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Physical dormancy in seeds of six genera of Australian *Rhamnaceae*

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Abstract

Physical dormancy (PY) was identified in six genera representative of Australian *Rhamnaceae* and subsequently was broken, based on identification of key seed dormancy characteristics: (1) isolation and classification of embryo features; (2) imbibition experiments to determine the rate and amount of water uptake in seeds; and (3) determination of optimum temperature regimes for germination. All six species had relatively large spatulate embryos. Imbibition studies showed all species possessed PY (i.e. a water-impervious seed coat) that was broken by a hot-water treatment. Alleviation of PY resulted in high germination (>70%) at 7/18°C, temperatures similar to winter in south-west Western Australia. Germination was suppressed at higher temperatures and in the presence of light. The study adds information to our knowledge of seed dormancy in Australian *Rhamnaceae*, and highlights the benefits of understanding dormancy states in seeds prior to evaluating dormancy-release mechanisms on wild species used in restoration ecology and horticulture.

Keywords: *Alphitonia incana*, *Cryptandra arbutiflora*, seed germination, physical dormancy, *Pomaderris paniculosa*, *Rhamnaceae*, *Siegfriedia darwinioides*, *Spyridium globulosum*, *Trymalium ledifolium*

Introduction

The *Rhamnaceae* is a worldwide family represented by over 900 species, 100 of which are endemic to Australia (Marchant *et al.*, 1987; Corrick and Fuhrer, 1996). *Spyridium*, *Cryptandra* and *Trymalium* are common genera in the biodiverse south-west of Western Australia, and species such as *C. arbutiflora*, *S. globulosum* and *T. ledifolium* are significant components of understorey plant communities and are in demand for post-mining restoration programmes. Other species, including *Siegfriedia darwinioides* and *Pomaderris paniculosa*, may have significant horticultural potential, due to their growth habit and showy flower displays. Several species, including *C. arbutiflora* var. *pygmaea*, *T. densiflorum* and *T. litorale*, are listed as Priority 1 taxa [i.e. taxa that are known from one or a few (generally less than five) populations, which are under threat] and are conservation-dependent (Western Australian Herbarium, 1998–). To utilize Australian *Rhamnaceae* effectively in conservation, restoration and horticulture, reliable seed propagation methods are necessary. Previous work by Bell *et al.* (1987, 1995), Ward *et al.* (1997) and Hanley and Lamont (2000) has reported that hot-water treatment, thermic pulsing or smoke increase seed germination of *T. ledifolium*. Dixon *et al.* (1995) reported that *S. darwinioides* and *S. globulosum* were smoke responsive. However, the mechanism(s) of dormancy and of dormancy release for seeds of Australian *Rhamnaceae* are yet to be generally established.

The family *Rhamnaceae* is one of 15 angiosperm families known to possess seeds with physical dormancy (PY) (Baskin and Baskin, 1998). Species with PY are characterized by a water-impermeable seed or fruit coat that consists of one or more palisade layers of lignified cells, or macrosclereids. Typically, these species possess a water gap, such as a strophiole or hilum, that acts as a water-regulating structure in the testa. The breaking of PY involves the disruption or dislodgment of this water plug or gap, thereby creating an entry point for water into the seed (Baskin

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et al., 2000). This event acts as an environmental 'signal detector' for germination to proceed.

Some *Rhamnaceae* also possess embryo-based dormancy in addition to PY. For example, the seed coat of *Discaria toumatou*, a New Zealand *Rhamnaceae* species, consists of a tightly packed palisade layer of macrosclereid cells and associated *linea lucida*, features typical of those found in other hard-seeded, physically dormant species (Keogh and Bannister, 1994). However, once PY is broken, seeds still require stratification at 5°C for germination to proceed (Keogh and Bannister, 1992). Thus, seeds of *D. toumatou* have not only seed-coat-imposed dormancy (PY), but also embryo dormancy (physiological dormancy), i.e. they exhibit combinational dormancy (PY + PD) (*sensu* Baskin and Baskin, 2004).

Light (Plummer and Bell, 1995), gibberellic acid (GA_3) (Hagon, 1976) and smoke (Dixon *et al.*, 1995) are common factors in promoting germination in many Australian plants. For example, *Erymophyllum ramosum*, *Millotia myosotidifolia* and *Podotheca chrysantha* (*Asteraceae*) are light responsive/requiring (Plummer and Bell, 1995; Schütz *et al.*, 2002); *Botriochloa macra* (*Poaceae*), *Brachyscome iberidifolia* (*Asteraceae*) and *Caltha introloba* (*Ranunculaceae*) are GA_3 responsive (Hagon, 1976; Wardlaw *et al.*, 1989; Bunker, 1994); and *Geleznowia verrucosa* (*Rutaceae*), *Anigozanthos manglesii* (*Haemodoraceae*) and *Stylidium affine* (*Stylidaceae*) are smoke responsive (Dixon *et al.*, 1995; Roche *et al.*, 1997a, b, 1998; Tieu *et al.*, 2001). Temperature is also crucial to successful germination of Australian species. Numerous studies (Bellairs and Bell, 1990; Bell and Bellairs, 1992; Bell *et al.*, 1995) have demonstrated a high correlation between habitat temperature during the rainfall season and optimal germination temperature.

This study investigates and describes seed dormancy and germination characteristics in Australian *Rhamnaceae* taxa to provide a more systematic approach for determining dormancy-breaking treatments. Specifically, the aims of this study were to: (1) determine the presence/absence of PY via imbibition experiments; (2) classify seed embryo type; (3) determine the optimal temperature regime for germination; (4) characterize the response of seeds to the common germination promoters, GA_3 and smoke; and (5) optimize the method employed to break PY.

Materials and methods

Seeds

Seeds from species in each of six genera [*Alphitonia incana* (Roxb.) Kurz, *Cryptandra arbutiflora* Fenzl, *Pomaderris paniculosa* Reissek, *Siegfriedia darwinioides* C.A. Gardner, *Spyridium globulosum* (Labill.) Benth. and *Trymalium ledifolium* Fenzl] from Western Australia were selected as representative of Australian *Rhamnaceae* in terms of habitat, dominance and restoration priority. Fruits were collected at maturity from *C. arbutiflora* and *S. globulosum* in January 2003 and from *A. incana* in December 2003. *T. ledifolium* fruits were obtained from a commercial seed supplier (collection date 2002). Seeds from these species were removed from fruits manually, by rubbing on a rubber mat. *P. paniculosa* and *S. darwinioides* seeds were obtained from the Kings Park germplasm collection, but their collection date is unknown. All seeds were stored at room temperature (*c.* 22°C) and ambient relative humidity (*c.* 50% RH).

Seed viability

Seed viability of each species was estimated using a cut test on a random sample of three replicates of 50 seeds, and scored based on the presence or absence of a white, turgid, fully formed embryo and endosperm. Average seed weight was determined on three replicates of 50 seeds and average seed length on three replicates of 20 seeds. To extract embryos, seeds were treated with hot water (88–92°C) for 5 min, cooled and incubated on pre-moistened Whatman filter paper (no. 182) for 48 h. Embryos then were gently excised from the imbibed seeds and classified according to Martin (1946).

Imbibition experiments

For each study species, six replicates of 10–20 seeds were weighed, moistened for 5 min in Petri dishes lined with irrigated seed germination papers, blotted dry and reweighed. Three replicates were then placed in hot water (88–92°C) for 5 min, removed and placed back onto moistened germination papers. Hot-water-treated seeds and non-treated seeds were removed from Petri dishes at regular intervals and weighed, following the same protocol.

Seed germination

Germination trials were undertaken on *C. arbutiflora*, *S. darwinioides*, *S. globulosum* and *T. ledifolium* seeds. A sufficient number of seeds of *A. incana* and *P. paniculosa* were not available for germination tests. To determine the effects of common germination stimulants on germination, seeds were surface-sterilized in a 1% (w/v) calcium hypochlorite [$Ca(OCl)_2$] solution for 30 min, then incubated immediately (control) or placed in hot water (88–92°C) for 5 min. Following the hot-water treatment, subsets of seeds were imbibed for 24 h in 1000 p.p.m. GA_3, 10% (v/v) smoke water, or a combination of GA_3 and

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smoke water. Straw was used to generate smoke, and the process for making the smoke solution used in this study was described by Dixon *et al.* (1995). The concentration of GA_3 selected for this study, while in the upper range of concentrations commonly evaluated (typically 10–1000 p.p.m.), nevertheless has proved to be very effective in stimulating germination responses in seeds of many different Australian native species (Turner *et al.*, unpublished results).

All solutions had been previously filter-sterilized using a 0.2 μm Acrodisc® 32 filter (Millipore S.A., Molsheim, France). Seeds were then placed into Petri dishes lined with germination papers and moistened with sterile, de-ionized water. Petri dishes were incubated in 12/12 hours light/dark (irradiance of 30 $\mu mol\, m^{-2}\, s^{-1}$, 400–700 nm), or in constant darkness, in one of three alternating (12/12 hours) temperature regimes of 7/18°C, 13/26°C or 18/33°C.

To determine the optimal duration of hot-water treatment, other seeds were exposed from 15 s to 8 min. Following this, seeds were incubated in darkness at 7/18°C (the optimal temperature). Five replicates of 20 seeds were used for all treatments. Seeds were considered germinated upon radicle emergence, and germination was scored every 7 d for 5–8 weeks.

Statistical analysis

Imbibition and germination data were analysed for statistical significance by analysis of variance (ANOVA). Percentage values for seed weight (imbibition) and germination were arcsine-transformed prior to analysis (non-transformed data appear in all tables and figures). Fisher's least significant difference ($P < 0.05$) was used to determine significant differences between treatments.

Results

Seed viability

Seed viability of all species was high (>80%) (Table 1). Seeds of most species were of similar size (Table 1), with the exception of those of *A. incana*, which were more than twice as large and substantially heavier. Embryos extracted from all species were fully developed, of the spatulate type and large (relative to the size of the seed), ranging from approximately 0.9 mm (*T. ledifolium*) to 3.1 mm (*A. incana*). The embryo length to seed length ratio (E:S ratio) ranged from 0.73 for *A. incana* to 0.83 for *P. paniculosa* (Table 1).

Imbibition experiments

There were limited increases in seed weight for non-treated (control) seeds (Fig. 1). Percentage increases in weight ranged from 0.12% (*P. paniculosa*) to 16% (*A. incana*). However, when seeds were exposed to a hot-water treatment, significant increases ($P < 0.05$) in subsequent water uptake were found (Fig. 1). Water uptake rates were variable between species, with *C. arbutiflora* showing a significant weight increase after only 1 h of imbibition, while *S. globulosum* significantly increased in weight only after 2 d of imbibition.

Seed germination

Germination of untreated seeds was very low (1–11%) for all species (Fig. 2). Hot-water treatment resulted in significantly higher germination ($P < 0.05$) than untreated seeds, particularly for seeds incubated at 7/18°C (Fig. 2). Germination was significantly less at

Table 1. Regional occurrence, average weight (mg ± SE), length (mm ± SE), embryo to seed ratio (E:S ratio) and percentage viability (±SE) of Western Australian *Rhamnaceae* seeds used in this study

Species	Location[1]	Average seed weight (mg ± SE)	Average seed length (mm ± SE)	E:S ratio	Viability (% ±SE)
Alphitonia incana	Northern Kimberley, Central Kimberley; Rainforest	18.4 ± 0.4	3.9 ± 0.0	0.73	81 ± 1
Cryptandra arbutiflora	Avon, Esperance, Geraldton, Swan Coastal Plain, Warren; Woodland–heathland	0.4 ± 0.0	1.2 ± 0.0	0.74	80 ± 5
Pomaderris paniculosa	Esperance; Heathland	0.7 ± 0.0	1.5 ± 0.0	0.83	97 ± 0
Siegfriedia darwinioides	Esperance, Avon; Heathland	0.9 ± 0.0	1.5 ± 0.0	0.82	100 ± 0
Spyridium globulosum	Hampton, Esperance, Geraldton, Swan Coastal Plain, Warren; Forest–coastal heath	1.3 ± 0.0	1.5 ± 0.0	0.83	98 ± 1
Trymalium ledifolium	Avon, Esperance, Geraldton, Swan Coastal Plain, Warren; Forest–woodland	0.3 ± 0.0	1.2 ± 0.0	0.78	85 ± 1

[1] After Paczkowska and Chapman (2000).

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13/26°C and 18/33°C than at 7/18°C for all species ($P < 0.05$). For *C. arbutiflora*, *S. globulosum* and *T. ledifolium*, germination in light was significantly less ($P < 0.05$) than in darkness for some treatments (those without GA_3) at 13/26°C and 18/33°C.

Exposure to light did not affect the final germination percentage at 7/18°C, but reduced the rate of germination at 7/18°C for all species. Treatment with GA_3 increased the germination rate of all species at 7/18°C (for both light and dark treatments), particularly for *S. darwinioides*, and partially overcame the light and temperature suppression of germination of *C. arbutiflora*, *S. globulosum* and *T. ledifolium* seeds at 13/26°C and 18/33°C (Fig. 2). Treatment with smoke water had no effect on seed germination rates or percentages across all temperature and light/dark regimes examined.

Exposure of seeds to hot water for as little as 15 s was sufficient to induce significant germination for all species (Fig. 3) ($P < 0.05$). Only seeds of *S. globulosum* required a longer exposure (2 min) for maximum germination (Fig. 3). Hot-water treatment of seeds for up to 8 min made little difference to germination, although a gradual reduction in germination of *C. arbutiflora* seeds was observed following exposure times greater than 1 min.

Discussion

Using a systematic approach based on identifying key seed characteristics, PY was identified and subsequently alleviated in six genera of Australian *Rhamnaceae*. Previous to these findings, *Rhamnaceae*

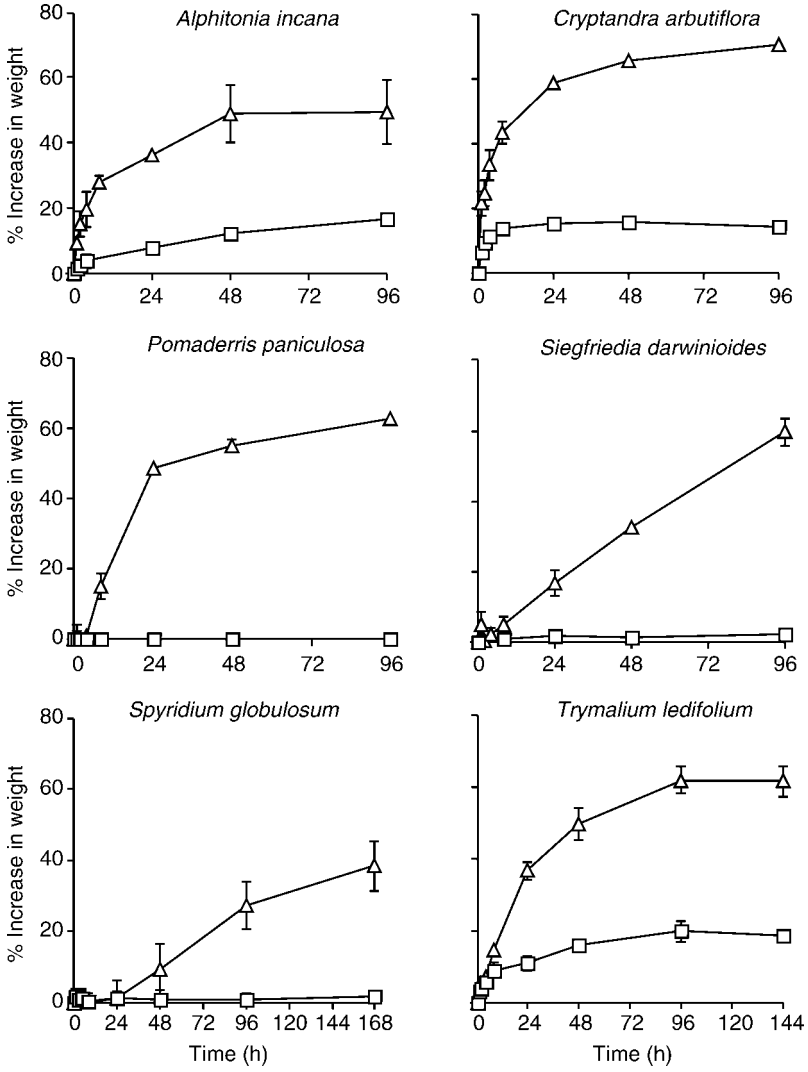

Figure 1. Average percentage increase in weight (±SE) of control (□) and hot-water-treated (△) seeds from six Australian *Rhamnaceae* species.

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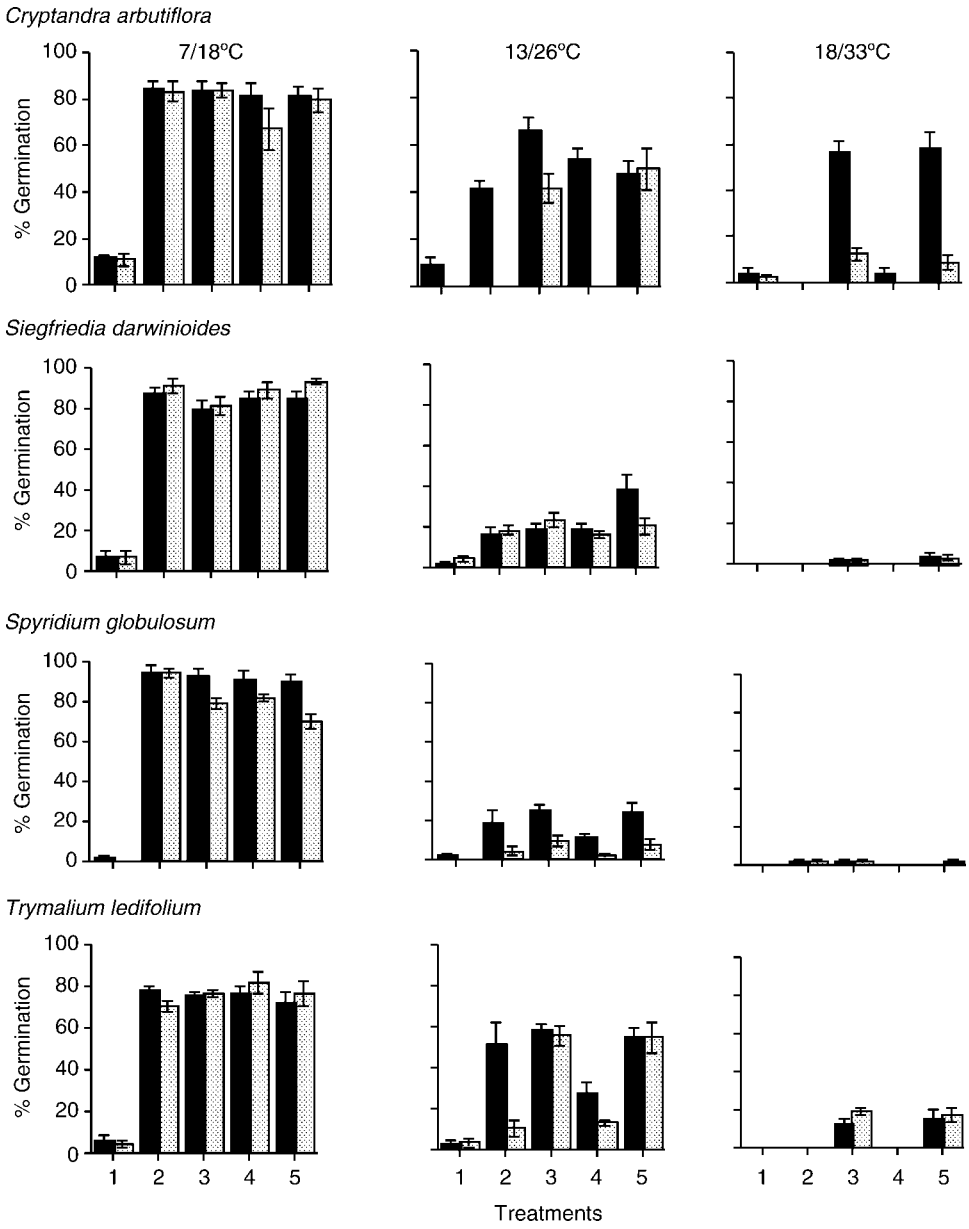

Figure 2. Average percentage germination (±SE) for seeds of four Australian *Rhamnaceae* species subjected to five treatments: 1, control; 2, hot water; 3, hot water + GA_3; 4, hot water + smoke; and 5, hot water + GA_3 + smoke, at three temperature regimes (7/18, 13/26 and 18/33°C) and exposure to 12/12 hours photoperiod (hatched bars) or constant darkness (black bars) during germination for up to 56 d.

species, such as *Trymalium ledifolium*, *Siegfriedia darwinioides* and *Spyridium globulosum*, were known to be heat and/or smoke responsive (Bell *et al.*, 1987, 1995; Dixon *et al.*, 1995; Ward *et al.*, 1997; Hanley and Lamont, 2000). However, germination percentages achieved using these methods were low, and the true nature of seed dormancy in these species was not fully understood.

Imbibition experiments demonstrated that water uptake of non-scarified seeds was clearly negligible, indicating the presence of water-impermeable tissue. PY was effectively and easily broken by a single treatment with hot water in all six species. The morphological structure of the water-impervious tissue layer in these species is presently unknown, but an anatomical study of the physically dormant New Zealand *Rhamnaceae* species, *Discaria toumatou*, provides evidence of a palisade layer of macrosclereid cells in the testa (Keogh and Bannister, 1994), and it is likely that the six species of *Rhamnaceae* in our study

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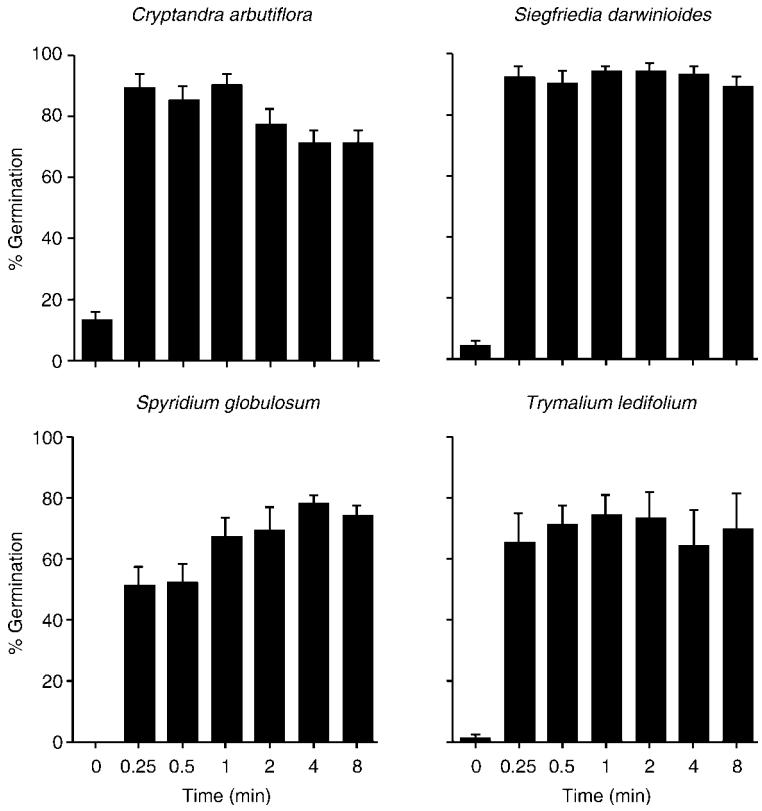

Figure 3. Average percentage germination (±SE) for seeds of four Australian *Rhamnaceae* species subjected to hot-water treatment in a 88–92°C water bath for 15 s to 8 min. Germination was scored up to 56 d after treatment at 7/18°C.

have a similar anatomy. Once PY was alleviated, water uptake increased substantially, to between 41% (*S. globulosum*) and 75% (*C. arbutiflora*), and seed germination proceeded. A very brief exposure to hot water (15 s) was sufficient to break PY for all species. Other studies on physically dormant, native Australian species have found similar results, with *Davesia cordata* and *Templetonia retusa* seeds (Bell and Williams, 1998) requiring only a 30 s exposure to hot water to germinate to high levels, and *Dodonaea viscosa* requiring only a 1–5 s exposure for dormancy-break (Hodgkinson and Oxley, 1990; Baskin *et al.*, 2004).

Water uptake of non-dormant seeds was most rapid for *C. arbutiflora* and *A. incana* (evident after 1 h) and most gradual for *S. globulosum* (only evident after 2 d). Slow water uptake rates have been suggested to be associated with the prevention of germination following brief, intermittent showers during the beginning of the wet season, or at other inappropriate times of the year for seedling establishment, when rainfall is sporadic (Thanos *et al.*, 1989; Baskin *et al.*, 2004). Such a mechanism would be useful for delaying germination until sufficient soil moisture is available to ensure seedling survival. This may partly explain the slow uptake of water in non-dormant *S. globulosum* seeds. This species grows in coastal regions with highly leached soils (predominantly white sand with little organic matter), high summer temperatures, desiccating winds and a limited overstorey. A slow rate of imbibition, acting as a moisture gauge in this seasonally wet–dry environment, would help ensure that seed germination occurs only when sufficient soil moisture is available for seedling establishment (Baskin *et al.*, 2004). However, other species that imbibed rapidly (e.g. *C. arbutiflora*) also occur in highly seasonal rainfall environments, where such a mechanism would be advantageous. Thus, it appears to be difficult to generalize the nature of the driving forces behind water uptake of physically dormant species. Both the natural timing of PY break and the exact environmental cues (e.g. fluctuations in daily temperature regimes, soil moisture) required to overcome PY in these species are unknown. Studies on these aspects may provide clues as to the reasons for varying imbibition rates between species.

For all six species tested, seed germination was greatest at the 7/18°C temperature regime. A relatively small temperature increase of 6–7°C resulted in a >50% reduction in germination, in most cases. Other studies on the germination biology

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of species from south-west Western Australia have demonstrated a similar, narrow temperature range for optimal germination. Bell *et al.* (1995) found that an increase in temperature from 15 to 23°C resulted in greatly reduced germination of the legume species *Acacia drummondii* ssp. *candolleana*, *Acacia lateriticola*, *Bossiaea ornata*, *B. aquifolium* and *Hovea trisperma*. Bellairs and Bell (1990) and Bell and Bellairs (1992) have reported the same phenomena for many other legumes and non-dormant, serotinous species, and concluded that the highly seasonal nature of rainfall in this region is the major contributing factor. In south-west Western Australia, around 80% of the annual rainfall occurs during late autumn and winter (May–August), when the temperatures are 7–10°C at night and 16–20°C during the day. The 7/18°C temperature regime used in this study is representative of the temperatures to which seeds are exposed during the wet season, and germination appears cued for this period to maximize the chances of seedling survival.

Light inhibited germination of most of the species in many of the treatments, especially at the warmer temperatures (13/26°C and 18/33°C). This finding is unusual, as physically dormant species are generally neither suppressed nor promoted by the presence of light (Baskin *et al.*, 2004), and in many cases, germination requirements of seeds with PY are highly non-specific (Baskin *et al.*, 1998; Li *et al.*, 1999). Once PY is broken, seeds are usually capable of germinating over a wide range of constant or alternating temperatures, and various types of photoregimes (Baskin *et al.*, 2004). However, light suppression of seed germination, particularly at higher germination temperatures, is a commonly reported phenomenon for south-west Australian species, including many which are physically dormant (Bell *et al.*, 1995), and has also been shown for other Mediterranean climate species found in other parts of the world, such as *Glaucium flavum* (Thanos *et al.*, 1989). This appears particularly prevalent in species that produce small seeds (<10 mg) (Bell *et al.*, 1995), such as the *Rhamnaceae* in this study. It is likely that light inhibition is a secondary 'protective' mechanism that ensures seeds that have lost PY do not germinate at the soil surface, where they may be prone to desiccation. The light and temperature suppression of germination was partially overcome by GA_3, particularly for seeds of *C. arbutiflora*, *S. globulosum* and *T. ledifolium*. This phenomenon has been reported for other Australian species, including *Juncus pallida* (Bell, 1993) and *Rhodanthe floribunda* (Plummer and Bell, 1995), and may be suggestive of a possible involvement of phytochrome in the light response (Plummer and Bell, 1995; Bell, 1999).

Previous studies provide evidence that smoke application increases the germination of some *Rhamnaceae* species. Ward *et al.* (1997) found germination of *T. ledifolium* increased from 61 seedlings recorded from non-smoked control soils to 91 seedlings recorded from aerosol-smoked soils, while Dixon *et al.* (1995) found germination of *S. darwinioides* and *S. globulosum* to increase from *c.* 1 to 4%, and *c.* 8 to 20% respectively, following smoke application in glasshouse trials. Several other physically dormant species (e.g. *Bossiaea aquifolium*, *B. ornata*, *Gompholobium marginatum*, *Hovea chorizemifolia* and *Kennedia coccinea*) also respond to some degree to smoke application (with no heat involved) (Roche *et al.*, 1997a). The results presented here indicate that a 10% smoke solution does not stimulate germination of the species tested in this study, and that application of this smoke solution does not stimulate further germination under any temperature regime, once PY is broken. The reasons for smoke-induced germination of other physically dormant seeds have not been adequately explained and require further investigation.

The results from this study will significantly increase the number of *Rhamnaceae* species available for land restoration projects and native plant horticulture, and will help to further conservation efforts for threatened Australian *Rhamnaceae* taxa. Future research should focus on investigating the ecological cue(s) that naturally break dormancy in these species, and the circumstances and mode of action of smoke and smoke products that have been found to stimulate germination of physically dormant Australian *Rhamnaceae* species in previous studies.

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