# Physical dormancy in a changing climate

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## Abstract

Species with physically dormant (PY) seeds make up over 25% of plant species in a number of ecologically important ecosystems around the globe, such as savannah and Mediterranean shrublands. Many of these ecosystems are subject to temporally stochastic events, such as fire and drought; but are in areas projected to experience some of the most extreme climatic changes in the future. Given the importance of PY in controlling germination timing for successful recruitment, we ask how plastic the PY trait is, and if changes to the maternal environment from climate change could alter recruitment. This review focuses on: (1) the evidence for inter- and intraspecific variation in PY; (2) the genetic, maternal and environmental controls involved; and (3) the ecological consequences of (1) and (2) above. Evidence for (within-community) interspecific variation in conditions required to break PY is strong, but for intraspecific variation evidence is contradictory and limited by a paucity of studies. Identifying controllers of variation in PY is complex, there is some suggestion that conditions of the maternal environment may be important, but no consensus on the nature of effects. The implications of PY plasticity for the persistence of seed banks, species and communities under climate change are discussed. We highlight a number of key knowledge gaps, such as a lack of research estimating the components of variation in non-agricultural species, and identify a suite of seed attributes relevant to understanding the potential impacts of climate change on the population dynamics of PY species in the future.

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## Introduction

Climate change projections indicate that many environmental factors, including mean air temperatures, average rainfall and events such as drought, fire and heat waves, will change in the future (Alexander and Arblaster, 2009; Royer *et al.*, 2011; IPCC, 2014). In order to cope with these changes, species survival will be dependent upon their ability to migrate to track the changing climate, pre-existing phenotypic plasticity and/or their ability to adapt to the new conditions they are experiencing (e.g. Thomas *et al.*, 2004; Davis *et al.*, 2005; Jump and Peñuelas, 2005; Hof *et al.*, 2011). It is unlikely that many plant species will be capable of dispersal at a rate equivalent to that of projected climate changes (Honnay *et al.*, 2002; Van der Veken *et al.*, 2007; Morin *et al.*, 2008) and, as such, they will have to either maintain traits that enable them to persist, or adapt to the new conditions (Parmesan, 2006; Skelly *et al.*, 2007). Understanding the variation in important traits, the mechanisms underpinning this variation, and how this variation affects the demographic responses and persistence of plant populations to projected climate change is therefore one of the key challenges faced by researchers today.

Climate exerts a strong influence on seed dormancy and germination (Walck *et al.*, 2011). These early life-history stages are subject to strong selection pressure, as dormancy break and germination at the wrong time, or under sub-optimal conditions, can cause a sharp reduction in fitness. Consequently, these stages are likely to be sensitive to climatic changes (Nicotra *et al.*, 2010; Walck *et al.*, 2011; McLaughlin and Zavaleta, 2012). Dormancy can be classified into four main types, namely: (1) physiological, (2) physical, (3) morphological and (4) morphophysiological (Baskin and Baskin, 2014). To date, much of the research on the controls and variation in dormancy has been conducted on species with physiological dormancy mechanisms and on agricultural species. This has shown that

environmental factors have a key role in determining the prevalence of dormancy and associated traits (e.g. Fenner, 1991; Wulff, 1995; Probert, 2000; Hoyle *et al.*, 2008; Kochanek *et al.*, 2011; Rix *et al.*, 2012, Baskin and Baskin, 2014). However, while physical dormancy (PY, also known as hardseededness) has been relatively well studied in agricultural settings, much remains unknown about how and why PY varies inter- and intraspecifically in natural ecosystems.

Physical dormancy is the result of an impermeable seed coat (testa) or endocarp which prevents water from reaching the embryo, as required for germination (Baskin *et al.*, 2000; Baskin and Baskin, 2014). As PY is believed, in many cases, to have evolved to enable plants in temporally stochastic and harsh environments to survive (Baskin *et al.*, 2000; although see Paulsen *et al.*, 2013), it may be hypothesized that plants with PY would prosper under the more variable and warmer climate that is projected for the future (IPCC, 2014). However, a number of questions need to be considered before such a conclusion can be drawn. Therefore, this review seeks to ask, first, what characteristics of PY vary, and to what extent do they vary inter- and intraspecifically? Second, if inter- and intraspecific variation in the PY characteristics exist, is this variation genetic or environmental in origin, and to what degree is it heritable? Without understanding the heritability of these traits, predicting the long-term PY responses will not be possible. While variation may buffer the population in the short term, establishing what causes this variation is crucial to understanding the long-term advantage of the traits under a changing climate. Should environmental factors trigger changes in PY, then it may be expected that the population and community dynamics would also be affected.

Under a changing, and potentially more variable, climate (IPCC, 2014), understanding how PY characteristics may change is of particular interest for a number of reasons. First, physical dormancy is a polyphyletic trait, resulting from convergent evolution, thus occurring throughout a variety of life histories and taxonomic lineages (see Baskin *et al.*, 2000). It is also prevalent within a number of ecologically important ecosystems worldwide, particularly in Mediterranean-type climates and tropical deciduous woodland, where approximately 27% and 37% of plants species display PY, respectively (Baskin and Baskin, 2014). Many of these ecosystems are highly diverse in terms of plant life, particularly Mediterranean-type ecosystems (Cowling *et al.*, 1996), and also contain high numbers of threatened species. Second, physical dormancy can allow long-term seed banks to develop (Norman *et al.*, 2002; Van Assche and Vandelook, 2006; Ooi, 2012; Ooi *et al.*, 2012; Baskin and Baskin, 2014), and any alteration of PY traits by projected environmental changes may affect the functioning of these long-term seed banks. And, third, relatively little is known about the degree of variability in PY within wild species. While agricultural studies provide useful information for understanding PY, these species have undergone extensive breeding and selection processes, altering PY characteristics. Consequently, it is possible that the way they respond to climatic selection pressures during early life-history stages may differ to the response displayed by wild species.

## The physical dormancy traits

Physical dormancy is usually considered to be a heritable trait, controlled by the testa or endocarp, which are derived from integuments of the ovule and the inner epidermal layer of the ovary wall, respectively (Evenari *et al.*, 1966; Pérez-García and Escudero, 1997; Li *et al.*, 1999a). To date, numerous natural mechanisms of PY breakdown have been described, particularly relating to various combinations of temperature and moisture changes, including high temperatures from summer insolation or fire (e.g. Auld and O'Connell, 1991), temperature fluctuations (e.g. Vázquez-Yanes and Orozco-Segovia, 1982) and wet heat (e.g. van Klinken and Flack, 2005). The loss of dormancy is linked with structural changes to a specialized region of the testa known as the 'water gap' (Box 1). While the breakdown of PY is primarily an all-or-nothing event, with an irreversible change to the water-gap region occurring, there are a number of different traits of PY that can be measured. These include: (1) initial percentage of seeds dormant at dispersal (initial PY); (2) the conditions required to break PY; (3) the time taken for the loss of PY to occur under a described suite of conditions; and (4) changes to the conditions required to break PY over time. These four traits all act together to determine when a seed will lose its dormancy. How these traits vary, and the underlying causes of the variation in each trait, will therefore alter the environment into which a seedling develops, thus influencing its chance of survival (Donohue *et al.*, 2010). Consequently, how the traits vary, what causes the variation and if any variation interacts with environmental conditions to change the timing of PY break are key research questions.

## Variation in the physical dormancy traits

In many cases, the breaking of physical dormancy is in response to an environmental stimulus, and it has been suggested that thresholds may exist, which environmental conditions must cross in order for the breaking of physical dormancy to occur (Ooi *et al.*, 2012). Considerable variation in the conditions required to break PY has been recorded between species (e.g. Jeffrey *et al.*, 1988, Auld and O'Connell, 1991, Herranz *et al.*, 1998, Ooi *et al.*, 2009), with some authors

suggesting that this contributes to maintaining community diversity and coexistence, by providing differentiation within the regeneration niches (Trabaud and Oustric, 1989, Moreno and Oechel, 1991, Herranz *et al.*, 1998, Ooi *et al.*, 2014). However, PY may also vary intraspecifically, in that different populations or individuals within a population may also have different requirements for breaking dormancy, providing a form of bet-hedging. In seed ecology, bet-hedging is commonly associated with the spreading of germination over time in desert annuals (Venable, 2007; Ooi *et al.*, 2009; Baskin and Baskin, 2014), but it can also be applied to ensuring that only a proportion of a population's seed bank will germinate in response to any given dormancy-breaking event in many habitat types. For example, in fire-prone regions, heat shock from fire is usually required to break PY. However, fires are variable, ranging from low to high intensity and differing in duration, producing a range of potential temperatures that could be experienced within the soil (Whelan, 1995; Penman and Towerton, 2008). Bet-hedging within a population, manifested here as variation in the temperature required to break dormancy, would therefore increase the chance that dormancy in a proportion of seeds within the seed bank would be broken during any given fire event,

thus potentially increasing overall population fitness by ensuring some germination irrespective of the fire conditions experienced. At the between-population scale, with site-to-site environmental variation (e.g. over a climatic gradient), conditions required for breaking PY may also vary due to the influence of environmental factors on dormancy onset and formation (Ooi *et al.*, 2012).

Given the many factors that interact to cause the loss of PY (e.g. temperature, humidity, storage duration), variation within and between populations may result in different populations having different responses to climate warming and the associated extreme weather events. Consequently, it is important to understand, and if possible quantify, this variation, through investigating the variation that exists within and between populations in their dormancy-breaking requirements. Genetically determined interpopulation variation might reflect the effects of both genetic drift and localized adaption, while variation within populations may reflect the effects of disruptive selection or perhaps the input of variation from diverse populations. Additionally, potential environmental links to this variation will enable predictions of the changes to PY and seed banks resulting from projected climatic changes. Quantifying this variation between species will have wider implications through influences on community composition, as well as on the ability of habitats to regenerate in zones where PY occurs.

To investigate the level of variation currently known to exist in PY at the interspecific and interpopulation level, papers were searched for using ISI Web of Science and Google Scholar, using multiple variations of the search terms 'physical dormancy', 'hardseededness', 'populations' and 'environmental variation'. A total of ten papers were found, covering 25 species, with *Trifolium subterraneum* and *T. cherli* appearing multiple times (for *T. subterraneum* (Norman *et al.*, 2006), multiple cultivars, each collected from multiple sites, were included). Table 1 highlights the variation in the initial PY trait between populations, as well as the methodologies used. Comparing variation in PY traits across populations or species from different studies is inherently difficult, given the variety of dormancy-breaking techniques used (Table 1). But due to the variety of ecosystems in which PY occurs, a standard treatment for testing PY on all species would not be feasible. For example, an 80°C heat treatment may be required to break dormancy of *Acacia* species from fire-prone environments (Auld and O'Connell, 1991), yet this would kill a *Trifolium* embryo. Consequently, we suggest standardized, habitat-specific comparisons, and have grouped the studies as such. Even grouped by habitat type, simply the duration over which germination checks were conducted varied, from 28 to 90 d in studies from fire-prone environments

**Table 1.** Summary of the interpopulation variation in initial dormancy of PY species from the literature, where multiple populations had been assessed. This includes the dormancy-breaking methodologies used

| Reference | Species | Habitat type | Populations studied | Collection method | Seed storage period | Replication | Control conditions | Observation period | Variance in % dormant in control | CV of % dormant |
|---|---|---|---|---|---|---|---|---|---|---|
| Auld and | *Acacia suaveolens* | FP | 2 | Bulk | 0–1 years | 1 × 30 | 'Ambient room | 28 d | 20.48 | 4.68 |
| O'Connell, | *A. ulicifolia* | FP | 2 | Bulk | – | seeds | temperature' | | 9.68 | 3.18 |
| 1991 | *A. terminalis* | FP | 2 | Bulk | – | | | | 53.05 | 8.46 |
| | *A. myrtifolia* | FP | 2 | Bulk | – | | | | 0.25 | 0.52 |
| Moreira and | *Fumana thymifolia* | FP | 2 | Bulk | – | 4 × 50 | 20°C darkness | 90 d | 24.5 | 5.18 |
| Pausas, 2012 | *Cistus salviifolius* | FP | 6 | Bulk | – | seeds | | | 12.67 | 3.80 |
| | *C. albidus* | FP | 4 | Bulk | – | | | | 4.67 | 2.30 |
| | *C. creticus* | FP | 3 | Bulk | – | | | | 25.33 | 5.30 |
| | *Ulex parviflorus* | FP | 5 | Bulk | – | | | | 88.7 | 11.05 |
| Norman *et al.*, | *Trifolium glanduliferum* | A | 2 | | 1 month | 4 × 200 | 15°C | 28 d | 0.5 | 0.72 |
| 1998 | *T. purpureum* | A | 2 | | 1 month | seeds | | | 0.5 | 0.83 |
| | *T. cherleri* | A | 2 | | 1 month | | | | 4.5 | 2.25 |
| Norman *et al.*, | *T. subterraneum* | A | 5 | Bulk | – | 4 × 100 | 15°C | 14 d | 111.7 | 11.77 |
| 2002 | *T. cherleri* | A | 3 | Bulk | – | seeds | | | 28 | 5.51 |
| | *T. hirtum* | A | 5 | Bulk | – | | | | 30 | 5.83 |
| | *T. tomentosum* | A | 5 | Bulk | – | | | | 1.3 | 1.17 |
| | *T. lappaceum* | A | 2 | Bulk | – | | | | 0 | 0 |
| | *T. spumosum* | A | 6 | Bulk | – | | | | 1.47 | 1.27 |
| | *T. glomeratum* | A | 5 | Bulk | – | | | | 1.2 | 1.11 |
| | *T. angustifolium* | A | 2 | Bulk | – | | | | 8 | 2.89 |
| | *T. nigrescens* | A | 2 | Bulk | – | | | | 0 | 0 |
| Norman *et al.*, | *T. subterraneum* cv. Dalkeith | A | 3 | Bulk | – | 1 × 200 | 15°C | 14 d | 12.33 | 4.16 |
| 2006 | *T. subterraneum* cv. Geraldton | A | 3 | Bulk | – | seeds | | | 26.33 | 6.06 |
| | *T. subterraneum* cv. Dwalganup | A | 3 | Bulk | – | | | | 0.33 | 0.69 |
| | *T. subterraneum* cv. Nungarin | A | 3 | Bulk | – | | | | 56.33 | 9.92 |
| | *T. subterraneum* cv. Urana | A | 3 | Bulk | – | | | | 16.33 | 4.97 |
| | *T. subterraneum* cv. Izmir | A | 3 | Bulk | – | | | | 48 | 8.77 |
| Li *et al.*, 1999b | *Rhus aromatica* | – | 3 | Bulk | – | 4 × 50 | 25/15°C | 28 d | 32 | 6.02 |
| | *R. glabra* | – | 6 | Bulk | – | seeds | in light | | 10.92 | 3.42 |
| Burrows *et al.*, | *A. melanoylon* | FP | 3 | Bulk | – | 2 × 100 | 25°C | 40 d | 4.33 | 2.27 |
| 2009 | | | | | | seeds | | | | |
| Bolin, 2009 | *R. copallinum* | FP | 4 | Bulk | – | 3 × 50 | 25°C 12/12h | 28 d | 0.56 | 0.76 |
| | | | | | | seeds | light dark | | | |
| Majd *et al.*, | *Prospis farcata* | A | 2 | Bulk | 1 month | 1 × 25 | 25°C | 15 d | 0 | 0 |
| 2013 | | | | | | seeds | | | | |

**Table 1.** *Continued*

| Reference | Species | Habitat type | Populations studied | Collection method | Seed storage period | Replication | Control conditions | Observation period | Variance in % dormant in control | CV of % dormant |
|---|---|---|---|---|---|---|---|---|---|---|
| Nichols *et al.*, 2009* | *T. subterraneum* (year 3) | A | 2 | Bulk | – | – | Submerged in 15°C water | 2 d for control; 112 d incubation | 4.5 | 3.63 |
| | *T. subterraneum* (year 16) | A | 2 | Bulk | – | – | | | 41.41 | 10.95 |
| Average by habitat | | A | | | | | | | 18.70 | |
| | | FP | | | | | | | 22.20 | |

*Nichols *et al.* (2009) assessed the same two populations 3 years and 16 years after artificial establishment.
–, Data unavailable. Habitat type: FP, fire prone; A, agricultural.

and 14 to 28 d in agricultural studies. It is not clear how different the results would be if the shorter studies were run for the longer periods.

Across all the species studied, the average variance in initial dormancy (%) between populations of species was 19.9, with a range of 0–111.7. When categorized by habitat type, there were no major differences (Table 1). This would seem to suggest that there is little interpopulation variation in the percentage of seeds with PY at the time of release (or soon after); indeed, all coefficients of variation were less than 12%. In agricultural systems (5 of the 10 papers studied) this is not surprising, given that agricultural selection processes are often focused on attaining 100% soft seed or 100% hard seed, depending on the crop species (D'hondt *et al.*, 2010). Similarly, for those species from fire-prone habitats (4 of the 10 papers), this may be expected, given that PY in such a habitat is believed to be an adaptation enabling populations to survive fire, with little fitness advantage gained by germination occurring outside of post-fire conditions (Whelan, 1995; Ooi *et al.*, 2012, 2014). However, as only 3 of the 18 families with PY are represented in Table 1 (Fabaceae, Cistaceae and Anacardiaceae), and only two habitat types, given a broader sample size these patterns may not hold. Finally, while all of these studies compared different populations, the geographical distance between populations may have influenced the results. Populations closer together are more likely to have increased levels of gene flow and therefore could be expected to be genetically more similar, which may act to homogenize PY.

Compared to variation in initial PY between populations, it may be expected that large variation in the conditions required to break PY would exist within populations, as well as between species within a habitat. Such variation between individuals and between species within a given location would act to reduce competition among seedlings, by staggering germination when suitable conditions arrive, as well as by ensuring that a portion of the seed bank germinates. As with comparing initial dormancy variation, comparing intra- and interspecific variation in PY-breaking conditions across multiple papers, even grouped by habitat type, is difficult, due to wide variation in techniques. However, a number of individual papers have compared dormancy-breaking conditions for multiple species subjected to the same treatments. Focusing on fire-prone habitats, this can be manifested as different optimal heating temperatures required to break PY. Intraspecifically, Auld and O'Connell (1991) subjected seeds of two populations each of *Acacia suaveolens*, *A. ulicifolia*, *A. myrtifolia* and *A. terminalis* to different dormancy-breaking temperatures and different durations of the temperature treatments that may occur during natural fires. The populations were classed as 'geographically distinct'.

For all four species, the interaction between site, temperature treatment and treatment duration was significant ($P < 0.005$). Similar studies, including those by Moreira and Pausas (2012), Ooi *et al.*, (2012), Bolin (2009) and Farrell and Ashton (1978), have also shown similar intraspecific variation amongst populations of fire-prone habitats from bulk wild-collected seed. But Li *et al.* (1999b) found no variation in PY response between populations to different storage treatments in two of three *Rhus* (Anacardiaceae) species studied. Future studies should focus, where possible, on using seed collected from individual maternal plants within populations, to help quantify the variation in PY traits intraspecifically.

## Genetic versus environmental control of physical dormancy

To predict future changes to plant population dynamics and their persistence, it is necessary to understand both the basis of variation in key traits and the extent to which such variation can evolve. Physical dormancy expresses a large degree of phenotypic variation and is considered an inherited, quantitative trait (e.g. Evenari *et al.*, 1966; Hill *et al.*, 1986a, b; de Souza and Marcos-Filho, 2001). Furthermore, genetic effects on PY are often assumed to reflect only the maternal genotype, due to the importance of the seed coat (or endocarp) in PY, both of which are derived from parts of the maternal ovule (Roach and Wulff, 1987; Fenner, 1991; Li *et al.*, 1999a; Donohue, 2009; Baskin and Baskin, 2014). However, Ramsay (1997) has shown that hardseededness can also be passed through the paternal line in *Vicia faba*. Such conflicting assumptions raise the hypothesis that PY may be affected by changing climatic conditions through impacts on both the maternal and paternal plants and their respective genotypes.

Phenotypic variation in a trait can be the result of multiple factors, including genetic and environmental influences (Falconer, 1989). Put simply, the phenotypic variation ($V_P$) displayed in a trait can be expressed as:

$$V_P = V_G + V_E + V_{GE}$$

where $V_G$ is the genetic component, $V_E$ is the environmental component and $V_{GE}$ is the interaction term between genetic and environmental portions (Falconer, 1989). Isolating these factors to understand their relative contributions to trait variation will enable predictions of trait responses to selection (Frankham *et al.*, 2010). However, in considering such responses it is important to recognize that selection not only shapes additive genetic variation, but also the extent of phenotypic plasticity. In the short term, if PY traits (e.g. initial dormancy, the conditions required to break PY, time to loss of PY) show high phenotypic plasticity,

then the expression of PY may show an immediate response to climate change that may be important for long-lived species. However, in the longer term, if the climatic conditions become more stochastic, as predicted, selection may favour individuals or species with a high degree of phenotypic plasticity for PY traits, due to their ability to alter these traits in line with climate. Consequently, it is not only genetic control that must be considered when assessing PY characteristics, but also the genetic variation within any given population. High levels of population genetic variation for PY may provide a buffer against climate change by providing a wide base upon which selection pressures can act (Lacerda *et al.*, 2004).

Genetic sources of variation can be further divided into additive, dominant and interacting partitions, the relative proportions of which influence how heritable a trait is and, consequently, the potential a trait has to respond to selection (Frankham *et al.*, 2010). The greater the additive genetic contribution within a population to a phenotype under a given set of environmental conditions, the higher the heritability of that trait, and therefore the greater the selection effect for a given intensity of selection (Falconer, 1989; Frankham *et al.*, 2010). However, the intensity of selection (i.e. the proportion of a population with the trait value selected for) will also alter the degree of evolutionary change. The higher the heritability value, the greater the potential of the trait to respond to the selection pressure. Consequently, without estimating the degree of heritability for traits, it is not possible to predict trait response to selection (i.e. in this case, climate change effects).

The additive genetic contribution to a trait can be estimated through narrow-sense heritability ($h_2$). Table 2 contains studies on hardseeded species where an estimate of heritability was made on initial PY. Of the papers measuring $h_2$, the mean estimate is 88.19% with a range of 64–98.9%. Despite wide variation in the results, there is a general trend that PY characteristics have a high heritability, suggesting the potential for evolutionary change to occur given a selection pressure. However, as heritability estimates are only valid under the set of environmental conditions used, studies were classified based on the environment in which the parent plant was grown, with those conducted under glass/vinyl house expected to have a more stable growing environment compared to field-based studies. Glass/vinyl house studies had an average $h_2$ of 92.6%, compared with 84.9% for studies conducted in the field, suggesting that under more variable environmental conditions (as expected for wild species) genetic components of phenotypic variance may be lower and thus a reduced evolutionary response to selection would be possible. However, the small sample size here, and the fact that all these studies are based on highly selected

**Table 2.** Species for which broad sense ($H_2$) and narrow sense ($h_2$) heritability studies have been conducted for initial PY from the literature, including the dormancy breaking methodologies used

| Reference | Family | Species | Parent growth environment | Conditions | $H_2$ (%) | $h_2$ (%) |
|---|---|---|---|---|---|---|
| Furbeck *et al.*, 1993 | Malvaceae | *Gossypium hirsutum* | Field | 7 d at 18.3°C | | 64 |
| Nair *et al.*, 2004 | Fabaceae | *Trifolium michelianum* cv. Paradana | Field | 12 d at 22°C | | 90.5 |
| Nair *et al.*, 2004 | Fabaceae | *Trifolium michelianum* | Field | 12 d at 22°C | | 96.1 |
| Slattery, 1986 | Fabaceae | *Trifolium subterraneum* | Glass house | Unknown | 19 | |
| Humphrey *et al.*, 2005 | Fabaceae | *Vigna radiata* | Glass house | 72 h at 25°C | | 84 |
| Humphrey *et al.*, 2005 | Fabaceae | *Vigna radiata* | Field | 72 h at 25°C | | 89 |
| James *et al.*, 1999 | Fabaceae | *Vigna radiata* ssp. *subulata* × ssp. *radiata* cv. Berken | Glass house | 3 d at unknown | 99 | |
| James *et al.*, 1999 | Fabaceae | *Vigna radiata* ssp. *subulata* × ssp. *radiata* cv. Celera | Glass house | 3 d at unknown | 74 | |
| Sriphadet *et al.*, 2007 | Fabaceae | *Vigna radiata* | Glass house | 3 d at 23-25°C | | 98.90 |
| Sriphadet *et al.*, 2007 | Fabaceae | *Vigna radiata* | Glass house | 7 d at 23/25°C | | 94.80 |
| Isemura *et al.*, 2012 | Fabaceae | *Vigna radiata* | Vinyl house | 1 d at 15°C | 99.60 | |
| Isemura *et al.*, 2010 | Fabaceae | *Vigna umbelata* | Vinyl house | 1 d at 15°C | 97.20 | |
| Veasey and Martins, 1990 | Fabaceae | *Desmodium barbatum* | Field | 40°C for 21 d | 37* | |
| Veasey and Martins, 1990 | Fabaceae | *Desmodium tormentosum* | Field | 40°C for 21 d | 40* | |
| Veasey and Martins, 1990 | Fabaceae | *Desmodium tormentosum* | Field | 40°C for 21 d | 95* | |
| Veasey and Martins, 1990 | Fabaceae | *Desmodium incanum* | Field | 40°C for 21 d | 89* | |
| Veasey and Martins, 1990 | Fabaceae | *Desmodium discolour* | Field | 40°C for 21 d | 84* | |
| Mean | | | | | 77.76 | 88.19 |

*Calculated as coefficient of determination, regarded as an upper limit of broad sense heritability (not included in estimation of the mean).

cultivars/accessions/lines of the species, must be considered.

Estimates of additive gene action on genetic variation may allow estimates of heritability to be calculated, but selection (and therefore the potential for evolutionary change) will also be influenced by the presence of dominant gene interactions. Studies that look more specifically at estimating additive/dominant genetic control based either on general (gca)/specific combining ability (sca) estimates (additive/dominant gene action, respectively) or the actions of identified quantitative trait loci (QTLs) have found differing results for different PY traits. For example, both Morley (1958) and Furbeck et al. (1993) concluded that the genetic control of initial PY is mostly additive (based on gca/sca estimates), a result matched by Kaga et al. (2008). However, Kaga et al. (2008) also found that dominance effects were higher for QTLs linked to the loss of PY in the field than for initial PY, suggesting different controls for different traits, meaning that each trait would respond differently to selection pressures exerted by climate change. Where studies have attempted to identify QTLs or possible gene numbers involved in PY (Donnelly et al., 1972; Lee, 1975; Kilen and Hartwig 1978; Keim et al., 1990; Ramsay, 1997; Sakamoto et al., 2004; Humphrey et al., 2005; Li et al., 2012) all conclude that there is likely to be at least one major gene controlling PY, with minor genes interacting to confer dominance. Most studies agree that it is likely that only a few (usually 2 or 3) major genes are involved with the development of an impermeable seed coat (the dominant form). Given the low number of major genes potentially involved in PY, it may be a reasonable assumption that they are either linked with the formation of the water-gap complex (Isemura et al., 2012), or simply linked to whether a species has physically dormant seeds. Whether this follows on to the control of the different characteristics of PY beyond initial percentage hard-seededness requires further investigation.

A number of caveats need to be considered when assessing heritability of PY from the literature. Arguably the key point is that the majority of these studies are based on agricultural species, which have been subjected to intense selective breeding, often against PY. Even when recombinant inbred lines (RILs – 'a collection of strains used to map quantitative trait loci' (Pollard, 2012)) generated from 'wild' types or accessions are crossed with cultivated accessions, there are likely to have been genetic changes altering heritability, thus limiting the inferences that can be made about PY for wild species. The agricultural focus also neglects to account for site-to-site genetic variation that may exist; for example, in how phenotypically plastic a trait is. In natural environments under a changing climate, this is a major gap, which needs to be addressed. Second, the methods used throughout the literature vary widely, both across the genetic methods used and the methods to test for PY. For example, in Table 2, of the four studies that used Vigna radiata, only two used similar test conditions, limiting the cross-study comparisons.

## Maternal effects

Maternal effects include important genetic and environmental influences on PY. Roach and Wulff (1987) argue that these can be understood as 'cytoplasmic genetic, endosperm nuclear and maternal contributions to the phenotype', while Donohue (2009, p. 1061), highlights five sources of influence:

> i) the maternal genetic effects caused by the maternal inheritance of plastids, ii) the effects of endosperm, which is triploid, with two-thirds of its genotype of maternal origin, iii) the effects of the seed coat which is maternal tissue, iv) the effects of maternal provisioning during seed development, with nutrient resources, hormones, proteins & transcripts, all capable of being provisioned to seeds by the maternal parent, and v) the maternal determination of the post progeny environment via dispersal or phenology.

However, as with both classification systems, the factors are not independent. Because of the importance of the seed coat in PY control, and the fact that the seed coat is of maternal origin, it is commonly assumed that PY is under maternal control. To this end, a number of studies (e.g. Donnelly et al., 1972; D'hondt et al., 2010) do not control pollination in genetics studies, assuming no paternal effect. As previously mentioned, there is some evidence that PY can be passed through the paternal line in certain species (e.g. Ramsay, 1997), and paternal effects on seed size in general are well known (e.g. House et al., 2010), all suggesting that further research into the paternal role in PY is required.

In seed ecology, distinguishing between maternal effects and environmental effects is important but difficult (Roach and Wulff, 1987). Given that a seed is attached to the maternal plant until dispersal, factors that affect the maternal plant will also affect the seed; although if these effects occur through the maternal plant (e.g. via seed provisioning), or via the direct influence of the environment on the seed, is hard to split. Roach and Wulff (1987) therefore advocated that environmental effects during the period of embryo formation to seed dispersal should be considered as maternal effects. Under such criteria, the aspects of PY variation attributed to purely environmental effects can only occur post-dispersal and relate to seed storage conditions, while phenotypic variation resulting from environmental variation during seed fill should be attributed to maternal environmental effects. For certain

environmental effects and species this may be so, but for factors such as humidity, it may not be as clear cut.

## Environmental effects through the maternal plant

Given that climate is expected to change rapidly, understanding how much of an influence environmental maternal effects have on PY variation is crucial for predicting future response patterns. Rainfall, temperature and humidity are three main factors projected to change. However, while much of the existing literature considers these factors separately, interactions between them are likely to have a strong impact within natural ecosystems.

### Rainfall

Rainfall has a strong influence on seed weight (Baskin and Baskin, 2014), but has also been shown to influence seed dormancy in PY species. Overall, the current literature seems to suggest that lower rainfall during seed development increases initial PY (Hill *et al.*, 1986b; Smith *et al.*, 1998; Norman *et al.*, 2006; Gresta *et al.*, 2007), although this is not always so (Norman *et al.*, 2002; Michael *et al.*, 2006).

Norman *et al.* (2006) studied 20 *T. subterraneum* genotypes produced at three sites differing in annual rainfall. They found that seeds from the driest site had the highest level of initial PY, while seeds produced at the wettest site had lower initial levels of PY but maintained the dormancy for a longer period of time. Similar results were found when maternal plants of *Glycine max* were subjected to water stress; they produced seeds with a higher initial PY percentage (Hill *et al.*, 1986b). In contrast, in a long-term study by Nichols *et al.* (2009) on *T. subterraneum,* the same seed mix was planted at two sites differing in mean annual rainfall (and mean annual maximum temperature). After 16 years, seeds produced at the wetter site showed higher initial PY (63.3%) compared to those from the drier site (54.2%). After 16 weeks of storage, seed from the drier site was 41.3% dormant in contrast to only 6.7% of seed from the wetter site. Although it could be suggested that under increasing drought conditions plants with PY may produce a higher percentage of initially dormant seeds, it is important to note that within natural ecosystems seed lots are often 90–100% dormant at seed dispersal (Auld and O'Connell, 1991; Ooi *et al.*, 2014). Consequently, the impact of rainfall on the ability of seeds to maintain PY is more important than initial dormancy in many natural ecosystems.

In a study by Michael *et al.* (2006), *Malva parviflora* seeds produced at wet sites differed in their dormancy-breaking response after storage treatments under natural conditions compared to those produced at a dry site. Seeds from the wetter sites showed higher dormancy maintenance (>84% dormant) compared to those from drier sites (45–55%) after 1 year of storage, but after 2 years of storage differences in dormancy were less apparent, with less than 11% left dormant compared to less than 7% for drier sites. Despite the different time frames involved, the results of Michael *et al.* (2006) contradict those of Nichols *et al.* (2009), but both show that rainfall is likely to affect the ability of seeds to maintain PY. In ecosystems where seeds are required to remain dormant for extended periods of time, such as arid or fire-prone environments, changes to rainfall patterns could have important implications for seed-bank maintenance. Thus, the relationship between rainfall and the ability of seeds to maintain PY in the seed bank needs further investigation.

### Temperature

Few studies have experimentally tested the effects of temperature experienced by the maternal plant during seed production on physical dormancy; however, those that do, suggest that dormancy may be altered as a result. Argel and Humphreys (1983a) studied seeds of *Stylosanthes hamata* cv. Verano (Fabaceae) grown on plants subjected to temperature treatments of either 21°C, 24°C or 27°C during the flowering phase. Plants grown at 21°C produced seed lots with initial PY of less than 20%, compared to greater than 90% initial PY for those grown at 27°C. At 24°C the results depended upon pod position, but plants produced over 50% dormant seeds. Similarly, Piano *et al.* (1996) collected seeds of 374 lines of *T. subterraneum* from 61 sites around Sardinia, Italy, and found that initial hardseededness showed a strong positive correlation with April and October temperatures ($r = 0.29$ and 0.25, respectively). The range of temperatures used by Argel and Humphreys (1983a) are within those projected under the most extreme climate change scenarios for many Mediterranean regions (IPCC, 2014). Based on this and the similar pattern shown by Piano *et al.* (1996), there is some suggestion that species with PY may produce a higher proportion of dormant seeds under a future warmer climate. However, the very limited amount of data available highlights the need for considerably more research to be focused on these effects. As with rainfall effects, more focus on non-agricultural species, and on other PY traits, is required to enable more robust projections of responses under future climates.

### Humidity

The role of humidity in triggering the onset of PY during seed development is one of the best-investigated

aspects of PY. The link between the onset of PY and low humidity has been displayed in both agricultural and natural settings, with numerous studies showing the need for humidity to drop below a threshold value for PY to occur (Quinlivan and Nicol, 1971; Argel and Humphreys, 1983a; Bolingue *et al.*, 2010). Tozer and Ooi (2014) found that dormancy was induced in Australian *Acacia saligna* seeds once relative air humidity dropped below approximately 20%, usually prior to seed pod dehiscence. However, the effect of humidity-induced PY can occur pre- or post-dispersal (e.g. Bolingue *et al.*, 2010; Tozer and Ooi, 2014), suggesting that it may be less of a maternal environmental effect, and more closely linked with the direct influence of microclimate on moisture content of the seed. However, due to the presence of a distinct threshold in a number of species for the formation of PY, it is possible that this is maternally, or at least genetically, determined. Despite this, D'hondt *et al.* (2010) studied nine genotypes of *Trifolium repens* grown under 46.5–78.3%, 61.1–94.3% and 89–99.9% relative humidity (RH). The different treatments produced different levels of initial PY (high humidity, low PY; and low humidity, high PY), but there was no interaction between clone and humidity. Most of the PY variation was attributed to phenotypic plasticity. As most Mediterranean areas are projected to face an overall drying trend (IPCC, 2014), this would produce a reduction in RH. Consequently, based on the range of plasticity and the humidities shown in D'hondt *et al.* (2010), it may be expected that the level of initial PY would therefore increase. However, as with temperature and rainfall, predictions of the impacts that this will have on other PY traits are limited due to a lack of studies.

## Environmental effects post seed dispersal

According to Donohue *et al.* (2010), environmental effects post dispersal can be considered a form of maternal effect, given the role of the maternal plant in determining the post-dispersal environment. Here, we consider them independent of maternal effects, due, in part, to the significant influence that environmental effects can have on the seed bank of PY species. This is not to say that maternal effects are not present post dispersal, particularly as maternal preconditioning of response patterns may occur. Given the importance of environmental effects on the seed bank, most of the literature focus is on the impact of environmental conditions on the maintenance of PY, and changes to the conditions required to break PY with time, rather than initial PY. In some ecosystems, such as fire-prone environments, these effects can continue for several years after the death of the parent plant, distinctly separating maternal environmental conditions from post-dispersal conditions.

In the context of climate change, changes to temperature, rainfall and humidity will affect the ability of seeds to maintain PY, altering seed-bank accumulation, persistence, bet-hedging capacity and germination timing (Walck *et al.*, 2011; Ooi, 2012). In addition, these climatic changes will exert a strong selection pressure on populations, through their control over dormancy loss.

### Rainfall/soil moisture

In certain species, water availability during seed storage has been shown to influence dormancy loss. *Ipomoea lacunosa* seeds initially stored at 30°C in wet sand subsequently germinated to greater than 95% at a 25/15°C temperature regime. If seeds were initially stored in dry sand, germination did not occur (Jayasuriya *et al.*, 2008a). In this case, rainfall would be required for the effects of heat to cause seeds to break dormancy. In contrast, *Cuscuta australis* seeds required dry storage in order to break dormancy (Jayasuriya *et al.*, 2008b). Once in the seed bank, soil-moisture levels rather than rainfall *per se* will be important in PY loss; however, as a construct of laboratory incubator experiments, it is more common for studies to measure the effects of storage humidity on the ability of seeds to maintain PY. For example, Bolingue *et al.* (2010) found that time to 50% imbibition was 5 d for *Medicago trunculata* seeds stored at 57% RH, compared with 58 d for seeds stored at 5.5% RH. Moreover, the temperature at which seeds develop can interact with RH to affect the PY. *Stylosanthes hamata* plants were grown at 21°C, 24°C and 27°C during fruiting, then collected seeds were stored for 120 d under RHs of 77%, 32%, 15% or 6%. At 77% RH the seed lot developed at 21°C was 100% non-dormant, while the seeds developed at 27°C were only 24% non-dormant (Argel and Humphreys, 1983b), highlighting the strong effect of storage RH on PY maintenance. Ecologically, however, RH will reflect differing soil moisture conditions experienced in the soil seed bank, which may cause different patterns of PY maintenance than variation in relative air humidity and must be taken into account when assessing such studies.

The study of Argel and Humphreys (1983b) provides evidence of preconditioning by the maternal plant, in this case during fruiting, revealing that this alters the seeds' response to storage humidity. Consequently, while each climatic factor has been considered independently in this review, and a distinction has been made between post- and predispersal maternal effects, interactions between these factors will undoubtedly influence the response of PY traits, namely the time to loss of PY and the conditions required to break PY.

In addition to altering dormancy-breaking requirements, water availability is crucial for ensuring

germination once seeds have lost dormancy. Projections for future changes to rainfall patterns are highly variable between regions but, in general, there is consensus that more extreme rainfall events, combined with longer drought intervals, will occur (Heisler-White *et al.*, 2009). Kimball *et al.* (2010) showed that delayed arrival of winter rainfall in the south-western US over a 25-year period altered community composition, with physically dormant *Erodium cicutarium* one of the species benefiting from this change, possibly due to PY loss being related to summer conditions rather than winter (Meisert, 2002). However, while some species may benefit, an increase in sporadic rainfall may increase the prevalence of 'false start' rain events. These occur when rainfall post dormancy break provides enough moisture for seeds to imbibe, but insufficient moisture for germination to continue. Once PY seeds have lost dormancy, wet–dry cycling can reduce the viability of a seed lot, reducing the seed bank prior to the occurrence of sufficient rainfall for the germination process to complete (Ooi *et al.*, pers. comm.; although see Van Assche and Vandelook, 2010).

### Temperature

Temperature is the most widely cited mechanism of PY loss (Baskin and Baskin, 2014) and, as such, it may be predicted that temperature changes in the future will have large impacts upon seed-bank maintenance. Loss of physical dormancy is often related directly to temperature, with an increasing proportion of any seed lot losing dormancy as temperature increases (Martin *et al.*, 1975; Auld and O'Connell, 1991; Van Assche and Vandelook, 2006; Ooi *et al.*, 2012). The temperature experienced by the seeds once they are on the soil surface or in the seed bank, and the dormancy-breaking conditions that the seeds require, combine to ensure that germination occurs during the best period for recruitment. For example, PY species that recruit into gaps have dormancy-breaking requirements related to diurnal temperature fluctuations reflecting those that occur once a gap appears (e.g. Vázquez-Yanes and Orozco-Segovia, 1982). Projected increases in soil temperatures as a result of climate change could cause an increase in seeds from the seed bank losing dormancy outside of optimal conditions (Ooi *et al.*, 2009, 2012). For species whose dormancy is broken by a specific environmental trigger, such as gaps or a fire, loss of dormancy due to increased soil temperatures (resulting from climate change) between events could reduce the magnitude of successful recruitment after the next specific recruitment event. For example, *A. suaveolens* and *Dillwynia retorta* seeds from the fire-prone sclerophyllous woodland of eastern Australia did not lose dormancy when exposed to projected future average temperatures for the area, but under projected heat-wave conditions there was a significant increase in the loss of PY (Ooi *et al.*, 2012). For these species, whose adult plants are killed by fire and which rely on the seed bank for ensuring a post-fire generation, germination outside of the optimal post-fire environment may result in a net loss to the seed bank if these plants are unable to reproduce before the next fire event. This would reduce the number of seeds available to respond to the next fire event.

While in fire-prone regions germination outside of the post-fire environment is likely to result in a net loss to the seed bank, many species with PY in temperate areas also have physiological dormancy (PD) as an additional mechanism to control germination timing and subsequently recruitment success (Van Assche and Vandelook, 2010; Baskin and Baskin, 2014). In these situations (known as combinational dormancy) the embryo can become dormant, preventing germination, even if PY has been broken. For example, Van Assche and Vandelook (2010) found that in a number of winter annual Fabaceae, including *Vicia sativa, V. hirsuta* and *Medicago arabica,* PD was present in fresh seeds when held at 23°C, but not at temperatures lower than 15°C. For PD to be broken, dry storage for 3 months was required, although for *V. sativa* this treatment also broke PY (Van Assche and Vandelook, 2010). For these species, this may act as an additional buffering mechanism against the impacts of climate change compared to their PY-only counterparts.

Although several suggestions have been made regarding the mechanisms that determine PY break for individual species, e.g. Jayasuriya *et al.* (2009) for *Ipomoea*, the mechanisms for the majority of species remain unclear (Van Assche and Vandelook, 2010). Interestingly, however, Zeng *et al.* (2005) analysed the fatty acid composition in the seed coats of *T. subterraneum* and *Trifolium spumosum* from Western Australia, and found that the fatty acids within the seed coat had melting points ranging from 22°C to 85°C. This mirrors the temperatures seeds would be exposed to in the soil seed bank during the summer period. If dormancy loss in PY seeds is related to the fatty acid composition of the seed coat, then prediction of the conditions required for PY breakdown may be possible. Further research into correlations between fatty acid composition, seed dormancy and dormancy-breaking requirements could be of great benefit to understanding PY and related seed-bank dynamics.

### Physical dormancy response to climate change and its implications

Across the literature reviewed here, a number of broad generalizations can be made with regard to physically dormant species. First, evidence from heritability studies, based primarily on agricultural species, suggests that heritability (narrow-sense) for initial PY

is high (generally greater than 80%, Table 2), with a few major genes involved and a number of minor ones. Second, seeds produced under a higher maternal temperature, and low water availability, seem to produce seed lots with a higher initial percentage PY. The duration for which seeds are able to remain dormant is also affected by high maternal temperatures, although consensus on the direction of this effect is lacking, potentially reflecting species-specific variation (e.g. Argel and Humphreys, 1983a; Hill et al., 1986a, b; Keigley and Mullen, 1986; Piano et al., 1996; Norman et al., 2006; Jayasuriya et al., 2008a). Third, the humidity experienced by the maternal plant, and in some cases by the seeds post dispersal, determines PY onset (Tozer and Ooi, 2014) and, finally, the exact causes of the variation observed at the intraspecific level, genetically or environmentally, are not clear.

Although the genetic influence on all the PY traits is far from understood, initial PY does seem to be dominant and heritable, at least in agricultural species. There is also some support for this from studies of species in natural ecosystems. For example, Lacerda et al. (2004) compared PY (after 1 year of storage) in Senna multijuga and Plathymenia reticulata from individual maternal plants from two populations per species. Although collections were done over multiple years for S. multijuga, introducing maternal and non-maternal environmental differences, the coefficient of genotypic determination suggests that a large amount (0.91–0.97 and 0.86–0.95, respectively) of the trait variation is due to genetically based differences. However, while studies show a high genetic contribution to PY (at least initial PY), large variation in many other PY traits within a given seed lot is also often found (e.g. Salisbury and Halloran, 1983), suggesting that some PY traits display phenotypic plasticity. This may be the result of past selection to cope with the stochastic climates under which PY species often occur.

Phenotypic plasticity may buffer some PY species against the increasingly variable climatic conditions projected for the future (IPCC, 2014), providing a mechanism for coping with changing environmental conditions, at least in the short term. The level of buffering will be dependent on the extent of the increase in climatic variation. If the traits are not plastic, or only slightly plastic, then adaptation will depend on whether PY change can keep pace with the projected rate of climate change. For example, Nichols et al. (2009) showed that selection for changes to PY can occur over a relatively short time period in annuals. Within the 16-year time frame of their study, clear changes in initial PY and the ability of seeds to maintain PY had occurred, suggesting that relatively rapid changes to PY in annual species may result from selection pressures induced under future climate change. However, the ability of many perennial PY species to adapt to such rapid change is likely to be much lower, particularly in natural ecosystems where generational turnover is long or driven by intermittent processes, such as fire, which can occur only once every 10–30 years.

For 'wild' species in natural habitats, initial levels of PY, in particular, are less important, and understanding the impacts of climate change on dormancy-breaking requirements and the resulting population dynamics are of much greater significance for predicting species' persistence. Temperature, rainfall and humidity have all been shown to alter the ability of a seed in storage to maintain dormancy, and there is a significant chance that dormancy loss outside of optimal recruitment conditions may result. For example, an increase in the intensity and duration of heat-wave events, as suggested by Ooi et al. (2012), may deplete the seed bank during the inter-fire period. This could result in a much smaller seed reserve available for post-fire recruitment. Understanding the impacts of climate change on PY species in natural ecosystems will therefore depend on knowing if the variation in the conditions required to break dormancy is determined by a predominantly plastic response, and if so, how plastic the response is. Just as importantly, understanding seedling survival after dormancy loss is necessary, particularly due to the likely effects of changing rainfall regimes on germination from the seed bank and recruitment success.

## Future directions

Variation exists in the dormancy-breaking criteria for PY species, both intra- and interspecifically. Environmental conditions appear to play a major role in PY determination, particularly initial PY, although whether this is purely environmental or the result of phenotypic plasticity is uncertain. The PY literature is currently dominated by studies based on agricultural species, resulting in many of the genetic studies being based on inbred lines that have been subjected to years of artificial selection. There is also a strong bias towards annual species in the Fabaceae family (in particular the Papilinoideae clade), and a focus on the initial PY trait. While certain information can be transferred to natural ecosystems from these studies, there are limits. We therefore suggest that a key requirement of future study is to focus on species from natural ecosystems, with the aim to establish how PY traits, beyond that of simply initial levels of dormancy, vary in response to the different factors projected to change in the future. In particular, understanding how PY changes will affect natural seed-bank dynamics is critical for accurate modelling of population persistence in the future.

In addition to this broad suggestion, a number of more specific factors related to understanding PY and its variation would benefit from additional study. For example, it is often assumed in the current literature that paternal effects on PY are negligible. However, given the influence that paternal effects can have on seed size and other seed traits (e.g. Lacey *et al.*, 1997; Galloway, 2001; House *et al.*, 2010), it is possible that it may also influence PY, particularly with regard to morphological traits and control of dormancy-breaking conditions. Further investigation of this relationship would have clear consequences for the development of future experiments investigating the inheritance of PY and parental environment effects.

Studying the genetic variation in PY traits within natural ecosystems, particularly on perennial species, is inherently difficult, given the often long generation times and expense. However, without understanding the natural genetic intraspecific variation in PY traits, it will not be possible to properly account for the impact a new climate regime may have on their selection. With genomic methods this may be possible (see Storz, 2005 for discussion), allowing for a better understanding of natural selection on PY traits. Investigation into the genotypic variation of PY traits within populations could also be approached by conducting experiments on seed collected from multiple individual plants within a population. This will enable a better understanding of the proportion of maternal environmental, versus maternal genetic, contributions to PY. We recognize that seed numbers from individual maternal plants can be limiting, so this may be more difficult for some species. However, using methods like those highlighted in Hoyle *et al.* (2011), where lower seed numbers are used to conduct germination experiments, may offer one way in which this can be achieved for as broad a range of species as possible. Isolation of maternal environmental and maternal genetic effects will add greatly to the robustness of climate change response projections, by improving our understanding of population dynamics.

Finally, our ability to make generalizations from the literature reviewed, regarding the mechanisms underlying PY variation, was hindered by a lack of comparability between studies. We suggest that the use of a framework for studies of PY traits, where factors are delimited temporally from the stages of embryo formation to dormancy break, would improve comparability. This could be based around: (1) the initial proportion of seeds dormant at release from the maternal plant; (2) the conditions required to break dormancy, and (3) changes to the conditions required to break dormancy over time. Furthermore, it is important to report the time frames for all the stages studied, such as storage durations prior to dormancy tests, to get a clearer understanding of the processes determining PY trait variation, adaptation potentials of species and future population dynamics under a changing climate.

## Conflicts of interest

None.

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