Occurrence of Physical Dormancy in Seeds of Australian Sapindaceae: A Survey of 14 Species in Nine Genera

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• Background and Aims Sapindaceae is one of 16 angiosperm families whose seeds have physical dormancy (PY). However, the extent and nature of PY within this family is poorly known. The primary aims of this study were: (1) to evaluate seed characteristics and determine presence (or not) of PY within nine genera of Australian Sapindaceae; and (2) to compare the frequency of PY across the phylogenetic tree within Sapindaceae.

• Methods Viability, imbibition and seed characteristics were assessed for 14 taxa from nine genera of Sapindaceae. For five species of Dodonaea, optimal conditions for germination and dormancy break were evaluated. An in situ burial experiment was performed on D. hackettiana seeds to identify the factor(s) responsible for overcoming PY. Classes of dormancy and of non-dormancy for 26 genera of Sapindaceae were mapped onto a phylogenetic tree for the family.

• Key Results Mean seed viability across all taxa was 69.7%. Embryos were fully developed and folded (seven genera) or bent (two genera); no endosperm was present. Seeds of all five Dodonaea spp. and of Distichostemon hispidulus had PY. Hot-water treatment released PY in these six species. Optimal germination temperature for seeds of the four Dodonaea spp. that germinated was 15–20°C. Following 5 months burial in soil, 36.4% of D. hackettiana seeds had lost PY and germinated by the beginning of the winter wet season (May). Laboratory and field data indicate that dormancy was broken by warm, moist temperatures (≥50°C) during summer.

• Conclusions PY occurs infrequently in genera of Sapindaceae native to Australia. Seeds of Dodonaea and Distichostemon have PY, whereas those of the other seven genera did not. Seeds of these two genera and of Diploptelis (a previous study) are the only three of the 20 native Australian genera of Sapindaceae for which germination has been studied that have PY; all three belong to subfamily Dodonacoideae.

Key words: Dodonaea spp., physical dormancy, Sapindaceae, seed ecology, seed germination.

INTRODUCTION

Dormancy is defined as the inability of seeds to germinate when exposed to conditions (e.g. moisture, temperature and light) that are otherwise favourable for germination once the seeds become non-dormant. It is common in seeds of species that grow in environments in which conditions are unfavourable for successful plant establishment immediately following seed dispersal. Five classes of seed dormancy are now recognized (Nikolaeva, 1977; Baskin and Baskin, 1998, 2004). Seeds with physiological dormancy (PD) have a water-permeable seed coat, a fully developed embryo, and a physiological inhibiting mechanism that prevents radicle emergence. Morphological dormancy (MD) is due to an underdeveloped embryo that needs time to grow (= dormancy period) before the seed can germinate, and morphophysiological dormancy (MPD) to an underdeveloped embryo that is physiologically dormant. Physical dormancy (PY) is caused by a water-impermeable seed or fruit coat, and combinational dormancy (PY + PD) by a water-impermeable seed or fruit coat and a physiologically dormant embryo. The embryo is fully developed in seeds with PY and in those with (PY + PD).

PY is known to occur in seeds of one monocot and 15 eudicot families of angiosperms, and it is not known to occur in seeds of gymnosperms (J. Baskin et al., 2000, 2006). However, in most of these families other classes of dormancy also can be found, in addition to PY and/or (PY + PD). One of these families is the Sapindaceae. In this family, relatively little is known about the prevalence of PY. For example, PY or (PY + PD) has been documented for species in only five genera (Koelreuteria, Diploptelis, Dodonaea, Sapindus and Cardiopermum: Johnston et al., 1979; Munson, 1984; Park and Rehman, 1999; Rehman and Park, 2000; Baskin et al., 2004; Turner et al., 2006a), while seeds of several other species, including Acer spp., Aesculus hippocastanum, Artryera littoralis, Euphoria logan, Diploptelis diphylleigia and Sapindus mukorossi, have been shown to have PD or to be non-dormant (Nikolaeva, 1969; Ng, 1978; Chin et al., 1984; Hopkins and Graham, 1987; Negi and Todaria, 1993; Finch-Savage et al., 1998; Steadman and Pritchard, 2004). Thus, of the approximately 133 Sapindaceae genera worldwide (Harrington et al., 2005),

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class of dormancy has been tentatively determined for seeds in less than 10% of them (Baskin and Baskin, unpubl. database, 1998).

The Sapindaceae is a large predominantly subtropical–tropical family, with several common genera found in temperate regions as well, including the maples (Acer spp.) and horse chestnuts (Aesculus spp.; Harrington et al., 2005; Simpson, 2006). About 2000 species are currently known, many of which are cultivated for fruit production, e.g. Litchi chinensis (lychee); for horticultural purposes, e.g. Acer spp. (maples) or timber (Edwards and Gadek, 2001; Harrington et al., 2005; Krupnick and Kress, 2005; Simpson, 2006). A recent revision of Sapindaceae based on parsimony and Bayesian analysis of plastid matK and rbcL DNA sequences identified four sub-families: Sapindoideae, Dodonaeoideae, Hippocastanoideae and Xanthoceroideae; representatives of only the first two clades are native to Australia. By far the largest subfamily in Australia is Sapindoideae, with at least 23 genera, while the much smaller Dodonaeoideae has at least five genera (Harrington et al., 2005). Within the Australian flora, there are an estimated 150 species of Sapindaceae. Dodonaea (hop bushes) is the largest genus with approx. 70 species, primarily associated with more arid parts of the continent (Reynolds, 1985; Marchant et al., 1987). Several taxa of Australian Sapindaceae, including Alectryon, Cupaniopsis, Diploglottis, Harpullia and Jagera (Reynolds, 1985), have horticulture value, and eight species (Cupaniopsis shirleyana, C. tomentella, Diploglottis campbellii, Dodonaea procumbens, D. ripicola, D. subglandulifera, Toechima pterocarpum and Toechima sp. East Alligator River) are currently nationally listed as threatened (Department of Environment and Water Resources, 2007). The easiest and most economical way to propagate threatened and horticulturally significant Sapindaceae taxa is through seed propagation. Yet given the prominence of Sapindaceae in Australia, remarkably little is currently known about seed dormancy-breaking and germination requirements of Australian members of this family, making seed-based propagation methods for many Sapindaceae species problematic. Therefore, knowing which Australian genera are likely to possess seed dormancy will improve propagation and restoration outcomes for these and related species.

A key question tied to dormancy and germination in Australian Sapindaceae is the prevalence of PY, a condition that has already been demonstrated for seeds of two Australian genera in the family (Baskin et al., 2004; Turner et al., 2006a). Therefore, given the limited knowledge concerning seed dormancy amongst species of Sapindaceae in Australia, we hypothesized that water impermeability of the seed coat (PY) will be prevalent amongst species in the two clades of Sapindaceae that occur in Australia. The aims of this study were: (1) to estimate percentage seed viability and describe seed morphology and embryo type for 14 taxa of Sapindaceae native to Australia; (2) to determine which of these species have water-impermeable seed coats; (3) to test the effects of hot-water treatment and application of dry heat on dormancy-break in seeds of Dodonaea spp.; (4) to evaluate the effect of incubation temperature on germination of seeds of Dodonaea spp. following hot-water treatment; (5) to identify the factor(s) responsible for natural dormancy-break in buried seeds of Dodonaea hackettiana; and (6) to investigate phylogenetic origins of PY in the two subfamilies of Sapindaceae native to Australia.

MATERIALS AND METHODS

Species selection and seed sources

Seeds of 14 species from nine genera (Alectryon connatus F. Muell., Allophylus cobbe (L.) Blume, Atalaya hemiglaucus F. Muell., Cupaniopsis anacardioide A. Rich., C. parvifolia Bailey, Distichostemon hispidulus Endl., Ganophyllum falcatus Blume, Harpullia pendula Planchon ex F. Muell., Synima cordierorum F. Muell., Dodonaea aptera Miq., D. hackettiana W. Fitzg., D. petiolaris F. Muell., D. ptarmicaefolia Turcz. and D. stenozyga F. Muell.) representing the two subfamilies of Sapindaceae native to Australia were selected for this study. Fresh fruits and seeds were collected from the Daintree River, North Queensland (A. cobbe, S. cordierorum and G. falcatus) and Mt Annan Botanic Garden, New South Wales (H. pendula), depulped (A. cobbe, S. cordierorum and G. falcatus) in January, February and May 2007 and sent via express mail to Kings Park. Seeds from Alectryon connatus and Cupaniopsis parvifolia were supplied by the Brisbane Botanic Gardens, Queensland. These were collected fresh in January 2007 and stored at 5 °C until provided for this study. Atalaya hemiglaucus and C. anacardioidei seeds were purchased from commercial seed suppliers and were collected several years ago and stored at 5 °C until purchased for this study. Seeds from all five Dodonaea spp. and Distichostemon hispidulus were provided by the Seed Technology Centre, Kings Park and Botanic Garden. Seeds of the six species were collected in 1984 (D. petiolaris), 1986 (D. ptarmicaefolia and D. stenozyga), 1992 (D. hispidulus), 1999 (one accession of D. hackettiana), 2003 (D. aptera) and December 2006 (one accession of D. hackettiana). Following collection, they were stored at −18 °C until used in this study.

Seed viability

Seeds were initially evaluated for seed fill using a Faxitron X-ray machine. Unless otherwise stated, four replicates of 100 randomly selected seeds were X-rayed and the images were visually assessed to detect empty seeds or degraded embryos. Following initial X-ray screening, embryo quality was quickly assessed on several seeds from each accession, based on presence or absence of a white, fully formed embryo (Turner et al., 2005). Only seeds that appeared full and intact and possessed a turgid embryo were considered to be viable and used in further tests.

Embryo classification

Seeds were bisected longitudinally and the embryo observed and photographed to determine embryo type (Martin, 1946). Seeds of Alectryon connatus, Allophylus
Seed length and mass

For each study species, three replicates of 20 seeds were measured using a binocular microscope equipped with an ocular micrometer. From these data, mean seed length (± s.e.) was calculated. Measurements were also recorded for species with indehiscent fruits (i.e. *Allophyllus cobbe, Atalaya hemiglaucia, Ganophyllum falcatum*), both with the endocarp intact and removed. To calculate mean seed mass, three replicates of 20 seeds were weighed to the nearest 0.1 mg using a microbalance. From these data, mean seed mass (± s.e.) was calculated. Masses were also determined for species with indehiscent fruits, both with and without the endocarp removed.

Seed moisture content

Three replicates of 20 seeds each of 11 of the 14 species were initially weighed (to the nearest 0.1 mg) using a microbalance, then placed in an oven at 103 °C for 17 h. Upon removal, seeds were immediately reweighed, and then seed moisture content was determined gravimetrically (gH₂O g⁻¹ d wt; ISTA, 1999). Seed moisture content was not determined for *A. conatus, C. anacardioides* and *D. hispidulus* due to insufficient quantities of seeds.

Imbibition

Imbibition tests were done to determine whether seeds were permeable or impermeable to water. These tests were carried out under ambient room conditions (~23 °C). For each study species, seeds were initially X-rayed to select only filled seeds. From these filled seeds, three replicates of 10–20 seeds each were weighed (to the nearest 0.1 mg), moistened for 5 min in 90-mm Petri dishes. Treated seeds (hot-water treatment) were dipped in hot water (88–92 °C) for 30 s (all species) or 2.5 min (*D. petiolaris* only) prior to the imbibition test. The same imbibition protocol was followed as outlined above for control seeds.

Seed dormancy-break and germination

The effects of hot-water treatment and incubation temperature were evaluated on all five *Dodonaea* species. Non-treated (control) seeds were firstly surface-sterilized in 2 % (w/v) calcium hypochlorite [Ca(OCl)₂] solution for 30 min (10 min with vacuum + 10 min normal + 10 min with vacuum), rinsed three times in sterile distilled water and plated onto 0.8 % (w/v) water agar plates in 90-mm Petri dishes. Treated seeds (hot-water treatment) were dipped in hot water (88–92 °C) for 30 s, removed and surface-sterilized, and plated onto water agar plates as previously described. Each treatment consisted of three replicates of 25 seeds each. Seeds were incubated in constant darkness (except when they were checked for germination) after 4 d and then daily for 19 d (23 d total) to provide cumulative germination, maximum germination and a germination rate index (GRI) calculated from the following formula (Maguire, 1962):

\[
\text{GRI}(\%\text{d}^{-1}) = \sum[(G_i - G_{i-1})/i]
\]

where \(i\) is the germination count-day, \(G_i\) the percentage of seeds germinated at time \(i\) and \(G_{i-1}\) the percentage of seeds germinated the previous count-day.

The effect of hot-water treatments and dry alternating temperatures on breaking PY was determined by dipping *D. aperta, D. hackettiana, D. ptarmicaefolia* and *D. stenozyga* seeds in water at 20, 30, 40, 50, 60, 70, 80,
90 or 100 °C for 30 s or by exposing them dry to eight daily temperature cycles of 15/50 °C (12/12 h cycles). For D. hackettiana only, seeds were exposed to 1 h of dry heat at constant temperatures of 20, 30, 40, 50, 60, 70, 80, 90 or 100 °C. Following treatment, seeds were surface-sterilized and plated onto 0.8 % water agar and incubated in darkness at 20 °C. Three replicates of 25 seeds were used for all treatments and for the control. Seeds were considered germinated upon radicle emergence, and germination was scored only after 3 weeks.

Seed burial experiment

Soil temperature, rainfall and seed germinability for D. hackettiana were monitored in the field to determine if PY is broken during the first summer. One-hundred-and-fifty seeds collected fresh in December 2006 from Kings Park were placed in each of three 75 μm nylon mesh bags that allowed water penetration but excluded soil and other particles. These bags were placed into three separate trays with drainage holes and buried at a depth of 20–30 mm at three sites (replicates) in natural bushland sites in Kings Park, Perth, Western Australia (in areas where D. hackettiana naturally occurs). After seeds were buried, plastic mesh was secured over the top of the soil to prevent disturbance by animals. Bags containing the seeds were buried in January 2007 and retrieved in May 2007.

Prior to burial, seed fill and germination were assessed by X-ray analysis (as described previously) followed by placing three non-treated (control) replicates of 25 seeds and three hot-water-treated (88–92 °C for 2 min) replicates onto 0.8 % water agar and incubating them at 15 °C. One bag of seeds was removed from each of the three sites on May 23, 2007 and the number of germinated seeds counted. All remaining whole seeds were counted and X-rayed to determine the number that was filled and to select filled seeds for a germination test. Three replicates of 25 filled seeds each were dipped into hot water (88–92 °C) for 2 min, surface-sterilized (as described above), plated onto 0.8 % water agar and incubated at 15 °C. Three replicates of non-treated seeds served as the control. Final germination was scored after 3 weeks.

A calibrated Tinytag Plus 2 data logger placed 10 mm below the soil surface adjacent to the bags of seeds recorded temperatures at 1-h intervals. Daily rainfall data for January–May 2007 was obtained from the Australian Bureau of Meteorology weather station located within 7 km of Kings Park (Fig. 1).

Construction of a phylogenetic tree of Australian Sapindaceae

A phylogenetic tree was constructed for all but three Australian Sapindaceae genera based on Harrington et al. (2005). Cossina, Dictyomeura and Heterodendrum were not included in the tree due to a lack of phylogenetic detail about these genera. Class of dormancy (sensu Baskin and Baskin, 2004) were assigned to each genus included in the tree, except Lepidopedalum, Tristiropis and Rhysotoechia, based on information in the present study and on that reported from the literature (Johnston et al., 1979; Munson, 1984; Nicholson and Nicholson, 1991a,b; 1992; 1994; 2000; 2004; Negi and Todaria, 1993; Rehman and Park, 2000; Woods, 2003; Baskin et al., 2004; Turner et al., 2006a; C. Baskin, pers com).

Statistical analysis

Imbibition (maximum seed mass), seed hydration, germination percentage and GRI were analysed by one-way ANOVA using Minitab® version 11. Prior to analysis, percentage data were arcsine-transformed, but non-transformed data appear in all figures. Hartley’s test was performed on all data sets to ensure that treatment variances were not significantly different prior to ANOVA. For experiments in which more than two treatments were assessed, Fisher’s least-significant-difference test was used to determine significant differences (P < 0.05) between individual treatments.

RESULTS

Seed viability

Seed viability was highly variable. Percentage viability (mean ± s.e.) of Cupaniopsis anacardioides and Alectryon connatus seeds was 3.0 ± 0.7 % and 9.0 ± 0.9 %, respectively, and that of the other 12 species ranged from approx. 40 % (Dodonaea ptarmicaefolia) to approx. 99 % (D. stenozyga; Table 1). Seed viability for D. hackettiana was 58.50 ± 2.60 % (1999 accession) and 98.7 ± 0.7 % (2006 accession). Average seed viability across all taxa was 69.7 ± 0.9 %.

Embryo classification

Six of the 14 study species have bent (coiled) embryos and the other eight folded embryos (Table 1).

Seed length and mass

Seed length ranged from 2.14 ± 0.03 mm (D. stenozyga) to 11.51 ± 0.04 mm (Harpullia pendula). Length of seeds with endocarp intact ranged from 8.37 ± 0.02 mm (Allophylus cobbe) to 38.33 ± 0.11 mm (Atalaya hemiglauca). Seed mass ranged from 1.65 ± 0.02 mg (D. stenozyga) to 681.34 ± 25.39 mg (H. pendula), and seed plus endocarp mass from 74.80 ± 1.01 mg (Allophylus cobbe) to 212.35 ± 2.68 mg (Ganophyllum falcatum; Table 1).

Seed moisture content

Moisture content of seeds at the start of experimentation ranged from 5.13 ± 0.23 % for Dodonaea aptera to 85.85 ± 2.06 % for H. pendula and 92.73 ± 2.99 % for Symina cordierorum (Table 1).

Imbibition

Percentage increase in seed mass for non-treated (control) seeds ranged from 3.0 % (Distichostemon
hispidulus) to 58.5 ± 5.8% (Alectryon connatus) and for scarified seeds from 30.9 ± 1.7% (Cupaniopsis parvifolia) to 101.1 ± 1.4% (Dodonaea hackettiana). The difference in mass between control and scarified seeds was significant for all species except Synima cordierorum (Table 1). $R^2$ for maximum mass increase of control versus scarified seeds after 30-s hot water treatment (Fig. 2). Seeds of the six species with PY (D. hispidulus, D. aptera, D. hackettiana, D. petiolaris, D. ptarmicaefolia and D. stenozyga) had imbibition ratios of 0.04 to 0.41, whereas the six species that did not have PY (A. cobbe, A. hemiglauca, C. parvifolia, G. falcatum, H. pendula and Synima cordierorum) had imbibition ratios of 0.56 to 1.29 (Table 1). Imbibition ratios >0.0 for seeds with PY was due to water uptake by a portion of seeds in the samples (see Fig. 4).

Hot-water treatment of seeds of all species with PY (D. hispidulus, Dodonaea spp.) resulted in an increase in seed mass ($P < 0.05$) that ranged from 61.3 ± 5.0% (D. petiolaris) to 104.0 ± 2.0% (D. aptera; Fig. 3). Hot-water-treated seeds from all five Dodonaea spp. imbibed more water than control seeds ($P < 0.05$; Fig. 4). For the five species, the lowest percentage of non-treated (control) seeds that imbibed was for D. hackettiana (11.3 ± 6.7%), while the highest percentage was for those of D. petiolaris (33.3 ± 6.0%; Fig. 4). Dodonaea petiolaris had the lowest number of seeds that imbibed following 2.5-min hot-water treatment (75.0 ± 2.9%), although this was higher than the 58.0 ± 4.4% of the seeds of this species that imbibed following 30-s hot water treatment (data not shown). More than 80% of the seeds of each of the other four Dodonaea spp. had imbibed by day 24 (31-Jan) following hot-water (30 s) treatment (Fig. 4).

Seed dormancy-break and germination

The difference in germination percentage between control and hot-water-treated seeds was significant in four (D. aptera, D. hackettiana, D. ptarmicaefolia and D. stenozyga) of the five Dodonaea spp. evaluated for germination responses ($P < 0.05$; Fig. 5). No germination was observed in D. petiolaris seeds (data not shown). Germination of non-treated seeds was 0–8% for D. aptera, D. hackettiana and D. ptarmicaefolia at all three incubation temperatures, and 22–37% for D. stenozyga (Fig. 5). Hot-water-treated seeds of D. stenozyga germinated to 80–90%, with no significant difference ($P > 0.05$) between the three temperatures. All other species germinated to significantly higher percentages at 15°C and 20°C (68–100%) than at 25°C (0–25%; $P < 0.05$; Fig. 5). Days to first germination was fastest for Dodonaea ptarmicaefolia seeds treated with hot water and incubated at 20°C (5.7 ± 0.7 d). Germination had begun by day 16 in seeds of the four hot-water-treated Dodonaea spp. that germinated (Table 2), and maximum germination for all species was attained by day 23. Germination rate was fastest for D. aptera seeds (GRI = 9.7 ± 0.3) after hot-water treatment and incubation at 15°C ($P < 0.05$). Seeds of D. aptera and D. hackettiana germinated most rapidly at 15°C ($P < 0.05$), while those of D. ptarmicaefolia and D. stenozyga did so at 20°C, although the GRIs for hot-water-treated seeds of D. ptarmicaefolia and D. stenozyga were not significantly higher than those at several other incubation temperatures (Table 2).

Germination percentage of seeds of D. aptera, D. hackettiana and D. stenozyga subjected to different wet heat treatments was highest for those exposed to 100°C (boiling) water for 30 s ($P < 0.05$), but for D. ptarmicaefolia seeds germination was highest for seeds exposed to 90°C (Fig. 6). Seeds of D. aptera and D. hackettiana exposed dry to cycling temperatures (15/50°C) for 8 d or to wet heat of 20–60°C germinated to significantly lower percentages ($P < 0.05$) than those exposed to wet heat of 70°C or higher. A transition in germination percentage was observed at 50°C for D. hackettiana (37.3 ± 10.9%) and at 60°C for D. aptera (26.7 ± 3.5%; $P < 0.05$; Fig. 6).

Dry heat up to 70°C for 1 h was ineffective in breaking dormancy for seeds of D. hackettiana, producing <10%
Table 1. Characteristics of seeds 14 Sapindaceae species

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat</th>
<th>Dispersal unit</th>
<th>Seed length (mm ± s.e.)$^1$</th>
<th>Seed source</th>
<th>Seed weight (mg ± s.e.)</th>
<th>Moisture content (% ± s.e.)</th>
<th>Viability (% ± s.e.)</th>
<th>Embryo type</th>
<th>Maximum mass increase, fresh weight basis (imbibition; % ± s.e.)$^1$</th>
<th>Maximum mass increase, scarified seed/diaspores (% ± s.e.)$^1$</th>
<th>Imbibition ratio (max. mass increase, control/max. mass increase, scarified)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alectryon conutatus</td>
<td>Light rainforest</td>
<td>Seed with thin pericarp</td>
<td>4.422 ± 0.004</td>
<td>Collected in Feb 2007</td>
<td>30.77 ± 0.60</td>
<td>Insufficient seeds</td>
<td>9.00 ± 0.91</td>
<td>Folded</td>
<td>46.5 ± 6.2 (96 h)</td>
<td>Insufficient seeds</td>
<td>NA</td>
</tr>
<tr>
<td>Allophylus cobbe</td>
<td>Semi-deciduous vine forest, strand forest, edge of mangrove</td>
<td>Indehiscent single locule dropped to nearly dry fruit</td>
<td>8.368 ± 0.024</td>
<td>Collected in Feb 2007</td>
<td>74.80 ± 1.01</td>
<td>5.25 ± 0.10</td>
<td>94.50 ± 0.29</td>
<td>Folded</td>
<td>D: 59.4 ± 0.7 (552 h)</td>
<td>D: 69.0 ± 0.2 (552 h)</td>
<td>0.86</td>
</tr>
<tr>
<td>Alvarezia hemiglauca</td>
<td>Dry open mixed forest, desert</td>
<td>Indehiscent samara</td>
<td>38.333 ± 0.109</td>
<td>Commercial seed supplier</td>
<td>142.90 ± 3.78</td>
<td>7.60 ± 5.06</td>
<td>76.50 ± 2.02</td>
<td>Folded</td>
<td>D: 115.7 ± 1.2 (96 h)*</td>
<td>D: 94.8 ± 2.4 (72 h)*</td>
<td>0.82</td>
</tr>
<tr>
<td>Capparaceae anacardioides</td>
<td>Riverine forest, hilly scrubs, rocky beaches</td>
<td>Seed mostly enclosed by aril</td>
<td>9.630 ± 0.030</td>
<td>Commercial seed supplier</td>
<td>81.95 ± 2.58</td>
<td>3.00 ± 0.71</td>
<td>Insufficient seeds</td>
<td>9.00 ± 0.24</td>
<td>37.0 ± 1.5 (192 h)</td>
<td>Insufficient seeds</td>
<td>NA</td>
</tr>
<tr>
<td>Distichostemon connatus</td>
<td>Sandplains, sandstone rocks, rocky hills and plateaus</td>
<td>Arillate seed</td>
<td>3.462 ± 0.063</td>
<td>Seed Technology Centre (KPBG)</td>
<td>12.73 ± 0.53</td>
<td>Insufficient seeds</td>
<td>89.72 ± 4.73</td>
<td>Bent</td>
<td>3.0 (72 h)</td>
<td>79.4 (72 h)</td>
<td>0.04</td>
</tr>
<tr>
<td>Dodonea apera</td>
<td>Coastal limestone cliffs, open eucalypt woodland</td>
<td>Arillate seed</td>
<td>3.065 ± 0.017</td>
<td>Seed Technology Centre (KPBG)</td>
<td>9.81 ± 0.15</td>
<td>5.133 ± 0.23</td>
<td>90.50 ± 0.96</td>
<td>Bent</td>
<td>19.1 ± 0.5 (144 h)</td>
<td>95.9 ± 0.7 (48 h)*</td>
<td>0.20</td>
</tr>
<tr>
<td>Dodonea buckettiana</td>
<td>Limestone soils in open eucalypt forest</td>
<td>Arillate seed</td>
<td>2.494 ± 0.012</td>
<td>Seed Technology Centre (KPBG)</td>
<td>3.70 ± 0.05</td>
<td>7.98 ± 0.13</td>
<td>58.50 ± 2.60</td>
<td>Bent</td>
<td>32.9 ± 9.7 (144 h)</td>
<td>101 ± 1.4 (72 h)*</td>
<td>0.32</td>
</tr>
<tr>
<td>Dodonea petiolaris</td>
<td>Rocky hills, gidgee plains, in arid and semi-arid environments</td>
<td>Exarillate seed</td>
<td>3.343 ± 0.018</td>
<td>Seed Technology Centre (KPBG)</td>
<td>18.35 ± 0.32</td>
<td>7.98 ± 0.19</td>
<td>91.50 ± 0.87</td>
<td>Bent</td>
<td>35.0 ± 5.4 (96 h)</td>
<td>85.0 ± 1.0 (192 h)</td>
<td>0.41</td>
</tr>
<tr>
<td>Dodonaea ptarmicaefolia</td>
<td>Sandy or granitic loams in mallee scrub</td>
<td>Arillate seed</td>
<td>3.042 ± 0.050</td>
<td>Seed Technology Centre (KPBG)</td>
<td>6.00 ± 0.21</td>
<td>9.02 ± 0.27</td>
<td>40.75 ± 2.87</td>
<td>Bent</td>
<td>16.6 ± 6.5 (96 h)</td>
<td>88.7 ± 3.0 (144 h)</td>
<td>0.19</td>
</tr>
<tr>
<td>Dodonaea stenocarpa</td>
<td>Semi-arid, mallee scrub, open eucalypt forest</td>
<td>Arillate seed</td>
<td>2.135 ± 0.033</td>
<td>Seed Technology Centre (KPBG)</td>
<td>1.65 ± 0.02</td>
<td>11.18 ± 1.76</td>
<td>99.25 ± 0.25</td>
<td>Bent</td>
<td>15.3 ± 1.8 (96 h)</td>
<td>73.9 ± 8.3 (72 h)*</td>
<td>0.21</td>
</tr>
<tr>
<td>Ganophyllum falcatum</td>
<td>Monsoon forest, edge of rainforest and mangroves</td>
<td>Droopless fruit with indehiscent endocarp</td>
<td>13.377 ± 0.055</td>
<td>Collected in Jan 2007</td>
<td>212.35 ± 2.68</td>
<td>13.42 ± 0.80</td>
<td>96.75 ± 0.95</td>
<td>Folded</td>
<td>D: 44.0 ± 2.3 (192 h)</td>
<td>D: 34.0 ± 0.7 (72 h)</td>
<td>1.29</td>
</tr>
<tr>
<td>Harpullia pendula</td>
<td>Dry rainforest on basalt</td>
<td>Exarillate seed</td>
<td>11.513 ± 0.047</td>
<td>Collected in May 2007</td>
<td>681.34 ± 25.39</td>
<td>85.85 ± 2.06</td>
<td>73.00 ± 5.74</td>
<td>Folded</td>
<td>11.5 ± 2.2 (144 h)*</td>
<td>20.6 ± 1.2 (144 h)*</td>
<td>0.56</td>
</tr>
<tr>
<td>Synima cordifolium</td>
<td>Well developed rainforest</td>
<td>Arillate seed</td>
<td>11.098 ± 0.044</td>
<td>Collected in Jan 2007</td>
<td>221.22 ± 1.20</td>
<td>92.73 ± 2.99</td>
<td>79.00 ± 1.91</td>
<td>Folded</td>
<td>18.8 ± 2.4 (48 h)</td>
<td>22.4 ± 0.5 (72 h)</td>
<td>0.84</td>
</tr>
</tbody>
</table>

$^1$ D = diaspora (endocarp plus true seed); S = seed only (endocarp artificially removed).

* Germination occurred.
germination ($P < 0.05$). However, dry heat at temperatures $>80\,^\circ C$ resulted in higher germination (74.7 ± 1.3 %; Table 3).

Seed burial experiment

Prior to burial, $D.\ hackettiana$ seeds produced <6 % germination when non-treated, while hot-water treatment enabled 91 % of seeds to germinate ($P < 0.05$). During burial, 36.4 ± 12.3 % of seeds germinated. The seeds remaining after burial in soil for 4 months were unable to germinate when removed from bags and incubated at 15°C, and hot-water treatment enabled germination to >90 % ($P < 0.05$).

Soil temperatures during burial ranged from 62°C on 7 February to 7.7°C on 22 May (Fig. 1). Four rainfall events of 1.8–5.2 mm occurred during late-summer and early autumn (Fig. 1). On at least one of these occasions, soil temperatures within 24 h of precipitation increased to over 50°C for periods of 3 h.

Construction of a phylogenetic tree of Australian Sapindaceae

The three genera of Australian Sapindaceae with PY ($Dodonaea$, $Diplopeltis$ and $Distichostemon$) are in subfamily Dodonaeoideae, and they are sister genera within this subfamily (Fig. 7). Interestingly, the next most-related taxa to these three genera are $Harpullia$ and $\ldots$
Ganophyllum, both of which were shown in this study not to possess PY (Fig. 7). Indeed, based on this analysis, the other three genera where PY has been reported, i.e. Sapindus, Koelreuteria and Cardiospermum, belong to the subfamily Sapindoideae and are neither closely related to each other or to Diplopeltis, Dodonaea or Distichostemon. Embryo morphology was very similar between Diplopeltis, Dodonaea and Distichostemon [all had bent (coiled) embryos] with all other taxa evaluated possessing folded embryos. In comparison, only seeds from Koelreuteria have been shown to possess bent embryos, with seeds from Cardiospermum and Sapindus having folded embryos similar to the non-PY species evaluated in this study (Watson and Dallwitz, 1992 onwards). Taxa with non-dormant seeds, or PD, are scattered right across the phylogenetic tree with representative genera found extensively within both subfamilies.

DISCUSSION

Non-treated seeds from Alectryon connatus, Allophylus cobbe, Atalaya hemiglauca, Cupanopsis anacardioides, C. parvifolia, Ganophyllum falcatum and Synima cordierrorum imbibed water readily, and thus they do not have PY. Other reports on the germination characteristics of Sapindaceae supports our results that Ganophyllum, Alectryon, Cupanopsis and Harpullia do not have PY since fresh (non-treated) seeds in several species in each of these genera germinate readily (Nicholson and Nicholson, 1991a, b, 1992, 1994, 2000, 2004). On the other hand, the seed coats of Distichostemon hispidulus, Dodonaea aptera, D. hackettiana, D. petiolaris, D. ptarmicaefolia and D. stenozyga were water impermeable, and thus these seeds have PY. PY has previously

Fig. 4. Percentage (± s.e.) of seeds that imbibed following no treatment (control) or hot-water (88–92 °C) treatment for 2.5 min (D. petiolaris only) or for 30 sec (all other Dodonaea spp.) and then incubated at room temperature on irrigated germination papers for 72–144 h. Different letters denote significant differences within a species (P < 0.05).

Fig. 5. Percentage germination (± s.e.) of control and hot-water-treated seeds of four Dodonaea spp. after incubation for 23 d at three different temperatures. For each treatment combination, three replicates of 25 seeds were used. Different letters denote significant differences within each temperature and each species (P < 0.05).
been reported for seeds of *D. viscosa* from Hawaii (Baskin et al., 2004).

Based on results presented in this study and on those of others (Johnston et al., 1979; Munson, 1984; Rehman and Park, 2000; Baskin et al., 2004; Turner et al., 2006a; C. Baskin and J. Baskin, unpubl. database), occurrence of PY within Sapindaceae appears to be relatively rare. However, given the limited number of Sapindaceae species for which dormancy and germination have been evaluated these conclusions should be viewed with some caution. Nevertheless, based on available evidence within the Australian flora the only three genera that have been confirmed to have at least one species with a water-impermeable seed coat are *Diploptelis* (Turner et al., 2006), *Dodonaea* (Baskin et al., 2004; this study) and *Distichostemon* (this study).

For the five Sapindaceae genera previously reported to have water-impermeable seed coats, PY was confirmed in three of them, *Diploptelis*, *Dodonaea* and *Cardiospermum*, by imbibition experiments (Johnston et al., 1979; Baskin et al., 2004; Turner et al., 2006a). For each of these three genera, water impermeability vs. water permeability was evaluated for only one species (*Diploptelis huegelii*, *Dodonaea viscosa* and *Cardiospermum halicacabum*). For the other two genera *Koelreuteria* (C. pinnatifida) and *Sapindus* (*S. drummondi*, *S. trifolatus* and *S. saponaria*), PY is inferred through indirect assessment, since seeds that were mechanically or acid-scarified germinated to significantly higher percentages than non-treated seeds (Munson, 1984; Brahmam et al., 1996; Rehman and Park, 2000; Sautu et al., 2006). Thus, the presence of PY still needs confirmation in species in these two genera with an imbibition test since seeds with PD may also be stimulated to germinate following mechanical scarification (C. Baskin et al., 2006). Interestingly, neither seeds of *Koelreuteria bipinnata* (Fan and Wang, 2000) nor those of *K. henryi* (Yang et al., 2000; J.-C. Yang, Taiwan Forestry Research Institute, Taiwan, pers. comm.) seem to be dormant. Seeds of *K. bipinnata* germinated up to 88% (apparently without any pre-treatment) and those *K. henryi* to 98% (no pre-treatment).

In seeds of the four *Dodonaea* species for which dormancy-break was evaluated in the present study, optimal water temperature for breaking PY was 90–100 °C. However, for the two more coastal species (*D. aptera* and *D. hackettiana*) germination (and hence PY loss) was significantly improved after exposure of *D. hackettiana* seeds to water at 50 °C (37% germination) and of *D. aptera* seeds to water at 60 °C (27% germination); non-treated seeds of *D. hackettiana* and *D. aptera* germinated to 11% and 1%, respectively. On the other hand, seeds of *D. hackettiana* required exposure to ≥80 °C dry constant temperatures to germinate to high

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**Table 2. Germination characteristics for four Dodonaea species derived from daily monitoring. Seeds of all four species were incubated at three temperatures (15, 20 and 25 °C) with a sub-sample also placed in hot water (88–92 °C) prior to incubation. There were three replications of 25 seeds for each treatment combination.**

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Germination temperature (°C)</th>
<th>Average number of days to first germination (± s.e.)</th>
<th>Average number of days to 50% germination (± s.e.)</th>
<th>Average number of days to max germination (± s.e.)</th>
<th>Average germination rate index (± s.e.)*</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dodonaea aptera</em></td>
<td>15 °C</td>
<td>13.0 ± 0.0</td>
<td>13.0 ± 0.0</td>
<td>13.0 ± 0.0</td>
<td>0.1 ± 0.1a</td>
</tr>
<tr>
<td>Control</td>
<td>20 °C</td>
<td>7.3 ± 0.3</td>
<td>10.7 ± 0.7</td>
<td>14.7 ± 1.5</td>
<td>9.7 ± 0.3d</td>
</tr>
<tr>
<td>HW</td>
<td>25 °C</td>
<td>10.0 ± 0.0</td>
<td>10.0 ± 0.0</td>
<td>10.0 ± 0.0</td>
<td>0.1 ± 0.1c</td>
</tr>
<tr>
<td>Control</td>
<td>20 °C</td>
<td>7.0 ± 0.6</td>
<td>12.0 ± 0.0</td>
<td>18.3 ± 0.3</td>
<td>8.8 ± 0.1e</td>
</tr>
<tr>
<td>HW</td>
<td>25 °C</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>0.0 ± 0.0a</td>
</tr>
<tr>
<td>Control</td>
<td>20 °C</td>
<td>25 °C</td>
<td>16.0 ± 0.6</td>
<td>18.0 ± 1.0</td>
<td>22.3 ± 0.7</td>
</tr>
<tr>
<td><em>Dodonaea hackettiana</em></td>
<td>15 °C</td>
<td>17.0 ± 3.3</td>
<td>19.0 ± 1.6</td>
<td>20.0 ± 1.6</td>
<td>0.4 ± 0.2a</td>
</tr>
<tr>
<td>Control</td>
<td>20 °C</td>
<td>11.7 ± 1.3</td>
<td>17.0 ± 0.0</td>
<td>21.3 ± 1.2</td>
<td>4.9 ± 0.4c</td>
</tr>
<tr>
<td>HW</td>
<td>20 °C</td>
<td>19.3 ± 1.2</td>
<td>20.3 ± 1.8</td>
<td>20.3 ± 1.8</td>
<td>0.4 ± 0.1a</td>
</tr>
<tr>
<td>Control</td>
<td>20 °C</td>
<td>20 °C</td>
<td>1.0 ± 0.0</td>
<td>18.7 ± 0.7</td>
<td>21.0 ± 1.0</td>
</tr>
<tr>
<td>HW</td>
<td>25 °C</td>
<td>19.0 ± 0.0</td>
<td>19.0 ± 0.0</td>
<td>19.0 ± 0.0</td>
<td>0.0 ± 0.0a</td>
</tr>
<tr>
<td>Control</td>
<td>25 °C</td>
<td>25 °C</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td><em>Dodonaea ptermicicifolia</em></td>
<td>15 °C</td>
<td>16.7 ± 2.3</td>
<td>17.7 ± 1.3</td>
<td>18.3 ± 0.7</td>
<td>0.5 ± 0.3ab</td>
</tr>
<tr>
<td>Control</td>
<td>20 °C</td>
<td>6.0 ± 0.0</td>
<td>13.0 ± 1.0</td>
<td>21.3 ± 0.3</td>
<td>6.4 ± 0.3c</td>
</tr>
<tr>
<td>HW</td>
<td>20 °C</td>
<td>9.5 ± 0.4</td>
<td>9.5 ± 0.4</td>
<td>16.5 ± 3.7</td>
<td>0.6 ± 0.6ab</td>
</tr>
<tr>
<td>Control</td>
<td>20 °C</td>
<td>20 °C</td>
<td>1.0 ± 0.0</td>
<td>10.3 ± 0.9</td>
<td>19.3 ± 0.9</td>
</tr>
<tr>
<td>HW</td>
<td>25 °C</td>
<td>20 ± 0.0</td>
<td>21.0 ± 0.0</td>
<td>21.0 ± 0.0</td>
<td>0.1 ± 0.1d</td>
</tr>
<tr>
<td>Control</td>
<td>25 °C</td>
<td>25 °C</td>
<td>10.3 ± 1.3</td>
<td>15.3 ± 1.2</td>
<td>19.3 ± 3.2</td>
</tr>
<tr>
<td><em>Dodonaea stenzyga</em></td>
<td>15 °C</td>
<td>7.3 ± 0.3</td>
<td>10.0 ± 1.2</td>
<td>16.7 ± 2.6</td>
<td>2.3 ± 0.4a</td>
</tr>
<tr>
<td>Control</td>
<td>20 °C</td>
<td>7.3 ± 0.3</td>
<td>11.3 ± 0.7</td>
<td>19.3 ± 1.8</td>
<td>8.1 ± 0.9b</td>
</tr>
<tr>
<td>HW</td>
<td>20 °C</td>
<td>6.0 ± 0.6</td>
<td>7.7 ± 0.3</td>
<td>17.3 ± 3.2</td>
<td>2.9 ± 0.1a</td>
</tr>
<tr>
<td>Control</td>
<td>20 °C</td>
<td>20 °C</td>
<td>6.7 ± 0.3</td>
<td>10.0 ± 0.0</td>
<td>21.7 ± 0.9</td>
</tr>
<tr>
<td>HW</td>
<td>25 °C</td>
<td>6.3 ± 0.3</td>
<td>10.3 ± 2.4</td>
<td>23.0 ± 0.0</td>
<td>3.2 ± 0.2a</td>
</tr>
<tr>
<td>Control</td>
<td>25 °C</td>
<td>6.7 ± 0.3</td>
<td>11.7 ± 0.9</td>
<td>19.7 ± 1.9</td>
<td>7.5 ± 0.9b</td>
</tr>
</tbody>
</table>

* Different letters denote significant differences across treatments within each species (P < 0.05).
percentages. Thus, <10% of the seeds of this species germinated after exposure to 70 °C dry, whereas 75–93% germinated after exposure to 80, 90 or 100 °C dry heat.

Thirty-seven percent of the seeds of *D. hackettiana* retrieved from *in situ* buried bags had germinated by late May, compared to the <5% germination for seeds in the same seed lot prior to seed burial (non-treated control seeds). Temperatures during the time of burial (Jan–May 2007) did not rise above 62 °C, which is nearly 20 °C lower than the 80 °C dry heat exposure required to break PY in a high percentage of seeds of this species under laboratory conditions. However, rainfall data indicate that at least on two occasions 2–5 mm of rain fell during summer and that within 24 h of rainfall temperatures rose to >50 °C for at least 3 h. Interestingly, germination in the field (36%) was very similar to that (37%) of seeds exposed to water at 50 °C for 30 s. However, whether sufficient moisture was still present within the topsoil when

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**Table 3.** Effects of wet and dry heat on dormancy-break and subsequent germination (% ± s.e.) of seeds of *Dodonaea hackettiana*. For each temperature, seeds were exposed to water for 30 s or to dry heat for 1 h. There were three replicates of 25 seeds for each treatment.

<table>
<thead>
<tr>
<th>Treatment type</th>
<th>20 °C</th>
<th>30 °C</th>
<th>40 °C</th>
<th>50 °C</th>
<th>60 °C</th>
<th>70 °C</th>
<th>80 °C</th>
<th>90 °C</th>
<th>100 °C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water</td>
<td>5.3 (±1.3)_a</td>
<td>2.7 (±1.3)_a</td>
<td>6.7 (±4.8)_a</td>
<td>37.3 (±10.9)_b</td>
<td>65.3 (±6.7)_bc</td>
<td>88.0 (±6.1)_def</td>
<td>78.7 (±15.7)_def</td>
<td>86.7 (±7.1)_def</td>
<td>94.7 (±3.5)_ef</td>
</tr>
<tr>
<td>Dry heat</td>
<td>6.7 (±1.3)_a</td>
<td>12.0 (±6.1)_a</td>
<td>9.3 (±1.3)_a</td>
<td>2.7 (±1.3)_a</td>
<td>1.3 (±1.3)_a</td>
<td>9.3 (±1.3)_a</td>
<td>74.7 (±1.3)_ad</td>
<td>98.7 (±1.3)_f</td>
<td>93.3 (±3.5)_ef</td>
</tr>
</tbody>
</table>

Different letters denote significant differences when compared across all treatments (*P* < 0.05).
temperatures increased to this level is not known. Nevertheless, Turner et al. (2006b) found that in situ buried (non-PY) seeds of Acanthocarpus preissii were partially hydrated (20–60%) for at least 6 h when soil temperatures were between 40–55 °C. This suggests that hydrated soils at temperatures similar to those required under laboratory conditions for alleviation of PY in some D. hackettiana seeds may occur naturally, particularly where soils are directly exposed to solar radiation.

In other species with PY, the water gap opens after exposure to specific soil conditions such as temperature extremes (including fire), wetting and drying cycles, or warm moist conditions (Egley and Paul, 1981; Baskin and Baskin, 1998; Jayasuriya et al., 2007), although in most cases remarkably little appears to be known about the exact factors that overcome PY naturally. For example, PY in Ipomoea lacunosa seeds was effectively broken during moist incubation at 35/20 °C or at constant 35 °C on wet sand, whilst dry incubation at 35 °C was ineffective (Jayasuriya et al., 2007). Likewise, for the PY-dormant seeds of Acacia sylvestris, Dodonaea triquetra and Kennedia rubicunda intensity and duration of fire were key factors influencing seedling recruitment and post-fire species’ abundance (Floyd, 1966). Indeed, for D. triquetra...
seeds moist incubation on sand at 55 °C for at least 200 min resulted in partial removal of PY, although temperatures ≥60 °C were far more effective.

For the four *Dodonaea* species that germinated in our study, germination percentages were highest (68–100 %) when seeds were incubated at 15 °C, although for *D. stenozyga* germination at 25 °C was 80 %. The differing germination responses may reflect differences in geographical distribution and therefore in the climatic and seasonal conditions that initiate germination in nature. For example, *D. stenozyga* occurs over a broad geographical range from southern Western Australia to western Victoria in semi-arid mallee scrub and in open eucalypt woodland (Reynolds, 1985); thus, this species is likely to experience a broad range of temperature and moisture conditions. In comparison, *Dodonaea apierea* is restricted to the coastal region of south-west Western Australia, and *D. stenozyga* occurs along parts of the south coast of Western Australia, extending inland towards Kalgoorlie. *Dodonaea hackettiana* has the most restricted distribution and is found only within the immediate Perth region (Reynolds, 1985). Germination optima usually correspond to temperatures that coincide with the annual period of reliable rainfall where a species occurs naturally, and most species studied from southern Western Australia exhibit a summer-drought-avoiding germination strategy and have germination temperature optima between 10–20 °C (Bellairs and Bell, 1990; Bell and Bellairs, 1992; Bell, 1994; Bell et al., 1995).

Harrington et al. (2005) recently proposed division of the Sapindaceae into four subfamilies: Sapindoideae (including *Koelreuteria* and *Ungnadia*); Hippocastanoideae (including *Aceraceae* and *Hippocastanaceae*, plus *Handeliodendron*); Dodonaeoideae; and the monotypic Xanthoceroideae. Based on modification of this tree for all but three Australian Sapindaceae genera, Australian taxa occur within the two subfamilies Sapindoideae and Dodonaeoideae (Fig. 7). Taxa in this study whose seeds have PY (*Dodonaea* spp. and *Distichostemon hispidulus*) and *Diplopeltis huegelii* (Turner et al., 2006a) are in subfamily Dodonaeoideae and are more closely related to one another than to any other Sapindaceae genera. Interestingly, seeds of the two genera (*Ganophyllum* and *Harpullia*) investigated in this study that belong to this subfamily did not have water-impermeable seed coats. In particular, *Harpullia*, which is the next most-related genus to *Diplopeltis*, *Dodonaea* and *Distichostemon*, also appears to show some indications of seed recalcitrance (desiccation sensitive), based on high moisture content of freshly mature seeds and large seed size (Table 1), a seed trait that has been demonstrated in several other Sapindaceae taxa (Flynn et al., 2006).

All other species evaluated in this study belong to subfamily Sapindoideae, with no species exhibiting PY. The other three genera in which PY has been reported, *Koelreuteria*, *Cardiospermum* and *Sapindus* (Johnston et al., 1979; Munson, 1984; Rehman and Park, 2000), belong to subfamily Sapindoideae and so are not closely related to *Dodonaea*, *Diplopeltis* or *Distichostemon*; they appear to be only distantly related to each other as well (Fig. 7).

Additionally, there appears to be no pattern for the occurrence of PD and non-dormant seeds across the phylogenetic tree, with both states occurring in the two Australian subfamilies and most major phylogenetic branches (Fig. 7). PD is the most common type of dormancy amongst the angiosperms that is likely to have been the ancestral state for most angiosperm groups (Baskin and Baskin, 1998), and its regular occurrence amongst the various branches of the phylogenetic tree is to be expected. Production of seeds that are non-dormant is likely to reflect regular seed shedding into environments that are immediately conducive to germination. The fact that there is no discernable trend in either trait within the phylogenetic tree is therefore not surprising. Indeed, there is only a weak relationship between embryo morphology and the occurrence of PY as well with four (*Koelreuteria*, *Diplopeltis*, *Dodonaea*, and *Distichostemon*) of the six reported species with PY having bent (spirally coiled) embryos. The other two PY taxa (*Cardiospermum* and *Sapindus*) both appear to possess folded embryos, which were found to be the embryo type for all non-PY taxa in this study (Watson and Dallwitz, 1992 onwards) Interestingly, *Koelreuteria*, *Diplopeltis*, *Dodonaea* and *Distichostemon* are all more closely related to one another than to any other known PY taxa, and until the recent Sapindaceae revision *Koelreuteria* was placed in the Dodonaeoideae with *Diplopeltis*, *Dodonaea* and *Distichostemon* (Harrington et al., 2005).

Corner (1976) suggested that the seeds of *Dodonaea* spp. seem to be one of the more primitive seed types in the Sapindaceae. Seeds of *Distichostemon* and *Diplopeltis* have very similar features to those of *Dodonaea*, such as spirally coiled embryos, arillate structures and black/brown testa. Thus, these primitive traits appear to be prevalent in these genera as well. Corner (1976) also proposed that spirally coiled cotyledons, such as those in *Dodonaea*, *Distichostemon* and *Diplopeltis huegelii*, may represent the original sapindaceous embryo type and that thick or more-or-less transverse cotyledogenous embryos observed in all other genera in our study are the derived state.

Based on the results presented in this study it is likely that around 50 % of the Sapindaceae taxa found within Australia have seeds with PY, accounting for around 80 species of *Dodonaea*, *Diplopeltis* and *Distichostemon*. All the PY species tested appeared to respond readily to hot-water treatment, making this an easy and straightforward method for breaking PY in these and related species for the production of plants for restoration and horticulture. Additionally, all but one *Dodonaea* species (the exception being *D. petiolaris*) germinated easily over a range of temperatures. Thus, germination following PY removal is not likely to be a significant issue, and propagation of other *Dodonaea* species should be relatively straightforward. The reason for the poor germination response for *Dodonaea petiolaris* is currently unknown, although several other Sapindaceae are known to have combination dormancy (PY + PD). Thus, it is possible that these seeds require stratification or dry after-ripening to become germinable, as shown for *K. paniculata* and *D. huegelii*.
(Park and Rehman, 1999; Turner et al., 2006a). For the other taxa evaluated in this study PY is not present, so seed imbibition is not an issue for these species. However, there are some indications that PD may be present in some species or even recalcitrance (Flynn et al., 2006), so for propagation and conservation purposes these seed attributes need to be considered when planning seed-storage strategies and germination trials as these will influence the selection of seed-storage conditions, and PD-breaking treatments and the germination environment.

With the limited number of taxa investigated here, more research is required in this diverse family before firm conclusions can be reached regarding definitive phylogenetic relationships and origin of dormancy states. However, our findings raise several key questions. (1) Was non-dormancy the ancestral state in Sapindaceae and PY subsequently? (2) Alternatively, was PY the ancestral state in Sapindaceae and non-dormant taxa have developed the non-PY state independently? (3) Has PY been misreported in Koelreuteria, Cardiospermum and Sapindus, and would investigation of seed-coat anatomy, including the water gap (if present), within these genera provide clearer answers about type(s) of dormancy in these genera? (4) Is there any relationship between embryo morphology and PY, since it appears that Koelreuteria may also have coiled embryos (Watson and Dallwitz, 1992)? (5) If indeed Koelreuteria seeds do have spirally coiled embryos, then how does this correlate with Corner’s (1976) proposal that spirally coiled cotyledons represent the original Sapindaceae embryo type?

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LITERATURE CITED


