Interaction Between Seed Dormancy-release Mechanism, Environment and Seed Bank Strategy for a Widely Distributed Perennial Legume, Parkinsonia aculeata (Caesalpinaceae)

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INTRODUCTION

Dormancy is a characteristic of the seed that prevents it from germinating in conditions that otherwise would have been favourable (Vleeshouwers et al., 1995; Baskin and Baskin, 1998). Seed dormancy can serve at least two roles. First, it can restrict opportunities for germination to small windows in time (e.g. time of year) or space (e.g. seed burial depth) when seedling establishment is most likely to occur (Vleeshouwers et al., 1995; Benech-Arnold et al., 2000; Baker et al., 2005). In this case seeds may be expected to be short-lived in environments where suitable conditions for recruitment are frequent. Second, it can serve as a ‘bet-hedging’ strategy by delaying germination, even when suitable conditions for germination and seedling establishment are encountered, and thus spreading the risk of recruitment failure across years (Facelli et al., 2005; Lambers et al., 2005; Evans et al., 2007; Simons and Johnston, 2007). Bet-hedging, although rarely tested (Evans et al., 2007), is expected to become increasingly important as the probability of recruitment failure for a particular cohort increases, for example with increasing inter-year environmental variance. Seed dormancy and the mechanisms for dormancy release can therefore have an important role in modulating the distribution and abundance of a plant species (Baskin and Baskin, 1998; Cabin et al., 2000; Handley and Davy, 2005). Hardseededness, or physical dormancy, is a very common type of seed dormancy imposed by having a hard testa (or endocarp), especially among shrubs and trees (Baskin and Baskin, 1998; Morrison et al., 1998; Baskin et al., 2000). Seeds with physical dormancy are typically very long-lived (> 100 years) when stored under dry, cool conditions (Fenner, 1995), and are generally considered to be long-lived in the field (Baskin and Baskin, 1998; Morrison et al., 1998; Holmes and Newton, 2004). In contrast to many physiological dormancy mechanisms, the timing of release from physical dormancy is particularly critical as seeds lack secondary seed-dormancy mechanisms or cyclical dormancy (Baskin and Baskin, 2004; Baker et al., 2005). Seeds will therefore either germinate or die (rot) once the hard testa is compromised and there is sufficient moisture for seeds to imbibe water. Physical dormancy may therefore be expected to be important for optimizing the timing of germination events to maximize...
seedling establishment. The relative importance of bet-hedging, where a proportion of seeds would be expected to remain dormant even when conditions for seedling establishment were ideal, is less clear although it is commonly attributed to seeds with physical dormancy (Thompson et al., 2003).

A range of mechanisms has been proposed for dormancy release of seeds with physical dormancy, but they generally remain poorly understood (Baskin and Baskin, 1998; Morrison et al., 1998; van Klinken and Flack, 2005). However, a recent study has shown that wet heat (incubation under wet, warm-to-hot conditions) is an important dormancy-release mechanism for the perennial, tropical, leguminous tree Parkinsonia aculeata (Caesalpinaceae; van Klinken and Flack, 2005). The relationship between temperature and dormancy release approximates a sigmoidal curve for seed populations under wet conditions, with the most temperature-sensitive part of the relationship (approx. 80% of fresh seeds remain dormant under wet conditions at 25°C but only 20% at 40°C) coinciding with temperatures typically encountered in tropical regions (Nix, 1981). Conditions required for dormancy release are therefore tighter than those required for germination, which is optimal between 25 and 35°C (van Klinken and Flack, 2005), and can commence at lower moisture levels (L. Anderson, Pilbara Mesquite Management Committee, Australia, unpubl. res.) than dormancy release. In the wet-dry tropics this dormancy-release mechanism was demonstrated to result in low rates of dormancy release in situations where the environment was buffered from temperature extremes, such as under dense herbaceous or foliar cover, or deep burial (van Klinken et al., 2006). However, it is not known whether other mechanisms might also be involved in other climatic conditions such as dry heat, which has been reported for some legumes (Benech-Arnold et al., 2000; van Klinken et al., 2006), although results from most studies are difficult to interpret because dormancy release and germination (which is also temperature-sensitive) processes are often confounded (Benech-Arnold et al., 2000).

Studies on the interaction between dormancy release and the environment are typically restricted to one or a few sites (Hesse et al., 2007), which potentially limits our understanding of the ecological significance of particular dormancy-release mechanisms. For example, the seed bank strategies of plant species are often categorized as either transient or persistent (Csontos and Tamas, 2003), but how these strategies might be influenced by environmental context is rarely considered. We therefore conducted a seed-burial trial in Australia across the national distribution of P. aculeata. Parkinsonia aculeata is native to the Americas (Hawkins et al., 2007), but it is most widespread and abundant as an invasive in Australia where it occurs across a wide range of environments, from the arid zone to the wet-dry tropics, and in uplands and wetlands (Fig. 1). Seeds were buried across the full range of environments in which this species occurs in order to test three things. First, whether wet heat alone explains the dormancy-release patterns observed across the full range of natural environments encountered by this species (categorized by climate, habitat and burial depth). Second, whether a single dormancy-release mechanism can be sufficiently robust to ensure that seeds are released from dormancy at times and places when seedling establishment is most likely to occur (with respect to seed burial depth, temperature, soil moisture and competitors). Finally, whether there is any evidence that seed dormancy also acts to spread recruitment and therefore the risk of recruitment failure across years, even when ideal conditions for recruitment are experienced. If bet-hedging occurs, then we would expect a significant proportion of seeds to remain dormant following conditions that are ideal for establishment. The documented between-seed variation in response to wet heat (van Klinken and Flack, 2005) would be one mechanism for this to occur.

MATERIALS AND METHODS

Seeds

Two seed cohorts of Parkinsonia aculeata L. were used, one from the Victoria River District (Auvergne) of the Northern Territory and the other from Central Queensland (Taenus; Table 1, Fig. 1), because samples from these two regions had previously been shown to have contrasting sensitivities to wet heat (van Klinken and Flack, 2005) and therefore may respond differently in a seed burial trial. Seeds were collected on 7 November 2001 (Auvergne) and 13 January 2002 (Taenus), to correspond with peak pod loads on trees in each region (van Klinken and Flack, 2008). In each case, fully mature (straw-coloured) pods were collected from trees within a single population and air-dried in the laboratory upon collection. They were then shelled manually and undamaged, fully-formed seeds were stored in paper bags under ambient laboratory conditions (25 ± 5°C) together with insecticide strips to protect against seed-feeders. One week prior to seed burial, undamaged seeds (9 mm long, 4 mm wide) were randomly sub-sampled into lots of 50 seeds. Seed lots were placed in 15 × 15 cm packets made from plastic shade cloth (1.5 × 1.5 mm holes), folded over and stapled shut, for subsequent burial.

Treatments

Seed burial sites were located throughout the Australian distribution of P. aculeata so as to represent the range of climatic conditions and habitats in which it occurs (Table 1, Fig. 1). Climatic conditions ranged from arid to wet-dry tropics. Habitat comparisons at some locations contrasted either inundation patterns or soil type (Table 1). Habitat was defined by inundation regimes: uplands were never inundated (flooded); riparian sites were located on river banks and were subject to pulse inundation; wetlands were seasonally inundated for long durations (months); and lowlands were periodically inundated for long durations. However, only wetland habitats were inundated during the course of the study. Soil type was included as
a treatment at Alroy Downs as red (clay-loam) and black (heavy cracking clay) soils are the two most common but contrasting soils in that region (Barkly Region). Seed packets were buried at a depth of 2 cm at all sites, which is likely to be an optimal depth for germination (Cox et al., 1993). In addition, the effect of seed burial depth (0 cm, on the soil surface; 2 cm; 10 cm) was tested at two locations (Table 1).

Seeds were buried at the time of the year that corresponded with the end of peak pod-drop in each location (van Klinken and Flack, 2008). Seeds sourced from Auvergne were buried from December 2001 to January

Table 1. Site and treatment details for the seed burial trial

| Location     | Climate                      | Habitat                | Burial depth (retrieval events) |
|--------------|------------------------------|                       | Auvergne seed | Taemus seed |
| Beatrice Hill| 12°39' S 131°19'E            | Wet-dry tropics (warm winters) | Upland        | 2 cm (5) | 2 cm (5) |
|              |                              |                        | Wetland       | 2 cm (9) |            |
|              |                              |                        | Upland (black soil) | 0 cm (5) | 2 cm (5) |
|              |                              |                        | Upland (red soil) | 2 cm (6) |            |
|              |                              |                        | Upland         | 10 cm (5) | 2 cm (5) |
|              |                              |                        | Wetland        | 2 cm (7) |            |
| Auvergne     | 15°26' S 130°20'E            | Semi-humid wet-dry tropics (warm winters) | Upland        | 2 cm (5) | 2 cm (5) |
|              |                              |                        | Wetland       | 2 cm (6) | 2 cm (4) |
|              |                              |                        | 10 cm (5)     |            |            |
| Alroy Downs  | 19°18' S 136°04'E            | Semi-arid wet-dry tropics (warm winters) | Upland (black soil) | 2 cm (5) | 2 cm (4) |
|              |                              |                        | Upland (red soil) | 2 cm (5) | 2 cm (4) |
| Taemus       | 21°00' S 146°22'E            | Semi-humid wet-dry tropics (cool winters) | Upland        | 2 cm (5) | 2 cm (4) |
|              |                              |                        | Lowland       | 0 cm (5) | 2 cm (6) |
|              |                              |                        | 10 cm (5)     |            |            |
| Leura        | 23°10' S 149°34'E            | Semi-humid wet-dry tropics (cool winters) | Upland        | 2 cm (6) | 2 cm (6) |
|               |                              |                        | Lowland       | 2 cm (6) |            |
| Millstream   | 21°35' S 117°02'E            | Arid (warm winters)   | Upland        | 2 cm (4) | 2 cm (5) |
|              |                              |                        | Lowland       | 2 cm (5) | 2 cm (5) |
| Alcoota      | 22°49' S 134°27'E            | Arid (cool winters)   | Upland        | 2 cm (5) | 2 cm (7) |
|              |                              |                        | Riparian      | 2 cm (5) | 2 cm (7) |
2002 in locations with warm winters, and those sourced from Central Queensland were buried at all locations from March to April 2002.

Ten to 16 seed packets of each seed source (depending on the number of planned retrieval events) were wired to steel pickets and buried at three replicate sites in the various location–habitat–burial depth combinations (Table 1). Replicates within a location were placed between 100 and 5000 m apart. Where possible, habitat treatments were paired, with treatments being placed 50–200 m apart (Auvergne, Taemus and Alcoota). Sites were placed away from the canopy of shrubs and trees to minimize potential shading effects.

Two (or one, on only 10% of occasions) randomly selected packets were periodically retrieved from each site between 35 and 1281 d after burial. Results from duplicate packets were averaged in the analysis. The exact retrieval schedule varied between treatments, depending on the number of packets buried, the expected rate of seed dormancy release at a particular site, and the pattern of seasonal changes at each location. Control seed packets (one per replicate) from each seed source were stored under ambient laboratory conditions (25 ± 5°C) and processed with each batch of retrieved seeds (four replicates).

Seed evaluation

All intact seeds were air-dried in the laboratory within 2 d of retrieval and their viability and dormancy were determined, together with those of their controls. Seeds that were no longer intact had imbibed and either germinated or died (rotted) within the burial packet, although there was no way of telling which at the time of retrieval. A standard protocol (van Klinken and Flack, 2005; van Klinken et al., 2006) was used to determine the proportion of seeds in each sample that were dormant, and the proportion of non-dormant and dormant seeds that was viable. Dormancy was defined as those seeds that had not imbibed following 4 d submerged in water at 20°C. Rates of dormancy release are constant below approx. 25°C, and most seeds that will imbibe at 20°C will do so within 4 d (van Klinken and Flack, 2005). Imbibed seeds were removed daily and allowed to germinate in Petri dishes lined with paper and kept moist at 25°C, which is within the optimal range for germination (25–35°C; van Klinken and Flack, 2005). Seeds classed as dormant had their seed coats individually nicked, were submerged in water at 20°C for a further 24 h and, once imbibed, processed for germination. Seeds were considered to be viable once the radicle was half the seed length. Any imbibed seeds that had not germinated after 2 weeks were invariably mouldy and were classed as unviable.

The effects of seed source, census date and their interaction on the dormancy release of seeds in the control treatment were analysed using a repeated-measures generalised linear model (SAS MIXED procedure). In the model, seed retrieval date was applied as a fixed, repeated effect with an autoregressive covariance structure, seed source as a fixed effect, and replicate as a random effect.

Testing the effect of wet heat

The effect of wet heat on seed dormancy release over time was tested using proportional daily changes in dormancy release, which standardized the effect of variable sampling intervals. This was calculated by dividing the difference in seed dormancy between two successive seed retrieval dates (averaged for the two bags retrieved from each site on each date) by the number of days that had elapsed since the previous census. The resultant value was slightly negative on 46 of the 244 collections used in the analyses. This was attributed to sampling error, as the process of dormancy release can not be reversed in this species and, consequently, these values were truncated at zero. Dormancy levels of control seeds (95.5% at day zero) were used as an estimate of seed dormancy at the time of burial.

Two types of analyses were conducted: an analysis of variance to investigate the effect of moisture and heat combinations (i.e dry and wet, and cool and warm), and a multiple regression to more explicitly examine the relationship between soil moisture and temperature on dormancy release (using SAS release 8.2; SAS Institute, Cary, NC, 1999). Climate data for each location was obtained from SILO, a database of historical climate data interpolated at 0.05 degree intervals across Australia (Jeffrey et al., 2001). Soil moisture was modelled using a daily tipping bucket model for the top 200 mm of soil, assuming run-off above saturation (200 mm), 25 mm d⁻¹ drainage between saturation and field capacity (150 mm) and 3-2 mm evapotranspiration between field capacity and dry soil (110 mm; van Klinken et al., 2006). Analyses only included seeds buried at 2 cm as it was not possible to model microclimate at the soil surface, and microclimate at 2 and 10 cm was expected to be qualitatively similar (van Klinken and Flack, 2006). Seeds buried in the wetland habitats at both Auvergne and Beatrice were excluded because the seeds were subjected to prolonged inundation and microclimate could therefore not be modelled with the available data. Data were also excluded for intervals with too few seeds remaining at the start of the interval (10%) to realistically assess rates of dormancy release.

For the analysis of variance, environmental conditions experienced by the buried seeds between seed retrieval dates were categorized as wet and warm, dry and warm, wet and cool, or dry and cool. Time periods were categorized as wet and warm if any 3 days in that period were wet (soil moisture greater than 130 mm) and warm (average temperature at least 25°C), or categorized in one of the remaining groups if one or more of those criteria were not met. Wet and warm conditions were defined to capture conditions under which dormancy release is sensitive to wet heat (van Klinken and Flack, 2005). Only one site on a single occasion was categorized as wet and cool (Leura, 0–113 d after burial), so those three replicate data points were excluded from the analysis. A three-factor ANOVA (SAS MIXED procedure) was used to examine whether the daily rate of dormancy release was affected by heat type (three types), location (seven types) and burial duration (buried less than or more than 12 months). Heat type and burial duration were applied as a fixed
effect and location as a random effect. Interaction terms could not be modelled due to the unbalanced nature of the design (with respect to heat types in each region). Dormancy release data were transformed prior to analysis to satisfy the assumptions of normality and homoscedasticity, and we found that log (x + 0.000025) was more suitable than arcsine transformation.

A multiple linear regression (SAS REG procedure) was performed to examine the relationships between temperature, soil moisture and their interaction on rate of dormancy release. Average temperature and average soil moisture conditions over the period since the last census date were modelled as continuous variables. No data transformation was required to satisfy the assumptions of the analysis.

**Effect of habitat and depth**

The effects of seed depth (two locations) and habitat (six locations; Table 1) on dormancy release were tested using a one-way ANOVA on rank-transformed data for each date that seeds from different depth or habitat treatments were retrieved at the same time from a particular location.

**RESULTS**

**Seed dormancy and viability**

**Controls.** Most seeds in the controls were dormant when tested through the course of the trial (91%, n = 3200). Seed dormancy was significantly affected by time \((F_{9,42} = 4.92, P = 0.0002)\), with seed dormancy dropping approximately 6% over a 1200-d period. However, there was no effect of seed source \((F_{1,6} = 0.60, P = 0.4685)\) and no interaction between seed source and time \((F_{5,42} = 1.95, P = 0.1061)\). Seed source was therefore not considered as a factor in subsequent analyses. Most dormant (96%, n = 2771) and non-dormant (83%, n = 278) seeds were viable.

**Buried seeds.** Approximately 34% of the 32,050 buried seeds were intact upon retrieval of seed packets. Of the intact seeds, 81% were still dormant and 16% were non-dormant and viable. Of the dormant seed, 89% were viable. The remaining analysis is of seed dormancy as a proportion of total seeds buried.

**Relationship between wet heat and dormancy release**

The analysis of variance showed that heat type \((F_{2,139} = 30.7, P < 0.0001)\) had an effect on seed dormancy release, but region \((F_{6,139} = 2.0, P = 0.07)\) and burial duration (buried less than or more than 12 months; \(F_{1,139} = 1.5, P = 0.22\)) did not. Pooled across the various locations and burial durations, a greater reduction in daily proportional dormancy release occurred when environmental conditions were wet and warm (mean ± s.e., 0.0063 ± 0.0009, n = 63), compared with dry and warm (0.0016 ± 0.0003, n = 72) \((t_{139} = -6.7, P < 0.0001)\) and dry and cool (0.0009 ± 0.0004, n = 15; \(t_{139} = -6.0, P < 0.0001)\), and when conditions were dry and warm compared with dry and cool \((t_{139} = -2.0, P = 0.048)\). Visual assessment of these data also shows a clear relationship between dormancy release and wet and warm conditions (Figs 2–5; see below). However, there were three exceptions for Taemus-sourced seeds: at upland Auvergne

![Fig. 2.](http://aob.oxfordjournals.org/ at University of Melbourne on June 7, 2013)
between day 0 and 89 (Fig. 2B); at upland and lowland Taemus between day 0 and 38 (Fig. 3); and at upland Millstream between day 182 and 465 after burial (or 273–556 d from commencement of the trial; Fig. 2D). This unexplained dormancy release may be real, or could be due to assumptions in the soil moisture model and the interpolated rainfall data it relied upon (e.g. 111 mm of rain fell over the relevant period at Millstream, but was not sufficient to meet our criteria for wet and warm according to the soil moisture model).

The multiple linear regression showed that the daily rate of seed dormancy release was strongly dependent on the combined effects of average temperature, soil moisture and their interaction ($F_{7,247} = 107.9$, $P < 0.0001$, $r^2 = 0.68$; Table 2). There was a clear relationship between dormancy...
release and increasingly wet and warm conditions (Fig. 6). However, the microclimate data used in this analysis were averaged over each seed burial interval, but in reality fluctuated considerably from day to day (especially soil moisture). If the extreme moisture values are driving release from dormancy, this focus on averages will underestimate the actual moisture and heat required for dormancy release.

**Relationship between climate, burial date, habitat and depth and dormancy release**

Most seeds were released from dormancy within the first year of burial (Fig. 7). Of seeds sourced from Auvergne and buried in December to January, the greatest proportion of them (11%) was still dormant after the first year at the most arid site (Fig. 7). However, there was greater variation in seed dormancy levels between soil types within a single climatic region (at Alroy Downs) than between climate regions. There was no relationship between dormancy release and decreasing aridity for seeds sourced from Taemus and buried later in the wet season. More seeds sourced from Taemus were still dormant after 1 year across all climate zones, when compared with those sourced from Auvergne (Fig. 7). The response of seeds from the two seed sources to immersion at 20 °C was identical under controlled conditions. However, it is possible that seeds buried later in the wet season were longer-lived because the herbaceous cover had more chance to regrow and buffer the microenvironment (see Discussion).

The pattern of dormancy release through time was greatly affected by time of seed burial (Fig. 2), as might be expected by the relationship with wet heat (Fig. 6). Most seeds buried in upland habitats at a depth of 2 cm early in the wet season were no longer dormant within a few months, while most of those buried late in the wet season remained dormant until the following wet season.

The interaction between habitat (inundation patterns and/or soil type) and dormancy release of seeds buried at 2 cm was tested at six of the seven locations (Table 1). Habitat had little or no effect at three locations, Taemus (upland vs lowlands), Millstream (uplands vs wetlands) and Alroy Downs (black soil vs red soil; Fig. 3). However, mesic habitats at Taemus and Millstream were never inundated during the trial. This contrasted with Alcoota, where dormancy release was slower in the riparian habitat, despite never being inundated (Fig. 4).

**TABLE 2. Multiple linear regression on the relationship between the daily rate of seed dormancy release, the effects of average temperature, soil moisture, and their interaction**

<table>
<thead>
<tr>
<th>Coefficient</th>
<th>Estimate</th>
<th>s.e.</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>0.378</td>
<td>0.067</td>
<td>5.63</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Temperature</td>
<td>-0.0142</td>
<td>0.0022</td>
<td>-6.36</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Soil moisture</td>
<td>-0.00344</td>
<td>0.00061</td>
<td>-5.66</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Temperature × Soil moisture</td>
<td>0.00013</td>
<td>0.00002</td>
<td>10.12</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

Fig. 5. The effect of seed burial depth on the proportion of seeds that remain dormant at upland sites at (A) Auvergne and (B) Taemus. Values represented by different letters indicate that dormancy release within the census dates varied significantly between burial depths (P < 0.05). Data for 0 d since burial refers to the ‘control’ seeds. Horizontal bars indicate when conditions were wet and warm.

Fig. 6. A contour-surface plot of the relationship between rate of dormancy release and temperature and soil moisture (averaged over the burial duration). The parameter estimates were taken from the multiple regression model (Table 2).
between habitats (Fig. 4). Less than 5% of seeds were still dormant at upland sites within the first 3 months. In contrast, most wetland seeds were still dormant after the first wet season at Auvergne, and in Beatrice 12% were still dormant at the final retrieval date during the fourth wet season (1094 days after seed burial). The greatest drops in the proportion of dormant seeds in wetland habitats coincided with the start of the rains and/or with the wetlands drying out. However, there was little reduction at Beatrice after the second wet season.

The interaction between burial depth and dormancy release was tested in upland habitats in two regions (Table 1; Fig. 5). Dormancy release was significantly ($P < 0.05$) affected by seed depth across both regions on eight of the 11 dates examined. There was little difference in dormancy release between seeds buried at 2 cm and 10 cm. In contrast, seeds on the soil surface persisted at much higher levels. For example, at Auvergne less than 3% of seeds were still dormant after 37 d at 2 cm, but 30% of seeds were still dormant after 736 d on the soil surface (Fig. 5).

**DISCUSSION**

The results suggest that wet heat is the primary mechanism for dormancy release for *P. aculeata* across all environmental conditions that it is likely to encounter. Furthermore, the available evidence suggests that wet heat provides an elegant mechanism for ensuring that germination coincides with conditions that are optimal for seedling establishment across a diverse range of environments. In addition, seeds can be long-lived but there is little evidence that seed dormancy acts expressly as a mechanism to deal with inter-year variation in recruitment probabilities, as most or all buried seeds lose dormancy within a year when suitable recruitment conditions are encountered. Each of these three points is addressed in turn below.

**Wet heat as a dormancy-release mechanism**

The strong, empirically determined relationship between wet heat and dormancy release for *P. aculeata* explained the pattern of dormancy release of buried seed across the full range of climate zones and micro-environments in its Australian distribution. This relationship therefore provides a predictable and strongly graduated relationship between environment and seed longevity. This extends the conclusions drawn from physiological studies (van Klinken and Flack, 2005) and a seed burial trial conducted in the wet-dry tropics (van Klinken et al., 2006) on the same species. It also suggests that physical dormancy mechanisms are specialized adaptations (Morrison et al., 1998; Baskin et al., 2000). For example, there was no evidence that dry heat during hot–dry summer periods resulted in dormancy release in arid environments despite it being a commonly recorded dormancy-release mechanism for other legume species (Norman et al., 2002). The physiological mechanisms underlying wet heat as a dormancy-release mechanism have not been determined, but is likely to involve active, temperature-dependent changes in seed-coat porosity below a threshold (approx. 33.6°C) overlaying a linear physical relationship between temperature and water uptake (van Klinken and Flack, 2005).

Wet heat varied considerably across the environments and microclimates that we examined, and resulted in very different dormancy-release responses. Inundated wetlands provided the most stable micro-environment for buried seed (Handley and Davy, 2005), with those in the wet-dry tropics typically being approx. 31°C (R. van Klinken, unpubl. res.). Laboratory results suggested that approx. 60% of *P. aculeata* seeds will remain dormant when...
inundated for long periods at this temperature (van Klinken and Flack, 2005) and this prediction was supported at both of the wetland sites that were inundated for long periods. Seeds of other species with physical dormancy have also been reported to be very long-lived under water, only being released from dormancy once waters recede (Vitelli et al., 2006). In contrast, micro-environment varies considerably as wetlands flood and dry. For example, seeds can be exposed to very high daily peaks in temperature when located for extended periods in shallow water or saturated, bare soils prior to the wetlands filling or as the wetlands dry out. Reduction in seed dormancy was apparent as wetlands filled and dried out, although data were not collected at a sufficient temporal resolution to test this explicitly.

Dormancy release differed qualitatively in comparisons between other habitats that were not inundated during the course of the study. For example, dormancy release was slower in riparian sites than upland sites (which had less herbaceous cover) at Alcoota, and in red soil than black soil at Alroy. However, habitat differences were relatively subtle as were, presumably, the contrasts in wet heat exposure resulting from differences in vegetation cover and soil type.

**Timing of dormancy release to maximize seedling establishment**

Dormancy release was consistently timed to coincide with conditions that are likely to be optimal for seedling germination and establishment. Although germination and establishment were not measured in this study, this conclusion was strongly supported by the situations under which dormancy release occurred. Rates of dormancy release were greatest when seeds were buried (survival of seedlings that germinate at the soil surface is minimal; R. van Klinken, pers. obs.) but not inundated (P. aculeata seedlings can not germinate under water; van Klinken and Flack, 2005), when conditions are wet and warm-to-hot (optimal conditions for germination and subsequent recruitment; van Klinken and Flack, 2005) and when there is little herbaceous or foliar cover (Parkinsonia seedlings are poor competitors; S.D. Campbell, Queensland Department of Primary Industries, Australia, unpubl. res.). Furthermore, wet heat as a dormancy-release mechanism was very robust, ensuring that dormancy release occurred under optimal conditions across very diverse climates, environments and latitudes. This contrasts with other plant species where seed dormancy mechanisms have placed geographic or environmental constraints on plant distributions (Baskin and Baskin, 1998; Handley and Davy, 2005).

Seeds commonly have mechanisms to prevent germination when deeply buried and to maximize germination when there are gaps in the foliage. Three previously suggested mechanisms for this are inhibition of germination by light with a low red-to-far-red ratio, stimulation by fluctuating (or high) temperatures, and dormancy termination caused by nitrate or other chemicals (Fenner, 1995; Benech-Arnold et al., 2000; Baskin and Baskin, 2006). Our results suggest a fourth mechanism, wet heat, which has the added advantage of limiting dormancy release when seeds are still on the soil surface. Seedling establishment rates are often low for seeds on the soil surface because of difficulties in penetrating soil crusts and exposure to high temperatures and desiccation (Cox et al., 1993). Parkinsonia aculeata seeds were longest-lived on the soil surface, which is the opposite result from a previous study conducted in the wet-dry tropics (van Klinken et al., 2006). This was almost certainly the consequence of seed packets being placed on top of the soil in the current trial (therefore allowing seeds to dry out rapidly following rainfall) as compared with being covered with a thin film of soil (van Klinken et al., 2006). Seed burial depth (2 vs 10 cm) did not result in much change in dormancy release, suggesting that microclimatic differences between the two depths were limited. This compares with the study in the wet-dry tropics, where seeds buried at 20 cm were exposed to temperatures that were several degrees cooler than those buried at 3 cm, and also remained dormant for much longer (van Klinken et al., 2006).

**Bet-hedging**

Few or no seeds remained after 1 year in high rainfall upland habitats, despite considerable within-population variation between seeds in their sensitivity to wet heat (van Klinken and Flack, 2005). There was therefore no evidence for a trade-off between germinating when conditions are optimal and delaying some seed germination in order to protect against high inter-year variability in recruitment probabilities or with reproductive failure (bet hedging; Evans et al., 2007). This compares with other species where most seeds can still persist after 1 year (Baker et al., 2005; Thompson et al., 2003), and is contrary to common perceptions that P. aculeata, and a wide range of other species with hard-seeded dormancy, has long-lived or persistent seed banks (Baskin and Baskin, 1998). However, it does support the prediction that iteroparous perennials will gain little advantage from dormancy mechanisms that spread dormancy release across years, because risk is already spread through annual seed production (Evans et al., 2007).

Persistent seed banks were, however, apparent in some environments. This was most notable in wetlands at Beatrice (wet-dry tropics) where 9 % of seeds were still dormant after almost 4 years, with little reduction in seed dormancy in the prior year despite an intervening wet season. However, herbaceous regrowth following seed burial was not removed during our trial. The observed dormancy-release pattern is therefore likely to have been the consequence of the micro-environment becoming increasingly buffered by herbaceous regrowth, which was especially dense in the Beatrice wetland after the first year. Similarly, greater persistence after 1 year of seeds buried in autumn (March to April) is likely to be the result of herbaceous regrowth prior to the onset of the following wet season. Seed burial trials rarely control for such changes in microclimate through time, and may therefore frequently overestimate seed persistence under optimal conditions for germination.
The results suggest that wet heat represents an excellent dormancy-release mechanism for maximizing seedling establishment probabilities, at least for dry-tropic species such as *P. aculeata*. Persistent seed banks do occur, but only in circumstances where there is insufficient wet heat for dormancy release, which is also likely to correspond with conditions that are unsuitable or suboptimal for seedling establishment. This includes sites where temperatures are highly buffered, such as under water, in heavy shade or deep in the soil, or where conditions dry out rapidly, such as on the soil surface (although most seeds generally become incorporated into the soil within 1 year; R. van Klinken, unpubl. res.). Dormancy release of persistent seeds therefore requires the microclimate to change either temporally (e.g. through drying of wetlands or the death of parent trees) or spatially (through secondary seed dispersal). Such environmental seed refuges potentially offer an alternative mechanism to bet hedging, which is a property of the seed and relies on a trade-off between mean fitness and variance of fitness (Evans et al., 2007), to cope with annual variation in recruitment probabilities. Available evidence suggests that such environmental seed refuges are relatively common among plants (Fenner, 1995; Lambers et al., 2005; Baskin and Baskin, 2006). Caution is clearly required when classifying species according to seed bank strategy (Csontos and Tamas, 2003) and when considering the evolutionary significance of dormancy mechanisms (Evans et al., 2007), without due consideration of the full range of ecological contexts in which those species may occur.

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LITERATURE CITED


