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Habitat-specific seed dormancy-release mechanisms in four legume species

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Abstract

Physical seed dormancy is a common attribute among plants, and a wide range of dormancy-release mechanisms have been described, but their ecological significance is rarely tested through comparative study. This study tests whether dormancy-release responses to wet heat in four legume species with physical dormancy are correlated with habitat: two wetland species (*Mimosa pigra* and *Parkinsonia aculeata*, both dispersed primarily by water) and two terrestrial species (*Acacia nilotica* and *Prosopis pallida*, both dispersed primarily through vertebrate herbivores). Dormancy release was compared at three moisture levels (80% relative humidity, saturated and submerged) at constant (20–45°C) and diurnally fluctuating (20/40°C) temperatures for 14 d. Seed viability was tested by germinating at 25°C. The functional relationship between temperature and dormancy release after 14 d differed between species: submerged seeds of the two wetland species showed a quadratic response, with low rates of imbibition below 20–25°C and complete imbibition at around 40°C; *P. pallida* seeds showed a linear positive relationship, whereas there was no temperature response for *A. nilotica* seeds below 45°C. Surprisingly, dormancy release after 14 d was relatively insensitive to moisture levels, although rate of dormancy release was generally slower under drier conditions. Dormancy release was not influenced by fluctuating temperatures. Seed viability was largely unaffected by temperature or moisture regime, although it did differ with species and was lower for non-dormant seeds. Our results suggest that a functional dormancy-release response to wet heat provides important fitness benefits for wetland species, but not for species dispersed through vertebrate herbivores, for which it may be maladaptive.

Keywords: *Acacia nilotica*, imbibition, invasive plant, *Mimosa pigra*, *Parkinsonia aculeata*, physical dormancy, *Prosopis pallida*

Introduction

Physical dormancy occurs across at least 15 plant families (Baskin and Baskin, 1998; Baskin *et al.*, 2000). The seed coat confers physical dormancy through tightly packed palisade cells impregnated with water-repellent substances (Baskin and Baskin, 1998; Jayasuriya *et al.*, 2009). A wide range of dormancy-release factors for seeds with physical dormancy have been identified or proposed. Examples include high and diurnally fluctuating dry temperatures, short exposure to intense dry heat from fires, temperature fluctuations at cold temperatures, prolonged exposure to wet heat, fluctuating temperatures under wet conditions, and alternate wetting and drying (McKeon and Mott, 1982; Dillon and Forcella, 1985; Auld and O'Connell, 1991; Norman *et al.*, 2002; van Assche *et al.*, 2003; Baskin and Baskin, 2004; van Klinken and Flack, 2005). However, with the exception of simulated fires (Auld and O'Connell, 1991), there have been few attempts to test the ecological significance of these mechanisms by comparing species from contrasting habitats.

Numerous studies have examined the effect of moisture and temperature on seed germination for species with physical dormancy (e.g. Mareno-Casasola *et al.*, 1994; McDonald, 2002). However, factors required for dormancy release and for germination are often confounded (Thompson and Ooi, 2013). For example, a positive correlation under wet conditions between temperature and germination rate could be

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the result of greater dormancy release, better germinating conditions for species that are already non-dormant, or both. Nonetheless, dormancy release is commonly found to be positively correlated with temperature and with moisture availability, and their interaction (Baskin and Baskin, 1998; van Klinken and Flack, 2005; Hu *et al.*, 2009; Jayasuriya *et al.*, 2009). Dormancy release of seeds of one wetland species, *Parkinsonia aculeata* L., showed a quadratic response to wet heat, with the proportion released increasing strongly above a temperature threshold (van Klinken and Flack, 2005). Dormancy release was thereby minimized when seeds are under dense ground or canopy cover (where competition will be highest), under water (where seeds will rot or seedlings will drown), deeply buried or on the soil surface; and maximized when there is little competition and when temperature and moisture are not limiting (van Klinken *et al.*, 2006, 2008).

Habitat-dependent dormancy-release mechanisms can be expected, as the ultimate fate of seeds depends on their ability to time germination to maximize subsequent recruitment (Allen and Meyer, 1998). For example, exposure to dry heat from fires ('heat shock') is considered to be the principal dormancy-release mechanism for many species in Mediterranean-type ecosystems where seeds are exposed to hot, dry summers (Auld and O'Connell, 1991; Morrison *et al.*, 1998). Within-species variation in dormancy-release mechanisms has also been documented in response to habitat type, with seeds from two populations being sensitive to wet heat and only one to dry heat (Hu *et al.*, 2009). Sensitivity of dormancy-release mechanisms can also differ within species. For example, responses to dry heat varied within two species along an altitudinal gradient in south-east Australia (Ooi *et al.*, 2012) and wet heat responses differed between two *P. aculeata* populations in northern Australia (van Klinken and Flack, 2005). In contrast, a study comparing physical dormancy of multiple species across contrasting environments found no evidence among *Trifolium* (clover) species of ecotype-dependent dormancy-release mechanisms (Norman *et al.*, 2002).

In this paper we test for habitat-specific dormancy-release responses to wet heat among four species with physical seed dormancy. We contrast seeds from two wetland (*P. aculeata* and *Mimosa pigra* L.) and two terrestrial [*Acacia nilotica* (L.) Willd. Ex Delile and *Prosopis pallida* (Willd.) Kunth.] tropical shrub species that are all highly invasive in Australia (Thorpe and Lynch, 2000). All four species are legumes (Family Leguminosae), but *P. aculeata* belongs to a different subfamily (Caesalpinoideae) to the others (Mimosoideae), and *A. nilotica* belongs to a different tribe (Acacieae) from *M. pigra* and *P. pallida* (Mimoseae). *A. nilotica* is native from Africa to India (Mackey, 1995) and the other three are native to the Neotropics (Lonsdale, 1995; Hawkins *et al.*, 2007; van Klinken and Campbell, 2009). *P. aculeata* grows in diverse climates (arid to wet-dry tropics) and habitats (wetlands that are flooded several months of the year, riparian and terrestrial), but is mostly restricted to seasonally flooded habitats in its native range (van Klinken *et al.*, 2009), and does best in periodically flooded habitats in Australia (Smith *et al.*, 2012). *M. pigra* is primarily a wetland species in the wet-dry tropics (Lonsdale, 1995). Both *P. pallida* and *A. nilotica* are largely restricted to terrestrial habitats that are rarely, if ever, inundated. *P. pallida* is invasive in arid and semi-arid regions around the world (Tewari *et al.*, 1998; van Klinken and Campbell, 2009) whereas *A. nilotica* is principally invasive in subtropical and semi-arid Australia (Mackey, 1995). Seeds are borne in pods. Water is the most important dispersal agent for *M. pigra* and *P. aculeata* whereas most *P. pallida* and *A. nilotica* pods are consumed by vertebrate herbivores, with seeds being dispersed through the dung (Mackey, 1995; van Klinken and White, 2011).

Seeds with physical dormancy cannot become physically dormant again once the testa is compromised and there is sufficient moisture for imbibition (Baskin and Baskin, 2004; van Klinken *et al.*, 2008), and there is no evidence for physiological dormancy in our species (Dillon and Forcella, 1985; Mackey, 1995; Gardner *et al.*, 2004; van Klinken and Flack, 2005; and see Methods). We therefore tested whether dormancy-release responses to moisture and temperature differ between our wetland and terrestrial species. Available evidence suggests species differences in dormancy-release mechanisms. As already described, *P. aculeata* has a quadratic response to wet heat but is not sensitive to fluctuating temperatures *per se* (van Klinken and Flack, 2005; van Klinken *et al.*, 2006). In contrast, the available evidence suggests that *M. pigra* seeds are only sensitive to fluctuating temperatures in moist conditions, with little temperature effect on dormancy release when tested at constant temperatures (Dillon and Forcella, 1985; Lonsdale *et al.*, 1988; Lonsdale, 1993). Studies on the terrestrial species are more equivocal. Temperature and germination rate were positively and linearly correlated under wet conditions between 15 and 40°C (seeds were killed at 45°C) for *P. pallida* (Gardner *et al.*, 2004, but this study confounded dormancy release and germination), and we found no relevant studies for *A. nilotica*, although *Acacia* species are commonly sensitive to dry heat (Auld and O'Connell, 1991). Dormancy-release responses to wet heat can also be sensitive to moisture levels (Jayasuriya *et al.*, 2009), but this has not previously been tested for our study species. We expected dormancy release in our study species to be relatively insensitive to moisture, so as to minimize germination when moisture levels may be insufficient for recruitment.

Materials and methods

Seed source

Mature pods of each species were collected from at least five healthy, large-adult trees: *P. aculeata* at 20°49′S 144°12′E on 8 July 2011; *M. pigra* at 12°32′S 131°07′E in March 2011; *A. nilotica* at 22°30′S 141.06°E in November 2009; and *P. pallida* at 20°49′S 144°12′E on 28 November 2005. Pods were subsequently kept under ambient laboratory conditions (20–25°C) until commencement of the experimental work in July 2011. Seeds were removed from pods by hand, taking care not to scratch the seed coat, and only intact, filled seeds were used in experiments.

Germination experiment

Trials were conducted in a set of seven controlled-temperature cabinets. Dormancy-release responses were compared under humid (seeds on dry filter paper at 80 ± 10% relative humidity), saturated (seeds on wet filter paper, but no free water) and wet (seeds submersed in water) conditions at constant (20, 25, 30, 35, 40 and 45°C) and diurnally fluctuating (20/40°C, 12 h/12 h) temperatures (only 20, 40 and 20/40°C for the humid treatment). Experiments were conducted under constant (24 h) light conditions, as light has previously been shown not to affect release from physical dormancy or subsequent germination (Baskin and Baskin, 1998). Temperatures were checked daily with minimum–maximum thermometers to ensure the settings were accurate, and relative humidity in the humid treatment was confirmed using an iButton data logger (DS1921 G-F5; iButtonLink Technology, East Troy, Wisconsin, USA). Each treatment was replicated through time four times (only two for *P. aculeata*), with temperature treatments being randomly assigned to each cabinet on each occasion to avoid any cabinet effect.

Replicates of 25 seeds were randomly drawn from the total seed pool for each species and assigned to a treatment. Each replicate was placed in a separate plastic box (75 × 75 × 25 mm) each of which was filled either with distilled water preheated to the required temperature (submerged treatment), lined with filter paper moistened to saturation (saturated treatment), or lined with dry filter paper (humid treatment), and closed. Submerged and saturated seed replicates were then placed in a larger plastic box (215 × 215 × 105 mm) together with another open box with free water and sealed. Humid replicates were placed in a second large box without free water.

Fully imbibed (non-dormant) seeds in the saturated and submerged treatments were counted and removed daily for 14 d, by which time the rate of seeds still imbibing was expected to be low, based on a previous study (van Klinken and Flack, 2005). Seeds that had not imbibed after 14 d were therefore considered dormant. Imbibed seeds were easily identified because they had lost colour clarity, were rubbery to the touch and had swelled to at least 1.5 times their original size. Seeds in the humid treatment were treated differently as they did not imbibe under those conditions so it was not possible to tell visually when they were released from dormancy. In a previous study on *P. aculeata*, most seeds that would imbibe when immersed at 20°C would do so within 4 d (van Klinken and Flack, 2005). Dormancy release was therefore determined by submerging seeds for 4 d at 20°C after 14 d under humid conditions. Imbibed seeds were removed daily.

Viability of all seeds was determined through germination. Dormant seeds were first individually scarified by abrasion. Seeds were placed into Petri dishes lined with paper towel and kept moist with distilled water at 25°C, which was considered to be within the optimal range for germination (Mackey, 1995; van Klinken and Flack, 2005; van Klinken and Campbell, 2009), for up to 20 d. Germinated seeds (defined as when the radicle was longer than the seed) were counted daily and discarded. No physiological dormancy was expected, and this was the case as all seeds either germinated (were viable) or rotted, as determined through dissection (were unviable).

Statistical analysis

A two-factor ANOVA was used to test the effect of moisture and temperature on imbibition for each of the 14 d that seeds were exposed to a treatment. The arcsine square root transformation was required to make the variance independent. As a species by temperature interaction was always present, species were analysed separately. One analysis of variance was done for submerged and saturated seeds to compare all seven temperatures at which they were tested, and another to include all three moisture levels and the temperatures at which they were tested (20, 40 and 20/40°C). Polynomials were fitted to the dormancy release response to constant temperature at 14 d for each species, using the untransformed data.

The effect of moisture and temperature on viability of dormant and non-dormant seeds (after 14 d) was tested in separate ANOVAs after an arcsine square root transformation. Again, the effect of all seven temperatures on saturated and submerged seeds was tested separately to all moisture treatments and three temperatures. Differences between two values were determined using the least significant difference (LSD).

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Results

Dormancy release

The four species showed contrasting relationships between dormancy release after 14 d and moisture (saturated and submerged treatments) and temperature (Fig. 1). *P. aculeata* was only affected by temperature ($F_{3,\ 18} = 90.24$; $P < 0.001$), as was *A. nilotica* ($F_{3,\ 42} = 20.09$; $P < 0.001$). *M. pigra* was affected by temperature ($F_{3,\ 42} = 162.33$; $P < 0.001$), humidity ($F_{1,\ 42} = 4.67$; $P < 0.05$) and their interaction ($F_{1,\ 42} = 5.46$; $P < 0.05$). *P. pallida* was also affected by temperature ($F_{1,\ 44} = 64.48$; $P > 0.001$) and humidity ($F_{1,\ 44} = 4.89$; $P < 0.05$), but there was no interaction.

The two wetland species showed similar dormancy release responses to temperature after 14 d (Fig. 1). *P. aculeata* was fitted with a cubic polynomial (b1 = −78.23 ± 19.02; b2 = 30.17 ± 6.09; b3 = −2.74 ± 0.58) (Rsq = 93.4%) whereas *M. pigra* was fitted as a cubic polynomial (b1 = −537 ± 0.16; b2 = 0.25 ± 0.052; b3 = −0.02 ± 0.005) with an interaction with moisture (b = 0.022 ± 0.01) (Rsq = 92.2%). For both species, dormancy release increased rapidly above a threshold temperature (*c.* 30 and 25°C, respectively) with all seeds released from dormancy by *c.* 45 and 40°C, respectively. That is, *P. aculeata* seed were released from dormancy at a higher temperature than *M. pigra* seed. Dormancy release for submerged seeds was only significantly different (higher) from that of saturated seed for *M. pigra*, and then only at 30°C (Fig. 1).

The relationship between temperature and dormancy release was also best described as a cubic polynomial (b1 = 55.58 ± 21.76; b2 = −18.30 ± 9.96; b3 = 1.91 ± 0.66; Rsq = 58.7%) for the terrestrial species, *A. nilotica* (Fig. 1c). However, dormancy release was only significantly different at 45°C. In contrast, the relationship was linear for *P. pallida* seed (b = 0.0931 ± 0.0116), with a slight effect of moisture apparent across all constant temperatures (Rsq = 61.47%) (Fig. 1d). For both species some seeds were still dormant at 45°C (12.8 ± 4.5% and 12.5 ± 4.5%, respectively).

Dormancy release through time could only be compared between saturated and submerged seeds as they were assessed daily (Fig. 2). Imbibition began within a day of immersion for all species. A temperature effect was significant from day 1 for all species (Fig. 2). In contrast, moisture was only

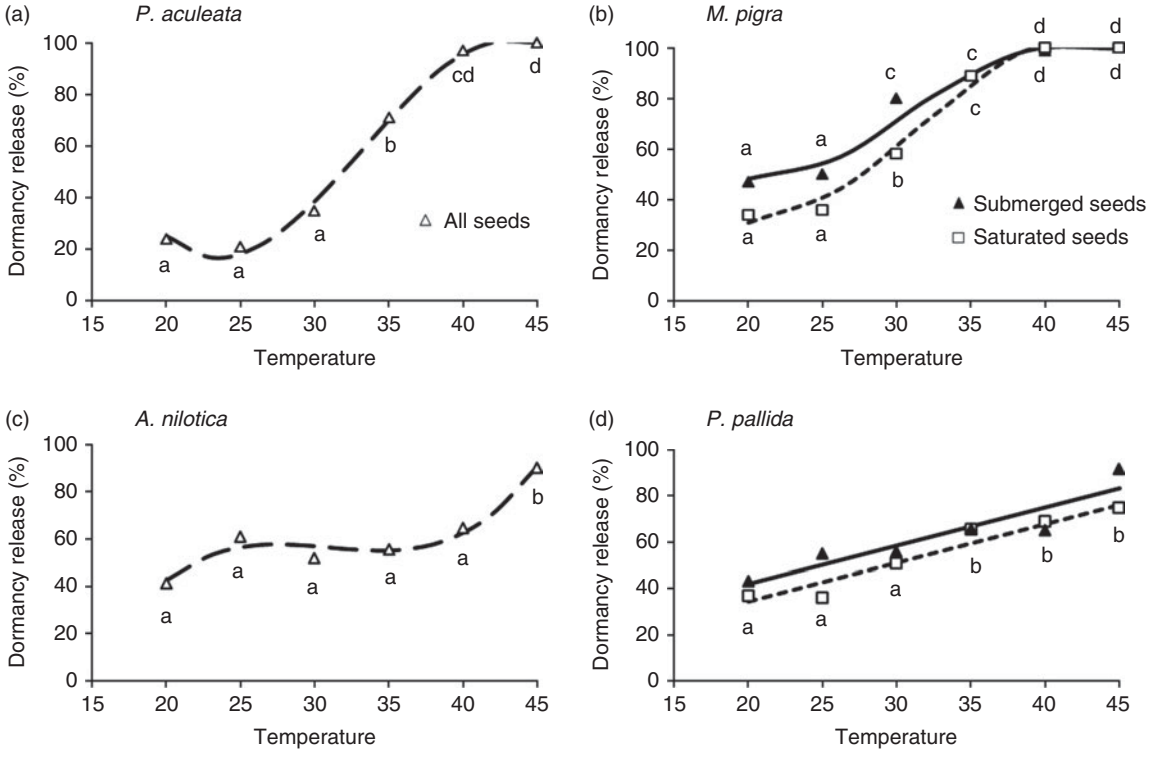

Figure 1. The effect of 14 d of exposure to constant temperature and moisture (saturated and submerged) conditions on dormancy release for two wetland (a and b) and two terrestrial (c and d) species. The relationship between temperature for seeds exposed to saturated or submerged treatments is shown when significant. Moisture treatments are pooled ('all seeds') when there was no moisture effect. Different letters indicate significant difference ($P < 0.05$) between temperatures for the combined moisture treatments, except for *M. pigra* (b) for which there was a significant temperature–moisture interaction (see text).

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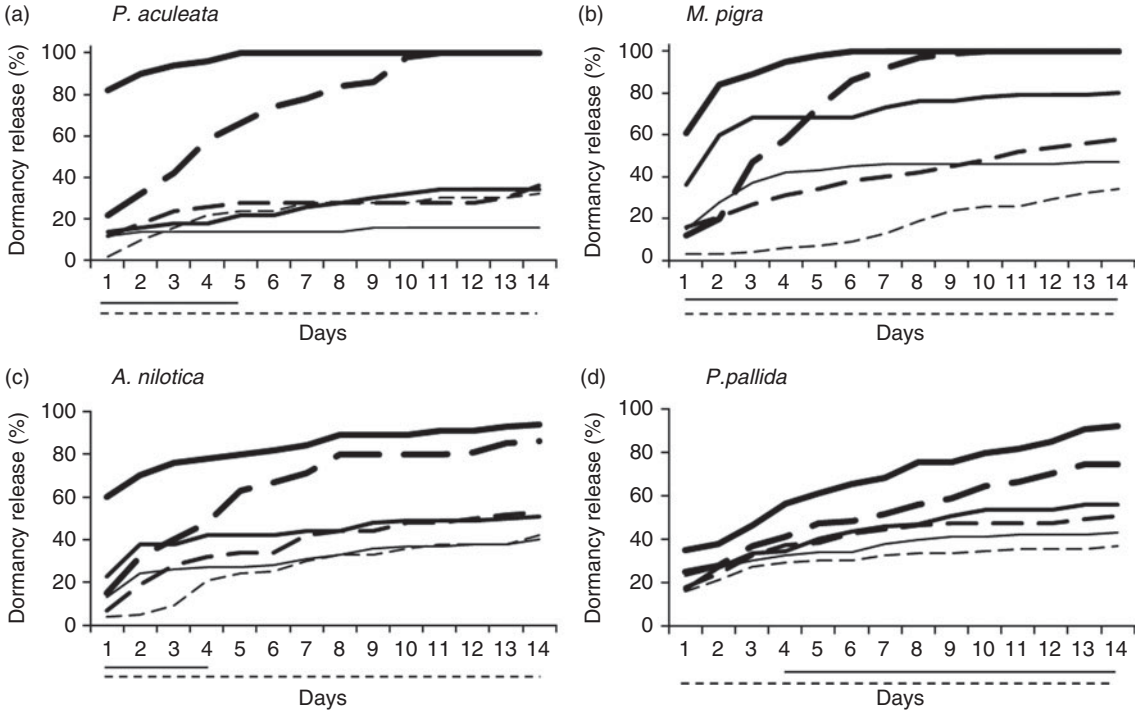

Figure 2. Dormancy release through time for the two wetland (a and b) and two terrestrial (c and d) species for saturated (dashed lines) and submerged seeds (solid lines) illustrated for three temperatures (20, 30 and 45°C, represented by increasingly thick lines). ANOVAs calculated individually for each day were significant for temperature (dashed lines) and humidity (solid lines) on the days indicated on the *x* axis.

significant in the first 4 or 5 d for *A. nilotica* and *P. aculeata*, respectively, the last 10 d for *P. pallida*, and throughout the 14-d period for *M. pigra*. Rate of dormancy release was much slower under saturated conditions at 45°C for the two wetland species and *A. nilotica*, but was not different from that under submerged conditions for *P. pallida*.

The dormancy-release analysis comparing the three moisture levels at the three temperatures at which they were all tested (20, 40 and 20/40°C) yielded similar results (Table 1) to the analysis comparing the two moisture levels tested across all temperature treatments (Fig. 1). Again, temperature was significant for *P. aculeata* ($F_{2,\ 9} = 30.96$; $P < 0.01$) and *A. nilotica* ($F_{2,\ 27} = 3.97$; $P < 0.05$); *M. pigra* was affected by temperature ($F_{2,\ 27} = 139.08$; $P < 0.01$), by humidity ($F_{2,\ 27} = 7.79$; $P < 0.01$) and the interaction between these two factors ($F_{4,\ 27} = 4.50$, $P < 0.01$); and there was an effect of temperature ($F_{2,\ 27} = 11.72$; $P < 0.01$) and humidity ($F_{2,\ 27} = 3.95$; $P < 0.05$) for *P. pallida*. Where there was a significant moisture effect, the humid treatment at constant temperatures was no different to the saturated treatment.

Fluctuating temperature had no effect on dormancy release (Table 1). Dormancy-release under fluctuating temperature conditions (20/40°C) was the same as at 40°C or was intermediate (wetland species and *P. pallida*), or the same as at both 20 and 40°C (*A. nilotica*).

Seed viability

Most seeds that were still dormant after 14 d were still viable, although viability did differ with species ($F_{3,\ 82} = 8.41$, $P < 0.01$) and temperature ($F_{2,\ 82} = 4.43$, $P < 0.05$). Viability of dormant seeds was highest for wetland species (Table 2), which were also the

Table 1. The effect of temperature and humidity on mean (SE) percentage of seeds released from dormancy (imbibed) after 14 d. Different letters indicate significant differences ($P < 0.05$) within a species

		Dormancy release (%)		
Species	Temperature (°C)	Humid	Saturated	Submerged
P. aculeata	20	60 (4)^a	42 (6)^a	46 (6)^a
	40	92 (8)^b	100 (0)^b	100 (0)^b
	20/40	96 (0)^b	98 (2)^b	98 (2)^b
M. pigra	20	46 (8)^a	34 (6)^a	47 (10)^a
	40	93 (4)^c	100 (0)^c	99 (2)^c
	20/40	86 (4)^b	87 (12)^b	100 (0)^c
A. nilotica	20	50 (17)^a	42 (9)^a	40 (14)^a
	40	65 (3)^a	71 (13)^a	58 (9)^a
	20/40	51 (14)^a	56 (25)^a	58 (21)^a
P. pallida	20	32 (6)^a	37 (6)^a	37 (9)^a
	40	62 (16)^b	69 (11)^b	65 (15)^b
	20/40	37 (18)^a	60 (8)^b	55 (18)^b

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youngest seeds (see Methods). For non-dormant seeds, only species had a significant effect ($F_{3,\ 102} = 68.00$, $P < 0.01$), with viability being highest for *M. pigra*, intermediate for *P. aculeata* and lowest for the two terrestrial species (Table 2). Overall, viability of non-dormant seeds was much lower than for dormant seeds (Table 2). The same factors were significant when just saturated and submerged seeds were compared across all seven tested temperatures, with only species being a significant factor for both dormant ($F_{3,\ 148} = 6.45$, $P < 0.01$) and non-dormant ($F_{3,\ 185} = 103.12$, $P < 0.01$) seeds.

Discussion

Seeds that only have physical dormancy will either germinate or rot once the hard testa is compromised and there is sufficient moisture for seeds to imbibe water (Baskin and Baskin, 2004). The timing of dormancy release of seeds is therefore particularly critical for restricting opportunities for germination to small windows of time or space when seedling establishment is likely to occur (van Klinken *et al.*, 2008 and references therein). Our study describes diverse dormancy-release responses to two important environmental cues, temperature and moisture. A temperature threshold response to wet heat was evident for two unrelated wetland species but not for two terrestrial species. This supports our hypothesis that species with physical seed dormancy will have habitat-specific dormancy-release mechanisms. Surprisingly, however, the proportion of seeds released from dormancy was relatively insensitive to moisture levels, with similar responses to temperature being observed under high humidity (80% RH), saturated conditions and full immersion, although dormancy release rate was slower under drier conditions. Furthermore, fluctuating temperatures (20–40°C) were not found to be important, despite previous findings to the contrary (Dillon and Forcella, 1985).

Table 2. Mean (SE) viability of seeds (per cent) that were non-dormant or dormant after 14 d. There was no moisture effect, but temperature was significant for dormant seeds (see text). Different letters indicate significant differences ($P < 0.05$) among dormant and non-dormant seeds, respectively

	Seed viability (%)		
	Non-dormant seeds	Dormant seeds	
Species		20°C	40 and 20/40°C
P. aculeata	76.5 (4.1)[b]	97.1 (1.4)[b]	100.0 (0.0)[b]
M. pigra	90.1 (1.6)[c]	96.3 (1.8)[b]	97.7 (2.3)[b]
A. nilotica	39.2 (3.0)[a]	85.7 (2.8)[a]	90.3 (2.9)[a]
P. pallida	37.8 (4.1)[a]	76.3 (4.4)[a]	84.9 (2.5)[a]

Although dormancy release in all four species was positively correlated with wet heat, only the two wetland species showed the strong quadratic relationship with wet heat that has previously been found to be an effective mechanism for *P. aculeata* (van Klinken and Flack, 2005). However, inter-species differences in responses were still apparent, with more *M. pigra* seeds being released from dormancy at lower temperatures (20–25°C) and the temperature threshold for increased dormancy release being lower (25–30°C rather than 30–35°C). Further testing would be required to determine whether these are species-level or population-level differences. Similar differences have been noted previously between different *P. aculeata* populations, possibly due to environmental differences during seed set (van Klinken and Flack, 2005). In contrast, the wet heat relationship in terrestrial species was relatively weak, with at least 12% of seeds still dormant after immersion for 14 d at 45°C. Furthermore, no temperature response threshold was apparent for *P. pallida*, and was only apparent above 40°C for *A. nilotica*.

High, diurnally fluctuating temperatures have been shown to release seeds of some species from physical dormancy, thereby providing an effective gap-detection mechanism (Baskin and Baskin, 1998). A diurnal temperature fluctuation of 20°C (20/40°C; see also Lonsdale, 1993) was also identified as a dormancy-release mechanism for *M. pigra* (Dillon and Forcella, 1985). However, this was not supported by our study, which found that it was cumulative exposure to wet heat, not fluctuating temperatures *per se*, that was important. These contradictory results remain unexplained, but sensitivity cycling in response to field or or storage conditions is a possibility (van Assche *et al.*, 2003; Jayasuriya *et al.*, 2009). Furthermore, seeds can be naturally exposed to more extreme microclimates where fluctuating temperatures may become important. For example, soil surface temperatures above 60°C are not uncommon in northern Australia (McKeon and Mott, 1982; Lonsdale, 1993). Prolonged exposure to greater hot-dry temperature extremes ('dry heat' > 50°C) is an important dormancy-release mechanism for some terrestrial species (McKeon and Mott, 1982; Baskin and Baskin, 1998; Ooi *et al.*, 2012), but remains to be properly tested for our study species.

Wet heat responses have previously been demonstrated for submerged *P. aculeata* seeds (van Klinken and Flack, 2005), but our results demonstrate similar responses under saturated and humid (80% relative humidity) conditions. This supports results from a detailed physiological study on *Ipomoea lacunosa* (Convolvulaceae) which demonstrated a wet heat response commencing between 79 and 88% relative humidity, although those seeds had already been made sensitive by storage on wet sand for 2 months,

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and were only exposed to up to 5 h of the treatment (Jayasuriya *et al.*, 2009). Water availability did affect the time it took for dormancy-release in our study, resulting in up to a delay of several days for three of the four species (most notably at 45°C). This has important implications under natural conditions. For example, weaker dormancy-release cues at lower moisture levels may still reduce the risk of seeds germinating when conditions for establishment are poor (van Klinken *et al.*, 2008).

Our findings on habitat-specific dormancy-release mechanisms extend knowledge on dormancy-release mechanisms obtained in other studies, such as those focused on the role of fire as a dormancy-release trigger (Auld and O'Connell, 1991). A threshold response to wet heat has previously been demonstrated for *P. aculeata* to be an excellent strategy for maximizing the likelihood that germination will coincide with good recruitment conditions in diverse climates (arid to the wet-dry tropics) and habitats (wetlands, riparian and terrestrial) (van Klinken *et al.*, 2008). It is therefore unsurprising to observe the same relationship for another wetland species, albeit from another subfamily. However, the same functional response to wet heat was not apparently important in the two terrestrial species we tested, at least below 45°C, even though it can be an effective mechanism for optimizing germination timing in terrestrial habitats (van Klinken *et al.*, 2008). One possible reason is that both our terrestrial species are dispersed through vertebrate herbivores (Mackey, 1995; van Klinken and White, 2011). Although consumption by animals is an important dormancy-release mechanism for both our study species (Haas *et al.*, 1973; Mooney *et al.*, 1977; Mackey, 1995; van Klinken and Campbell, 2009), the mechanism is probably through a combination of mechanical action and acidity (Baskin and Baskin, 1998). In contrast, a threshold response to wet heat in these species could in fact be maladaptive, resulting in dormancy release and possible imbibition of all seeds following exposure to hot (38.6°C) wet conditions when passing through the digestive system. This would leave no means for optimally timing subsequent germination events, and seeds would germinate simultaneously, resulting in stronger sib-competition. This study together with similar studies on dry heat (Auld and O'Connell, 1991; Ooi *et al.*, 2012) open the way for comprehensive studies aimed at revealing the full suite of dormancy-release mechanisms for seeds with physical dormancy, and, most importantly, their ecological significance.

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