characterised include embryo type, the effects of incubation temperature, gibberellic acid, and KAR$_1$ on germination percentage and speed, and seed dormancy type was determined. We expected to find a high frequency of dormancy among the seeds of the various species, fast germination of non-dormant seeds, optimum germination at high temperatures, stimulation of germination by fire cues (smoke), and a higher proportion of developed embryos than under-developed embryos (hence a greater proportion of physiological than morphological or morphophysiological dormancy).

Methods

Study site and seed collection

The study site was the vegetation community surrounding Telfer Gold Mine, in the Great Sandy Desert (GSD), Western Australia (Fig. 1). Its climate is arid tropical with summer rain (Dec-Mar). Average annual rainfall is 371 mm, but varies from 114 to 817 mm, and on average, 9.8 days per year receive ≥10 mm (Bureau of Meteorology 2014). Mean maximum and minimum temperatures are 40.5 and 10.6 °C in the hottest (Jan) and coolest (Jul) months, respectively (Bureau of Meterology 2014). Temperatures are lower on days that receive rainfall, for instance in December (wet season) 2013, maximum and minimum temperatures on days with <1 mm of rain were 40 and 27 °C, respectively, but 36 and 22 °C, respectively, on days with ≥1 mm of rain. This temperature difference is relevant as these cooler temperatures occur when water is available and germination could occur. Landforms include stony hills, linear sand dunes separated by flat sandplains, and low lying areas with

Fig. 1 Map showing the location of the Great Sandy Desert (Interim Biogeographic Regionalisation for Australia version 7) within Australia

clayey soils (Hart Simpson and Associates Pty Ltd. 2002). A total of 292 species have been recorded in the Telfer vicinity, with Fabaceae (54 species), Poaceae (40), Malvaceae (29), Chenopodiaceae (19), Myrtaceae (13), Amaranthaceae (13) and Goodeniaceae (13) the dominant families (Golos 2013; Hart Simpson and Associates Pty Ltd. 2002; Mattiske Consulting Pty Ltd. 2004).

Seeds of 43 species from 14 families required for restoration and representing the common species and including all dominant families (except Amaranthaceae) were collected between November 2008 and October 2010 within approx. 20 km of Telfer Mine Site (21.725059S, 122.214432E). Herbarium specimens were collected, and species were verified by the Western Australian Herbarium. Plant life-form for the study species was obtained from the Western Australian Herbarium (1998). Following collection, seeds were removed from dehiscent fruits, and stored at 15 °C and 15% RH until used for experiments. Seeds were x-rayed using a Faxitron Specimen Radiography System (MX-20 Cabinet X-ray Unit) (Faxitron, Wheeling, Illinois, USA) with empty and predated seeds discarded.

Experimental approach

In this study we investigated the effects of KAR_1, gibberellic acid (GA_3) and temperature on germination percentage and rate of species from the Great Sandy Desert. We also classified embryo type to enable us to identify physiological dormancy through eliminating the possibility of morpho- or morphophysiological dormancy (an under-developed embryo).

Specifically, we assessed the effect of KAR_1 and GA_3 on germination percentage and rate of 43 and 40 species, respectively (3 species were omitted in the GA_3 trial due to insufficient seeds). Prior to incubation on KAR_1 and GA_3, we pre-treated seeds in the families which are well known to exhibit physical dormancy (PY) (Baskin and Baskin 2014) (Fabaceae, Malvaceae and Sapindaceae), with hot water, which has been shown to overcome PY. Following the assessment of KAR_1 and GA_3, low germination of seeds in the Malvaceae was observed, hence, we then undertook an imbibition experiment to assess water uptake of 4 Malvaceae species to determine whether or not hot water treatment did enable imbibition. Also following

the assessment of KAR_1 and GA_3, we selected 8 species with high germination to investigate the effect of temperature (10, 15, 20, 25, 30, and 30 °C) on germination percentage and rate. Of those 8 species, four were incubated with and without KAR_1 to investigate potential interaction between temperature and KAR_1. Finally, we undertook a meta-analysis on seed dormancy and life-form for species in this study, as well as additional species from the region.

Effects of Karrikinolide and gibberellic acid on germination percentage and rate

Seeds in all families were surface sterilised with 2% calcium hypochlorite (bleach) for 30 min and rinsed three times with water. Seeds were incubated in 90 mm Petri dishes on either water agar (0.7%, w/v), agar containing 1 mM gibberellic acid (GA_3, Sigma-Aldrich) or agar containing 1 μM Karrikinolide (KAR_1, the butenolide, 3-methyl-2H-furo[2,3-c]pyran-2-one, synthesised in pure form as described in Flematti et al. (2005)). All seeds in the Fabaceae, Malvaceae and Sapindaceae were treated with hot (>90 °C) water for 1 min prior to incubation. Four replicates of 25 seeds were used for each treatment. Petri dishes were incubated at constant 25 °C with 12 h light/12 h dark, as this is within the range of temperatures experienced on rain days in the wet season (Bureau of Meterology 2014). Germination was defined as the emergence of the radicle and was monitored 3–5 times per week. Final germination was recorded after 28 days of incubation. For some species where seed availability was low, 10 seeds per replicate (*Eragrostis eriopoda*, *Hybanthus aurantiacus*, *Scaevola parvifolia,* and *Thysanotus exiliflorus*), 23 seeds per replicate (*Senna symonii*), or 20 seeds per replicate (the three *Triodia* species) were used. For the seeds of *Triodia* spp. germination testing encompassed only water and KAR_1 agar.

Imbibition of Malvaceae species

Seeds of some species in the Malvaceae showed low germination in the first germination test, indicating that perhaps the hot water treatment may not have overcome dormancy. Hence, an imbibition test was undertaken to confirm the presence/absence of a water impermeable testa and determine the efficacy of the hot water treatment. For species of Malvaceae (*Hibiscus burtonii*, *Abutilon otocarpum*, *Sida cardiophylla*,

and *Sida echinocarpa*) three replicates of at least 0.2 g (at least 100 seeds) were either non-treated, or treated with hot (>90 °C) water for 1 min (Turner et al. 2006). Seeds were then placed on moist filter paper in Petri dishes, weighed after 1, 2, 3, 4, 5, 6, 7, 24, 48, 72, and 96 h, and the percent increase in mass was calculated (Turner and Merritt 2009). At the conclusion of the experiment, the proportion of imbibed seeds was calculated based on the number of germinated seeds plus the number of imbibed seeds that had not germinated (ungerminated seeds were cut with a scalpel to determine whether or not they had imbibed, and whether or not they were alive by inspecting the colour of the embryonic tissue), out of the total number of filled, live seeds.

Seed dormancy classification

Seeds and embryos were measured using a microscope (Leica DFC 450). Embryo types were classified according to Martin (1946) and Baskin and Baskin (2007), and seeds were considered to have under-developed embryos if the embryos were less than half the length of the seeds.

Dormancy was classified according to Baskin and Baskin (2004), which is based on embryo morphology, permeability of the seed or fruit coat to water, and whether or not seeds germinate within 28 days. Seeds were considered dormant if their germination was <75% and non-dormant if germination was >75% after 28 days of incubation.

Effects of temperature and/or Karrikinolide on germination percentage and rate

Eight species which exhibited high germination percentages in the initial germination experiment were then selected to study the effect of temperature and/or KAR_1 on germination percentage and rate. The effects of incubation temperature on germination was examined in four species with physical dormancy (*Jacksonia aculeata*, *Acacia colei* var. *colei*, *Senna notabilis*, and *Senna glutinosa* subsp. *glutinosa*), and seeds of these species were treated with hot water prior to being incubated on water agar. The effects of temperature and KAR_1 on germination were also examined in three non-dormant species (*Corymbia opaca*, *Eucalyptus odontocarpa*, *and Hakea lorea*), and one species stimulated by KAR_1 (*Streptoglossa macrocephala*).

Seeds of these four species were incubated on water agar and on KAR_1 agar to determine whether KAR_1 increased the range of temperatures over which seeds could germinate. Prior to incubation, all seeds were surface sterilised and rinsed with sterile water as described above. Seeds were incubated at six constant temperatures (10, 15, 20, 25, 30, and 35 °C) in 12 h light/12 h dark. Germination was observed daily for the first few days, then 3–5 times per week, and final germination was determined after 28 days of incubation. Time to 50% germination (t_{50}) was calculated by interpolating from cumulative germination curves of each replicate (using 50% of the total number of seeds per replicate) and the germination rate (GR50) was calculated by the inverse of time to 50% germination.

Meta-analysis

In order to investigate the relationships between dormancy and life-form, a meta-analysis was performed on species in this study combined with other species in the Telfer region. In total, 189 of the 292 species that have been identified in the region were analysed. Dormancy classes were assigned based on inferences at a genus or family level (similar to Kos et al. 2012; Ooi 2007) from data from this and other studies (Baker et al. 2005a, c; Commander et al. 2009b). If no information on dormancy was available at a family level, or if species within families exhibit different dormancy classes, species were excluded from the analysis.

Data analysis

Imbibition of seeds of Malvaceae was analysed using a two-sample binomial test to compare the total number of imbibed seeds vs the total number of live seeds. Final germination of seeds treated with hot water, KAR_1 or GA_3 was analysed using generalised linear modelling of binomial data with a logit link-function (GenStat 11th Edition, VSN International Ltd.). If required, levels of treatments were compared using a two-sample binomial test. Final germination of seeds incubated six constant temperatures (10, 15, 20, 25, 30, and 35 °C) was analysed using generalised linear modelling of binomial data with a logit link-function. GR50 of seeds incubated at six constant temperatures (10, 15, 20, 25, 30, and 35 °C) was analysed using one-way Analysis of Variance (ANOVA) and means were

separated using Fishers protected least significant difference test (GenStat 11th Edition, VSN International Ltd.).

Results

Effect of Karrikinolide and gibberellic acid on germination percentage and rate, and seed dormancy classification

Germination of six of the seven species of Goodeniaceae was variable, with germination on water agar ranging from 0 to 62% (Fig. 2), and as seeds had fully developed embryos, the seeds were considered physiologically dormant (Table 1). GA_3 promoted germination of four species; *Goodenia armitiana*, *Goodenia azurea* subsp. *hesperia*, *Goodenia stobbsiana*, and *Velleia connata* ($P < 0.001$) (Fig. 3). KAR_1 only promoted germination of *Goodenia armitiana* ($P < 0.001$) (Fig. 2).

Seeds of all species in the Poaceae (except *Aristida inaequiglumis*) were physiologically dormant, as they had fully developed lateral embryos and germination was 0–12% (Fig. 2; Table 1). KAR_1 increased germination of all three *Triodia* species ($P < 0.05$) (Fig. 2) and GA_3, but not KAR_1 increased germination of *Enneapogon caerulescens* (Figs. 2, 3). GA_3 and KAR_1 did not increase germination of *Amphipogon caricinus* var. *caricinus*, *Eragrostis eriopoda*, and *Eriachne aristidea* (Fig. 2).

In the Proteaceae, all three *Grevillea* species (*Grevillea eriostachya*, *Grevillea stenobotrya*, *and Grevillea wickhamii*) exhibited 0–30% germination on water or GA_3 agar, but >50% germination when incubated on KAR_1, which was significantly higher than germination on water ($P < 0.001$) (Figs. 2, 3). These three species had fully developed (investing) embryos (Table 1) and are therefore physiologically dormant.

Seeds of *Halgania solanacea*, *Eremophila latrobei* subsp. *glabra*, *Eremophila tietkensii*, and *Thysanotus exiliflorus* failed to germinate within 28 days and had fully developed embryos (*H. solanacea* had investing and the other three had linear embryos) and are therefore considered to be physiologically dormant (Fig. 2; Table 1). *Solanum diversiflorum* and *Hybanthus aurantiacus* did not germinate on water agar, however GA_3 promoted germination ($P < 0.05$)
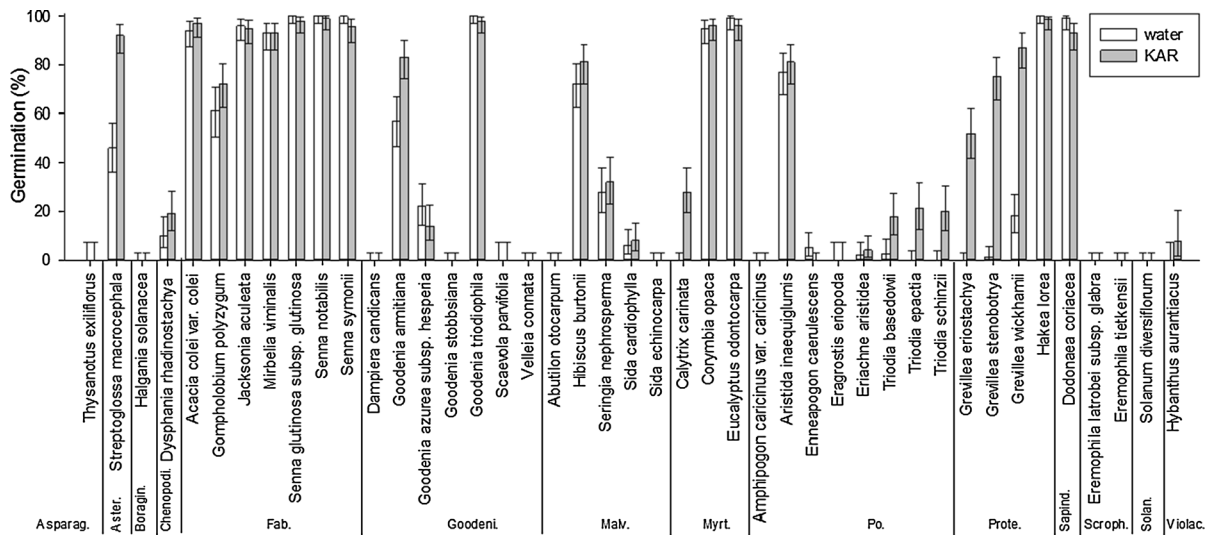
Fig. 2 Germination (%) of 43 species in 14 families incubated on water agar and agar containing Karrikinolide (KAR$_1$) for 28 days. *Bars* indicate the 95% confidence interval. Number of seeds per species and treatment was 100, except *Eragrostis eriopoda*, *Hybanthus aurantiacus*, *Scaevola parvifolia* and *Thysanotus exiliflorus* (40 seeds), *Senna symonii* (92 seeds), and the three *Triodia* species (80 seeds)

(Figs. 2, 3) and embryos were fully developed (linear and spatulate respectively) (Table 1), so both species are also considered physiologically dormant. GA$_3$ also increased germination ($P < 0.001$) of *Dysphania rhadinostachya* subsp. *rhadinostachya* (Fig. 3), which had a fully developed (peripheral) embryo (Table 1) and is hence physiologically dormant. Germination of *Streptoglossa macrocephala* was doubled with both GA$_3$ and KAR$_1$ and embryos were linear (Fig. 2,3, Table 1). Seeds of *Calytrix carinata* germinated to 0–28% and KAR$_1$ promoted germination (Fig. 2). Embryos were linear, and seeds were considered physiologically dormant (Table 1).

High germination percentages (>75%) were obtained for five species on water agar and their seeds were considered to be non-dormant; Goodeniaceae: *Goodenia triodiophila* (100%); Myrtaceae: *Corymbia opaca* (95%) and *Eucalyptus odontocarpa* (99%); Poaceae: *Aristida inaequiglumis* (77%); Proteaceae: *Hakea lorea* (100%) (Fig. 2).

Germination of seeds of four of the five Malvaceae species was low (0–32%) under all conditions (Fig. 2), hence the need for the subsequent experiment to test imbibition. Imbibition testing of four Malvaceae species revealed that very few seeds (3–6%) imbibed if they were not treated with hot water (Fig. 4), hence they are considered physically dormant. A two-sample binomial test determined that a greater number of

seeds imbibed following HW treatment than untreated seeds of each of the four species ($P < 0.001$) (Fig. 4). In addition, HW had no effect on seed viability ($P > 0.05$). Hence, seeds are considered physically dormant. However, HW was not completely effective in overcoming water-impermeability, with only 26–85% of seeds imbibing (Fig. 4).

For species with >75% germination, seeds germinated quickly (time to 50% germination was 1–5 days on water agar) (data not shown). Average time to 50% germination was 3 days (data not shown).

Effects of temperature and/or Karrikinolide on germination percentage and rate

Temperature did not significantly affect germination of two species, *Senna notabilis* and *Corymbia opaca*, as seeds germinated to ≥90% from 10 to 35 °C (Fig. 5). Temperature significantly affected germination percentage of the remaining six species. However, five of these species still germinated over a fairly wide range of temperatures, with germination ≥90% from 15 to 35 °C for four species (*Acacia colei* var. *colei*, *Eucalyptus odontocarpa*, *Hakea lorea*, and *Senna glutinosa*) and 20 to 35 °C for one species (*Jacksonia aculeata*) (Fig. 5).

KAR$_1$ did not significantly ($P > 0.05$) affect germination of three species (*Corymbia opaca*,

Table 1 Seed and plant traits of 43 species including dormancy class (according to Baskin and Baskin 2004) (*ND* non-dormant, *PD* physiologically dormant, *PY* physically dormant), life-form (Western Australian Herbarium 1998), and embryo type (according to Baskin and Baskin 2007; Martin 1946)

Family	Species	Dormancy	Life-form	Embryo type
Asparagaceae	*Thysanotus exiliflorus* F. Muell.	PD	Perennial herb	Linear
Asteraceae	*Streptoglossa macrocephala* (F. Muell.) Dunlop	PD	Perennial herb	Linear
Boraginaceae	*Halgania solanacea* F.Muell.	PD	Perennial herb	Investing
Chenopodiaceae	*Dysphania rhadinostachya* subsp. *rhadinostachya* (F. Muell.) A.J. Scott	PD	Annual herb	Peripheral
Fabaceae	*Acacia colei* var. *colei* Maslin & L. Thomson	PY	Shrub/tree	Investing
	Gompholobium polyzygum F. Muell.	PY	Shrub	Bent
	Jacksonia aculeata W. Fitzg.	PY	Shrub	Bent
	Mirbelia viminalis (Benth.) C.A.Gardner	PY	Shrub	Bent
	Senna glutinosa var. *glutinosa* (DC.) Randell	PY	Shrub	Investing
	Senna notabilis (F. Muell.) Randell	PY	Shrub	Investing
	Senna symonii (Randell) Randell	PY	Shrub	Investing
Goodeniaceae	*Dampiera candicans* F. Muell.	PD	Shrub	Linear
	Goodenia armitiana F. Muell.	PD	Perennial herb	Spatulate
	Goodenia azurea var. *hesperia* L.W. Sage & Albr.	PD	Perennial herb	Linear
	Goodenia stobbsiana F. Muell.	PD	Shrub	Linear
	Goodenia triodiophila Carolin	ND	Perennial herb	Spatulate
	Scaevola parvifolia Benth.	PD	Perennial herb	Linear
	Velleia connata F.Muell.	PD	Annual herb	Spatulate
Malvaceae	*Abutilon otocarpum* F. Muell.	PY	Shrub	Folded
	Hibiscus burtonii Bailey	PY	Shrub	Folded
	Seringia nephrosperma F. Muell.	PY	Shrub	
	Sida cardiophylla F. Muell.	PY	Shrub	Folded
	Sida echinocarpa F. Muell.	PY	Shrub	Folded
Myrtaceae	*Calytrix carinata* Craven	PD	Shrub	Linear
	Corymbia opaca (D.J. Carr & S.G.M. Carr) K.D. Hill & L.A.S. Johnson	ND	Tree	Folded
	Eucalyptus odontocarpa F. Muell.	ND	Tree	Folded
Poaceae	*Amphipogon caricinus* var. *caricinus* F. Muell.	PD	Grass	Lateral
	Aristida inaequiglumis Domin	ND	Grass	Lateral
	Enneapogon caerulescens (Gaudich.) N.T. Burb.	PD	Grass	Lateral
	Eragrostis eriopoda Benth.	PD	Grass	Lateral
	Eriachne aristidea F. Muell.	PD	Grass	Lateral
	Triodia basedowii E. Pritz.	PD	Grass	Lateral
	Triodia epactia S.W.L. Jacobs	PD	Grass	Lateral
	Triodia schinzii (Henrard) Lazarides	PD	Grass	Lateral
Proteaceae	*Grevillea eriostachya* Lindl.	PD	Shrub/tree	Investing

Table 1 continued

Family	Species	Dormancy	Life-form	Embryo type
	Grevillea stenobotrya F. Muell.	PD	Shrub/tree	Investing
	Grevillea wickhamii Meisn.	PD	Shrub/tree	Investing
	Hakea lorea (R. Br.) R. Br.	ND	Tree	Investing
Sapindaceae	*Dodonaea coriacea* (Ewart & O.B. Davies) McGill.	PY	Shrub	Linear
Scrophulariaceae	*Eremophila latrobei* var. *glabra* (L.S. Sm.) Chinnock	PD	Shrub	Linear
	Eremophila tietkensii F. Muell. & Tate	PD	Shrub	Linear
Solanaceae	*Solanum diversiflorum* F. Muell.	PD	Shrub	Linear
Violaceae	*Hybanthus aurantiacus* (Benth.) F. Muell.	PD	Perennial herb	Spatulate
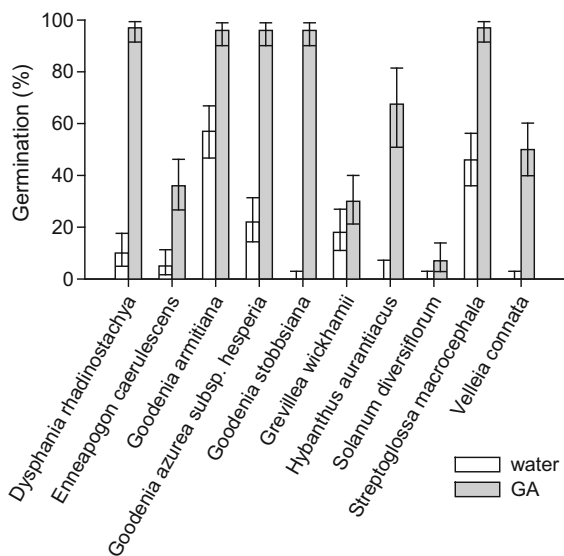
Fig. 3 Germination (%) of 10 species incubated for 28 days on water agar and agar containing gibberellic acid (GA₃). *Bars* indicate the 95% confidence interval. Number of seeds per species and treatment was 100, except *Hybanthus aurantiacus* (40 seeds). Only species for which GA₃ increased germination are shown


Fig. 4 Imbibed seeds (%) of four species in the Malvaceae either not treated (control) or pre-treated (HW) by soaking seeds in hot (>90 °C) water for 1 min. Seeds were placed on moist filter paper and allowed to imbibe for 4 days prior to being cut test to determine the proportion of seeds that had imbibed. *Bars* indicate the 95% confidence interval

Eucalyptus odontocarpa, *Hakea lorea*) (Fig. 5). In contrast, *Streptoglossa macrocephala* had a narrow temperature range for germination, with >90% germination only at 20 °C, however KAR₁ significantly increased germination percentage ($P < 0.05$), and also increased the range of temperatures at which ≥90% germination occurred to 15–30 °C.

Temperature affected the germination rate of all eight species ($P < 0.05$). In general, germination rate increased with increasing temperature (Fig. 5). Although high germination percentages were obtained over a wide temperature range, high germination rates occurred over a relatively narrow range. Highest germination rates were at 25 and 30 °C (*Senna glutinosa* and *Hakea lorea*), 30 °C and 35 °C (*Corymbia opaca* and *Jacksonia aculeata*), 35 °C (*Eucalyptus odontocarpa* and *Acacia colei* var. *colei*), and 20–35 °C (*Senna notabilis*). KAR₁ only significantly increased the germination rate of *Streptoglossa macrocephala*.

Meta-analysis

Across the whole community ($n = 189$), shrubs and shrub/trees mostly produced seeds with physical dormancy, while seeds from trees were mostly non-
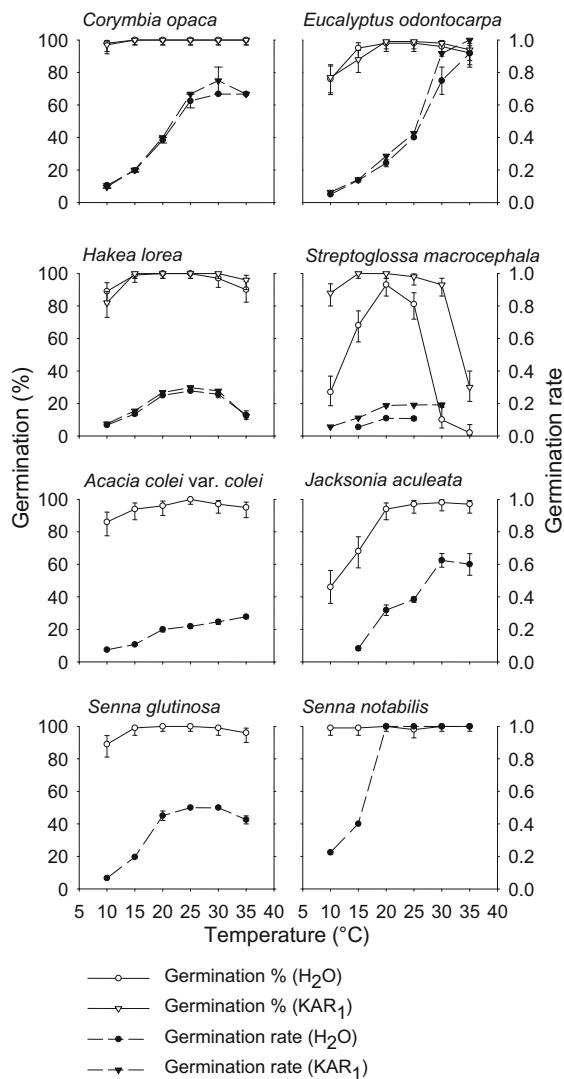
Fig. 5 Germination percentage (%) and germination rate (GR50—the inverse of time to 50% germination) of seeds of *Corymbia opaca*, *Eucalyptus odontocarpa*, *Hakea lorea*, and *Streptoglossa macrocephala*, incubated on water agar and KAR$_1$ agar and *Acacia colei* var. *colei*, *Jacksonia aculeata*, *Senna glutinosa*, and *Senna notabilis* pre-treated with hot water and incubated on water agar at 10, 15, 20, 25, 30, and 35 °C for 28 days. Number of seeds per species and treatment was 100

dormant and seeds from herbs were mostly physiologically dormant (Fig. 6).

Discussion

This study demonstrates that a range of seed regeneration traits exists amongst the species of the Great

Sandy Desert. While some seed traits differed between species (dormancy vs non-dormancy, and different dormancy classes), other traits were similar (germination at high temperatures and fast germination). Most species (38) had dormant seeds, with seeds of only five species exhibiting high (>75%) germination without treatment, and considered non-dormant. Non-dormant seeds, and seeds pre-treated to overcome physical dormancy, germinated quickly, with time to 50% germination ranging from 1 to 5 days. For the eight species for which the effects of incubation temperature were examined, it was evident that seeds can germinate over a wide range of temperatures, with the optimal germination being ≥25 °C. KAR$_1$ promoted seed germination of species in five families and across all life-forms, except trees. Two classes of dormancy, physical and physiological dormancy, were experimentally determined, with a meta-analysis revealing dormancy class differed between life-forms and families.

The proportion of dormancy classes in this ecosystem was similar to other drylands and deserts. These proportions, 12% ND, 30% PY and 58% PD, fit within the ranges found in the Southern Kalahari, hot deserts and savannas (Baskin and Baskin 1998; Kos et al. 2012). This study did not identify any species with MD, MPD or PY + PD, which may be the result of collection bias, and the relatively few number of species for which dormancy was determined experimentally (*n* = 43). Also, the lack of MD and MPD may be due to a requirement for embryos to grow within seeds that exhibit these classes of dormancy, and the soil may not remain moist for long enough to enable this to occur.

In this study, we found that seeds from tree lifeform species had proportionally more ND than those from grass, herb and shrub species. This finding corresponds with global trends of woody plants having proportionally more species with non-dormant seeds than herbaceous plants (Jurado and Flores 2005). Specifically in an arid environment, Kos et al. (2012) found that in the Kalahari desert, with increasing longevity, species are more likely to possess non-dormant seeds and less likely to have seeds with PD. Although the three trees included in our study do not have dormant seeds, they may have other traits to reduce the risk of reproductive failure in a given year, such as serotiny (persistent seeds are stored on the parent plant rather than in the soil seed bank), long
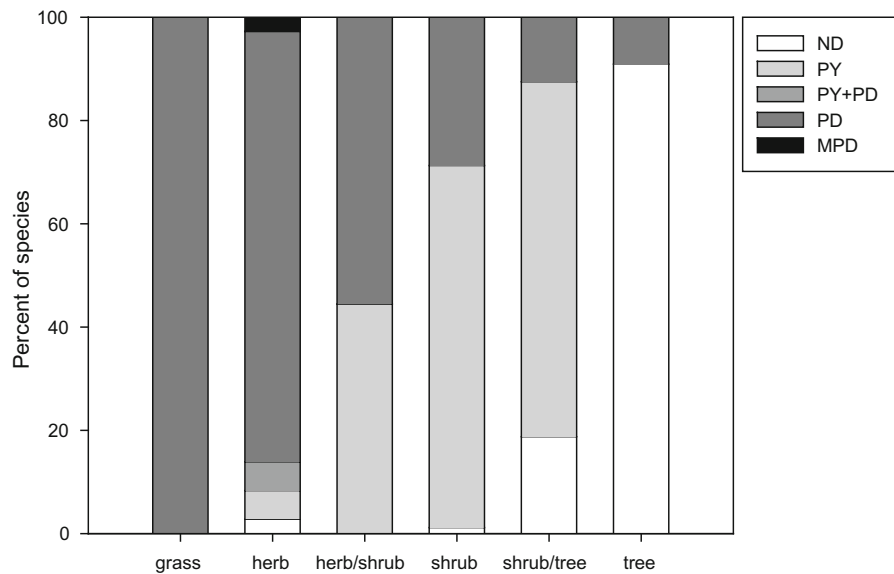
Fig. 6 Dormancy class including non-dormancy (*MPD* morphophysiological dormancy, *ND* non-dormancy, *ND/PD* non-dormancy or physiological dormancy, *PD* physiological dormancy, *PY* physical dormancy, and *PY + PD* combinational dormancy) for species recorded in the Telfer vicinity, in the Great Sandy Desert (*n* = 189) for different life-forms (as defined by Western Australian Herbarium (1998), grass (*n* = 21), herb (*n* = 36), herb/shrub (*n* = 18), shrub (*n* = 87), shrub/tree (*n* = 16), and tree (*n* = 11). Dormancy classes were assigned based on inferences at a genus or family level from data from this and other studies. If no information on dormancy was available at a family level, or if species within families exhibit different dormancy classes, species were excluded from the analysis

adult life span and capacity to resprout after fire. The tree species in the region, and also in the meta-analysis, include 4 *Corymbia* spp., 5 *Eucalyptus* spp. (both Myrtaceae), *Hakea lorea* (Proteaceae), and *Codonocarpus cotinifolius* (Golos 2013; Hart Simpson and Associates Pty Ltd. 2002; Mattiske Consulting Pty Ltd. 2004). Non-dormant seed in the Myrtaceae and Proteaceae may be serotinous (Merritt et al. 2007). However, the three tree species examined here appeared to be weakly serotinous with fruits spontaneously opening and shedding seeds as they ripened and dried (Golos 2013), they are resprouters, and at least two of them have a non-persistent seed bank (Golos 2013; Nano and Clarke 2011). In contrast, *Codonocarpus cotinifolius* (Gyrostemonaceae) is a fire ephemeral with PD seed (Baker et al. 2005a), indicating that it has a different strategy to remain a part of the community to the other tree species. So, it appears that most of the tree species exhibit traits such as a long adult life span, are weakly serotinous and are able to resprout, so that they do not need to rely on a soil seed bank for survival of the population.

Unlike trees, short-lived herbs, shrubs and grasses, do rely on a soil seed bank, as they germinate immediately post fire, and are likely to have a shorter life span than the average fire interval. Hence, unless, like *Scaevola parvifolia*, they have the ability to reproduce clonally (Golos 2013), their seeds must persist in the soil seed bank, and with germination likely be cued by fire (Wright and Clarke 2009). Interestingly, phenological patterns differ between grasses, herbs and shrubs, with grass seed reaching maturity in February and March but seeds of herbs and shrubs dispersing in September–November (Ritchie et al. 2017). Although this study found that *Triodia* seeds are dormant, this dormancy may not confer persistence, as previous research has postulated that *Triodia* seeds are short-lived (Wright and Clarke 2009). *Triodia* plants can be long-lived, and dominate the community after the short-lived ephemeral flora declines in abundance. Some *Triodia* species are capable of resprouting, however, *T. basedowii*, *T. epactia*, and *T. schinzii* are not resprouters (Rice and Westoby 1999). As plants are killed by fire, they are likely to rely on seed for recruitment. Based on our observations during seed collection, and those of others (Ritchie et al. 2017), *Triodia* species do not have serotinous seeds, as seeds disperse soon after

maturity. Hence, in contrast to trees which may be able to resprout following fire, are weakly serotinous, and may not need to rely on their seed bank; short-lived herbs and shrubs do rely on a seed bank to survive in the inter-fire intervals for the continuation of the species; and dominant *Triodia* species are long-lived, may not rely on a long-term persistent seed bank, but recruit from seed after fire.

Herbaceous species and grasses in this study mostly exhibited dormancy, but seeds of only nine species exhibited higher germination with the smoke cue, KAR_1. Germination of the *Triodia* species slightly increased with KAR_1 but seeds from the other grasses were not stimulated by KAR_1. For species with PD for which germination was not, or was only partly increased by KAR_1, manipulating temperature and moisture conditions, such as the use of after-ripening, stratification and/or wet dry may maximise germination (Hoyle et al. 2008). Given that herbaceous species and grasses disperse at different times of the year (Ritchie et al. 2017) and environmental conditions in the soil seedbank following dispersal overcome dormancy (Merritt et al. 2007), these different life-forms may have different requirements for dormancy-break. Response of seeds to smoke cues depends on the dormancy status of seeds (Baker et al. 2005c; Long et al. 2011a; Roche et al. 1997; Tieu et al. 2001b). Some seeds with PD do not have an inherent response to KAR_1, but seeds may become responsive to smoke when they have low levels of dormancy following soil storage, after-ripening or stratification. (Baker et al. 2005b; Long et al. 2011a). In fact, the stimulatory effect of KAR_1, particularly for grasses, may be underestimated, as previous studies and this one, have investigated the effect of KAR_1 on fresh seeds (Long et al. 2011b). Hence, some of the species in this study may respond to KAR_1 once dormancy has been alleviated.

In addition to KAR_1, gibberellic acid (GA_3) also stimulated germination of 10 species with PD. While the effect of GA_3 on germination of many of these species had not been tested, our results are in line with Commander et al. (2008) who found that GA_3 promoted germination of *Solanum diversiflorum*. Gibberellins can be used as a pre-treatment for seed-based restoration (Turner et al. 2013), and to further classify dormancy (Baskin and Baskin 2004). The 10 species in this study for which GA_3 stimulated germination are likely to exhibit non-deep or

intermediate PD, and species with PD for which GA_3 did not stimulate germination exhibit intermediate or deep PD. Further classifying species into these three levels can point to potential treatments to alleviate dormancy, such as dry storage and the length of time for stratification (Baskin and Baskin 2004).

In contrast to the interspecific variation in dormancy and response to KAR_1 and GA_3, the response to temperature was more similar between species. In this study, non-dormant and PY seeds germinated over a wide range of temperatures of 10–35 °C (2 spp.), 15–35 °C (4 spp.), and 20–35 °C (1 sp.), however, maximum germination rate was obtained at a narrower range of 25–30 °C (2 spp.), 30–35 °C (2 spp.), 35 °C (2 spp.) and 20–35 °C (1 sp.). These results are consistent with the findings for non-dormant seeds, as they germinate over the widest range of temperatures possible, with germination rate affected by temperature. Therefore, germination rate more clearly indicates the optimum germination temperature than germination percentage (Batlla and Benech-Arnold 2015). Interestingly, for *Streptoglossa macrocephala*, KAR_1 widened the range of temperatures over which high germination percentages were achieved, with increased germination rate. As expected, optimum germination temperatures of 20–35 °C were higher than optimum temperatures found in species from ecosystems of cooler climates further south (Bell and Bellairs 1992; Bellairs and Bell 1990; Cochrane et al. 2011; Plummer and Bell 1995), with the exception of those from the transition zone between south western Australia's mediterranean and arid zones (Whyte 2010). Few Australian species have been shown to have such high optimum germination temperatures, except *Solanum orbiculatum* (20–30 °C) (Commander et al. 2008), *Adansonia gregorii* (30–35 °C) (Turner and Dixon 2009), *Acacia stellaticeps* (20–35 °C), *A. stipuligera* (25–35 °C), *A. ancistrocarpa* (30–40 °C) (Golos 2013), and *Eucalyptus erythrocorys* (36 °C) (Cochrane 2017). These germination temperatures are also higher than the mean germination temperature of herbaceous species (24.5 °C), shrubs (23.7 °C) and trees (26.7 °C) in savannas across the globe (Baskin and Baskin 2014).

Fast germination was observed in non-dormant seeds and those treated to overcome PY, as hypothesised, with time to 50% germination ≤5 days. These results are similar to another study in arid Australia, where over half of the species achieved 50% (of their

final) germination within 3 days (Jurado and Westoby 1992). However, some desert species are able to germinate even faster, in <24 h (Liu et al. 2013). Evidence for a trade-off between germination percentage and speed, with fast germination associated with low final germination has been noted previously (Jurado and Westoby 1992), but the inverse has also been found (Morgan 1998). In addition, germination rate can increase as dormancy is lost (Commander et al. 2009a). With its sporadic rainfall, soil moisture in arid ecosystems may only be available for short periods (Kos and Poschlod 2010). So, although few dormant seeds may germinate in any single rainfall event, once seeds have become non-dormant, they may be able to germinate quickly, enabling their seedlings to establish during the brief period of moisture availability, an important trait in desert species (Liu et al. 2013).

Conclusion

Our study shows how seed traits such as dormancy, germination temperature and germination speed influence recruitment biology in an extreme environment. It has made a substantial contribution to the general knowledge of seed germination ecology of desert species, in terms of dormancy types, germination temperature, germination speed and response to the smoke cue, KAR_1. Our approach to strategically classify dormancy, determine optimum germination temperatures, assess the use of KAR_1 and GA_3 to increase germination could be used in other ecosystems where seeds are required for restoration. The information in this study will be useful to those undertaking restoration at mine sites in Australian deserts by identifying seed pre-treatments for seed broadcasting. The seed pre-treatments and information on germination temperatures will also be useful for those propagating seedlings for botanic gardens, amenity horticulture, floriculture or 'bush food' (native food) cultivation. Identification of dormancy types is critical for directing further research into pre-treatments for species for which germination was not maximised in this study.

References

Adondakis S, Venable DL (2004) Dormancy and germination in a guild of Sonoran Desert annuals. Ecology 85:2582–2590

Baker KS, Steadman KJ, Plummer JA, Dixon KW (2005a) Seed dormancy and germination responses of nine Australian fire ephemerals. Plant Soil 277:345–358

Baker KS, Steadman KJ, Plummer JA, Merritt DJ, Dixon KW (2005b) The changing window of conditions that promotes germination of two fire ephemerals, *Actinotus leucocephalus* (Apiaceae) and *Tersonia cyathiflora* (Gyrostemonaceae). Ann Bot 96:1225–1236

Baker KS, Steadman KJ, Plummer JA, Merritt DJ, Dixon KW (2005c) Dormancy release in Australian fire ephemeral seeds during burial increases germination response to smoke water or heat. Seed Sci Res 15:339–348

Baskin CC, Baskin JM (1998) Seeds: ecology, biogeography and evolution of dormancy and germination. Academic Press, San Diego

Baskin JM, Baskin CC (2004) A classification system for seed dormancy. Seed Sci Res 14:1–16

Baskin CC, Baskin JM (2007) A revision of Martin's seed classification system, with particular reference to his dwarf-seed type. Seed Sci Res 17:11–20

Baskin CC, Baskin JM (2014) Seeds: ecology, biogeography, and evolution of dormancy and germination. Academic Press, San Diego

Batlla D, Benech-Arnold RL (2015) A framework for the interpretation of temperature effects on dormancy and germination in seed populations showing dormancy. Seed Sci Res 25:147–158

Beard JS, Beeston G, Harvey J, Hopkins A, Shepherd D (2013) The vegetation of Western Australia at the 1:3,000,000 scale. Explanatory memoir. Second edition. Conserv Sci West Aust 9:1–154

Bell DT (1999) The process of germination in Australian species. Aust J Bot 47:475–517

Bell DT, Bellairs SM (1992) Effects of temperature on the germination of selected Australian native species used in the rehabilitation of bauxite mining disturbances in Western Australia. Seed Sci Technol 20:47–55

Bellairs SM, Bell DT (1990) Temperature effects on the seed germination of ten kwongan species from Eneabba Western Australia. Aust J Bot 38:451–458

Bureau of Meterology (2014) Climate and past weather. Commonwealth of Australia. www.bom.gov.au/climate/

Chesson P, Gebauer RLE, Schwinning S, Huntly N, Wiegand K, Ernest MSK, Sher A, Novoplansky A, Weltzin JF (2004) resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. Oecologia 141:236–253

Cochrane A (2017) Modelling seed germination response to temperature in Eucalyptus L'Her. (Myrtaceae) species in the context of global warming. Seed Sci Res 27:99–109

Cochrane A, Daws MI, Hay FR (2011) Seed-based approach for identifying flora at risk from climate warming. Austral Ecol 36:923–935

Cochrane A, Yates CJ, Hoyle GL, Nicotra AB (2015) Will among-population variation in seed traits improve the chance of species persistence under climate change? Glob Ecol Biogeogr 24:12–24

Cohen D (1966) Optimizing reproduction in a randomly varying environment. J Theor Biol 12:119–129

Commander LE, Merritt DJ, Rokich DP, Flematti GR, Dixon KW (2008) Seed germination of Solanum spp. (Solanaceae) for use in rehabilitation and commercial industries. Aust J Bot 56:333–341

Commander LE, Merritt DJ, Rokich DP, Dixon KW (2009a) The role of after-ripening in promoting germination of arid zone seeds: a study on six Australian species. Bot J Linn Soc 161:411–421

Commander LE, Merritt DJ, Rokich DP, Dixon KW (2009b) Seed biology of Australian arid zone species: germination of 18 species used for rehabilitation. J Arid Environ 73:617–625

Environmental Protection Authority (2014) Cumulative environmental impacts of development in the Pilbara region. Environmental Protection Authority, The Government of Western Australia

Erickson TE, Barrett RL, Merritt DJ, Dixon KW (eds) (2016) Pilbara seed atlas and field guide: plant restoration in Australia's arid Northwest. CSIRO Publishing, Clayton

Flematti GR, Ghisalberti EL, Dixon KW, Trengove RD (2004) A compound from smoke that promotes seed germination. Science 305:977

Flematti GR, Ghisalberti EL, Dixon KW, Trengove RD (2005) Synthesis of the seed germination stimulant 3-methyl-2H-furo[2,3-c]pyran-2-one. Tetrahedron Lett 46:5719–5721

Flematti GR, Merritt DJ, Piggott MJ, Trengove RD, Smith SM, Dixon KW, Ghisalberti EL (2011) Burning vegetation produces cyanohydrins that liberate cyanide and stimulate seed germination. Nature Commun 2:360

Geoscience Australia (2015) Deserts. http://www.ga.gov.au/scientific-topics/geographic-information/landforms/deserts

Golos P (2013) Restoring vegetation on waste rock dumps at the Telfer mine site in Australia's Great Sandy Desert: topsoil management and plant establishment. The University of Western Australia, Perth

Gutterman Y (2000) Environmental factors and survival strategies of annual plant species in the Negev Desert, Israel. Plant Species Biol 15:113–125

Hart Simpson and Associates Pty Ltd. (2002) Telfer Project Ecological Survey. Report prepared for Newcrest Mining Limited

Hoyle GL, Daws MI, Steadman KJ, Adkins SW (2008) Mimicking a semi-arid tropical environment achieves dormancy alleviation for seeds of Australian native Goodeniaceae and Asteraceae. Ann Bot 101:701–708

Jiménez-Alfaro B, Silveira FAO, Fidelis A, Poschlod P, Commander LE (2016) Seed germination traits can contribute better to plant community ecology. J Veg Sci 27:637–645

Jurado E, Flores J (2005) Is seed dormancy under environmental control or bound to plant traits? J Veg Sci 16:559–564

Jurado E, Westoby M (1992) Germination biology of selected central Australian plants. Aust J Ecol 17:341–348

Keith DA (2012) Functional traits: their roles in understanding and predicting biotic responses to fire regimes from individuals to landscapes. In: Bradstock RA, Gill AM, Williams RJ (eds) Flammable Australia: fire regimes, biodiversity and ecosystems in a changing world. CSIRO Publishing, Collingwood, pp 97–125

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. Restor Ecol 24:S36–S42

Kos M, Poschlod P (2007) Seeds use temperature cues to ensure germination under nurse-plant shade in xeric Kalahari savannah. Ann Bot 99:667–675

Kos M, Poschlod P (2010) Why wait? Trait and habitat correlates of variation in germination speed among Kalahari annuals. Oecologia 162:549–559

Kos M, Baskin CC, Baskin JM (2012) Relationship of kinds of seed dormancy with habitat and life history in the Southern Kalahari flora. J Veg Sci 23:869–879

Larson JE, Funk JL (2016) Regeneration: an overlooked aspect of trait-based plant community assembly models. J Ecol 104:1284–1298

Leyer I, Pross S (2009) Do seed and germination traits determine plant distribution patterns in riparian landscapes? Basic Appl Ecol 10:113–121

Liu K, Baskin JM, Baskin CC, Du G (2013) Very fast-germinating seeds of desert species are cryptoviparous-like. Seed Sci Res 23:163–167

Long RL, Stevens JC, Griffiths EM, Adamek M, Gorecki MJ, Powles SB, Merritt DJ (2011a) Seeds of Brassicaceae weeds have an inherent or inducible response to the germination stimulant karrikinolide. Ann Bot 108:933–944

Long RL, Stevens JC, Griffiths EM, Adamek M, Powles SB, Merritt DJ (2011b) Detecting karrikinolide responses in seeds of the Poaceae. Aust J Bot 59:610–620

Marques AR, Atman APF, Silveira FAO, de Lemos-Filho JP (2014) Are seed germination and ecological breadth associated? Testing the regeneration niche hypothesis with bromeliads in a heterogeneous neotropical montane vegetation. Plant Ecol 215:517–529

Martin AC (1946) The comparative internal morphology of seeds. Am Midl Nat 36:513–660

Mattiske Consulting Pty Ltd. (2004) Monitoring of vegetation regrowth after fire, Prepared for Newcrest Mining Limited

Merritt DJ, Dixon KW (2011) Restoration seed banks—a matter of scale. Science 332:424–425

Merritt DJ, Turner SR, Clarke S, Dixon KW (2007) Seed dormancy and germination stimulation syndromes for Australian temperate species. Aust J Bot 55:336–344

Morgan JW (1998) Comparative germination responses of 28 temperate grassland species. Aust J Bot 46:209–219

Myers JA, Harms KE (2010) Seed arrival and ecological filters interact to assemble high-diversity plant communities. Ecology 92:676–686

Nano C, Clarke P (2011) How do drought and fire influence the patterns of resprouting in Australian deserts? Plant Ecol 212:2095–2110

Nelson DC, Flematti GR, Ghisalberti EL, Dixon KW, Smith SM (2012) Regulation of seed germination and seedling growth by chemical signals from burning vegetation. Annu Rev Plant Biol 63:107–130

Ooi MKJ (2007) Dormancy classification and potential dormancy-breaking cues for shrub species from fire-prone south-eastern Australia. In: Adkins S, Ashmore S, Navie S (eds) Seeds: biology, development and ecology. CABI Publishing, Wallingford, Oxfordshire, pp 205–216

Ooi MKJ, Auld TD, Whelan RJ (2007) Distinguishing between persistence and dormancy in soil seed banks of three shrub species from fire-prone southeastern Australia. J Veg Sci 18:405–412

Peishi Z, Plummer JA, Turner DW, Choengsaat D, Bell DT (1999) Low- and high-temperature storage effects on viability and germinability of seeds of three Australian Asteraceae. Aust J Bot 47:265–275

Plummer JA, Bell DT (1995) The effect of temperature, light and gibberellic acid (GA$_3$) on the germination of Australian everlasting daisies (Asteraceae, Tribe Inuleae). Aust J Bot 43:93–102

Rice B, Westoby M (1999) Regeneration after fire in *Triodia* R. Br. Austral Ecol 24:563–572

Ritchie AL, Erickson TE, Merritt DJ (2017) Monitoring of plant phenology and seed production identifies two distinct seed collection seasons in the Australian arid zone. Rangel J 39:73–83

Roche S, Dixon KW, Pate JS (1997) Seed ageing and smoke: partner cues in the amelioration of seed dormancy in selected Australian native species. Aust J Bot 45:783–815

Rosbakh S, Poschlod P (2014) Initial temperature of seed germination as related to species occurrence along a temperature gradient. Funct Ecol 29:5–14

Saatkamp A, Affre L, Dutoit T, Poschlod P (2011) Germination traits explain soil seed persistence across species: the case of Mediterranean annual plants in cereal fields. Ann Bot 107:415–426

Tieu A, Dixon KW, Meney KA, Sivasithamparam K (2001a) The interaction of heat and smoke in the release of seed dormancy in seven species from southwestern Western Australia. Ann Bot 88:259–265

Tieu A, Dixon KW, Meney KA, Sivasithamparam K (2001b) Interaction of soil burial and smoke on germination patterns in seeds of selected Australian native plants. Seed Sci Res 11:69–76

Turner SR, Dixon KW (2009) Seed dormancy and germination in the Australian baobab, *Adansonia gregorii* F. Muell. Seed Sci Res 19:261–266

Turner SR, Merritt DJ (2009) Seed germination and dormancy. In: Offord CA, Meagher PF (eds) Plant germplasm conservation in Australia. Australian Network for plant Conservation Inc., Canberra, pp 87–108

Turner SR, Merritt DJ, Baskin JM, Baskin CC, Dixon KW (2006) Combinational dormancy in seeds of the Western Australian endemic species *Diplopeltis huegelii* (Sapindaceae). Aust J Bot 54:565–570

Turner SR, Steadman KJ, Vlahos S, Koch JM, Dixon KW (2013) Seed treatment optimizes benefits of seed bank storage for restoration-ready seeds: the feasibility of prestorage dormancy alleviation for mine-site revegetation. Restor Ecol 21:186–192

Venable DL (2007) Bet hedging in a guild of desert annuals. Ecology 88:1086–1090

Volis S, Bohrer G (2013) Joint evolution of seed traits along an aridity gradient: seed size and dormancy are not two substitutable evolutionary traits in temporally heterogeneous environment. New Phytol 197:655–667

Western Australian Herbarium (1998) FloraBase—The Western Australian Flora. Department of Parks and Wildlife. https://florabase.dpaw.wa.gov.au/

Whyte C (2010) The effects of water stress, salinity, and temperature on germination, seedling emergence, and seedling biomass: implications for restoration in the Shark Bay World Heritage Area. Honours Thesis. School of Plant Biology. The University of Western Australia, Perth

Wright BR, Clarke PJ (2009) Fire, aridity and seed banks. What does seed bank composition reveal about community processes in fire-prone desert? J Veg Sci 20:663–674