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Influence of maternal environment in developing different levels of physical dormancy and its ecological significance

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Abstract There is considerable literature on the ecology of seeds with impermeable coats, i.e., physical dormancy (PY), but the factors controlling the development of PY and their ecological importance have received little study. The differences in relative humidity, temperature, and rainfall of the maternal environment during seed development, which vary within year at different sites or between years within the same site, contribute to the number and level of PY are reviewed. These factors all influence the development of PY by lowering the level of moisture content in the seeds. Based on moisture content reached during maturation drying, two levels of PY can be recognized: (1) shallow and (2) absolute. Seeds with shallow PY are shed at higher water content, while seeds with absolute PY have lower moisture content at the time of shedding. However, if the moisture content maintained is higher than the 'shallow dormant' level, the seed coat remains permeable to water. It is suggested that this variation in the level of PY subsequently affects the dormancy loss mechanisms and determines the ability of seeds to establish a long-term persistent seed bank or germinate within few years of shedding.

Keywords Shallow and absolute dormancy · Evolution · Impermeable seed coat · Maternal effect · Physical dormancy

Introduction

Seeds of many genera belonging to 18 plant families develop impermeable seed (or fruit) coats, i.e., physical dormancy (PY) during the maturation drying phase of seed development (Baskin and Baskin 2014). At the time of PY acquisition, depending on the species, one or more palisade cell layers present in the seed/fruit coat contain water-repellent substances that prevent the penetration of water into the seed (Rolston 1978). During the final stage of PY acquisition, other structures such as the micropyle, hilum, and chalaza also close, but these structures serve as detectors of the external environment that guide the timing of dormancy break in PY seeds (Baskin et al. 2000). After dispersal, the presence of an impermeable seed coat precludes immediate germination, and these seeds persist in soil until suitable dormancy-breaking signal cues, such as seasonal temperature variation, high or low temperature, and/or other factors, like fire, open a 'water gap' marking the termination of dormancy (Baskin and Baskin 2014; Jaganathan 2015). Water

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first enters through this gap, hydrates the embryo, and triggers immediate germination if the embryo does not have physiological dormancy (PD), i.e., combinational dormancy (PY + PD) (Baskin and Baskin 2004). Such a trait noticeably increases fitness for colonization and maintains species in highly variable environments (Jaganathan and Liu 2014b; Van Assche et al. 2003).

The broadly accepted notion is that the seeds of PY species, collected before the maturation drying stage, have permeable seed coats and germinate when incubated at appropriate temperature, which is species specific (Baskin and Baskin 2014; Egley 1979; Gama-Arachchige et al. 2011; Helgeson 1932; Hills 1942; Quinlivan 1971). These seeds become impermeable only at the end of the maturation drying stage (Baskin and Baskin 2014; Baskin et al. 2000). Although seeds collected early in the maturation phase and tested for dormancy contributed to some misconception about the presence or absence of PY in a particular species, the number of PY seeds, and the level of hardseededness (collected even after maturation drying) produced by any given plant varies significantly between the sites, between years or even on the same plant depending on the location of seeds (Baskin and Baskin 2014; Smith et al. 1998; Hudson et al. 2015). This raises important questions: (1) why does the number of PY seeds vary between plants, sites, or years, (2) what factors control this variation, and (3) is there any ecological significance behind this? To date, most of the PY literature has had a primary interest in determining how PY is broken by any given set of artificial and/or natural conditions. Despite detailed research over the past several decades, knowledge of the factors regulating development of PY is still inconclusive. Consequently, addressing these questions may provide an opportunity to understand the ecological significance of PY.

Influence of environmental conditions on PY development

Although the trait of PY is mostly heritable, the maternal environment of the plant during seed development plays an important role in regulating its development. Environmental factors, particularly temperature, relative humidity, water stress, and length of growing season, contribute to the development of PY that can vary from no impermeable seeds to all seeds having an impermeable seed coat (D'hondt et al. 2010; Tozer and Ooi 2014). Nevertheless, which of these factors plays a more dominant role is often difficult to disentangle due to the species-specific variation that interacts with these factors (Argel and Paton 1999; Souza and Marcos-Filho 2001).

Numerous studies have shown that seeds maturing at higher temperature produce more impermeable seeds compared with the low-temperature environment (Gladstones 1958; Llorens et al. 2008; Jaganathan et al. submitted). In *Stylosanthes hamate* cv. Verano, for example, seeds that matured at 27 °C produced more impermeable seeds compared with those maturing at 24 °C (Argel and Humphreys 1983a). Based on the microscopic examination, these authors revealed that in the seeds matured under warmer temperature, palisade cells were shorter and contained less cellulose but increased levels of hemicellulose and lignin that contributed to the impermeable seed coat. However, given the difficulty in measuring temperature throughout the seed maturation period, direct information on this subject is mostly incomplete. Further, seasonal or location-specific variation of temperature around the parent plant may partly explain the development of both permeable and impermeable seed coat in the same species maturing at different times or in different places. Piano et al. (1996) reported that the number of impermeable seeds produced by *Trifolium subterraneum* decreased with increasing altitude indicating that the high temperature prevalent at lower altitudes contributes to the production of more impermeable seeds. Thus, it is reasonable to predict that seeds maturing at higher temperature are likely to lose more water and produce higher proportion of PY seeds than the seeds developing in a low-temperature environment.

The development of an impermeable testa is initiated only when the moisture content of the seeds falls below species-specific threshold levels. In *Trifolium repens*, *T. pratense*, and *Lupinus arboreus* during maturation drying, moisture content fell rapidly to approximately 25 % (dry weight basis), but this drop did not lead to the development of impermeable seed coats (Hyde 1954). However, towards the end of maturation drying, the moisture loss was slow and when the seeds reached 14 % moisture content, the epidermis became impermeable. Thereafter, water present in the seeds could only diffuse out through hilum when the external relative humidity was less, but at higher relative humidity the fissure closes preventing the movement of water in the form of vapor into the seeds (Hyde 1954).

Many studies established that the relative humidity (RH) of the seed maturation environment can affect the drying capacity of seeds, and that RH consequently plays a critical role in the development of impermeable seed coats (Barrett-Lennard and Gladstones 1964; Corner 1951). In Western Australia, seeds of *Ornithopus compressus* collected before maturation and stored at 76 % RH and above did not develop impermeable seeds, while storage at 44 % RH or below resulted in all seeds being impermeable (Barrett-Lennard and Gladstones 1964). By growing plants of *Trifolium repens* at three different relative humidities, D'hondt et al. (2010) found that seeds matured under wet conditions (relative humidity between 89 and 99.9 %) developed permeable seeds, compared with dry conditions (RH between 47 and 98 %) where few permeable seeds developed. At RH levels between 61 and 98 %, there were almost equal numbers of seed with permeable and impermeable coats. Similarly, Tozer and Ooi (2014) reported that seeds of *Acacia saliga* matured in a dry year produced more impermeable seeds, than in a year with higher relative humidity.

The development of an impermeable seed coat is affected by the temperature and RH prevailing at the time of seed maturation, but these factors continue to act on seeds and dry them even after they are shed from parent plant to the soil (Quinlivan and Millington 1962). While measuring these effects in the field is challenging, laboratory experiments storing seeds at different RH and temperatures provided support for this suggestion. In the case of *Melilotus officinalis*, seeds collected before maturation drying and stored at dry conditions became impermeable, but storing these seeds in a moist environment did not develop impermeability (Helgeson 1932). Seeds of *Lupinus luteus* maturing in Israel remained permeable to water during the maturation drying stage, but after removal from the mother plant, seeds stored at lower humidity became impermeable, whereas those under higher humidity conditions remained permeable (Hurwitz and Gabrielith-Gelmond 1952). In *Lupinus varius*, the moisture content of the seeds before shedding was 18–20 %, but after dispersal on to the ground, the moisture content of the seeds decreased to 10–12 % within 2–3 days. This loss of moisture was accompanied by the development of an impermeable seed coat (Quinlivan 1967). Working with nine varieties of garden bean seeds, Nutile and Nutile (1947) showed that no seeds collected before completing maturation drying and held at higher RH developed impermeable seed coats following 60 days of storage; however, the ability of seeds to develop impermeable seed coats increased with a decrease in RH, with some cultivar-specific variation. Nevertheless, there appears to be a threshold moisture content below which, irrespective of maternal environment, a high percentage of PY develops in the seed population (Hyde 1954). For example, although seeds of *Stylosanthes hamate* cv. Verano had various levels of PY at different temperatures, the effect of temperature became irrelevant, if the moisture content of the seeds fell below 7 %. Below this moisture all seeds developed impermeable seed coats, irrespective of ambient temperature (Argel and Humphreys 1983a).

It has been suggested that there is an inverse relationship between temperature and relative humidity in the development of impermeable seed coat. In general, seeds maturing at a low relative humidity and high temperature environment are more likely to form impermeable seed coats, whereas higher humidity combined with low temperature favors the development of a permeable seed coat (Biasutti Owen 1956). Hopkins et al. (1947) showed that storing freshly collected seed of *Phaseolus vulgaris* at 4.4 °C for 6 months at 0 and 80 % RH resulted in 61 and 0 % of impermeable seeds compared with 14.2 % impermeable seeds recorded before storage. However, storing the same batch of seeds at a higher temperature (26.6 °C) resulted in 85 % impermeable seeds at 0 % RH, but no impermeable seeds at 80 % RH.

In addition to the relative humidity and temperature, gases present in the atmosphere affect the development of an impermeable seed coat. For example, Marbach and Mayer (1974) found that seeds of *Pisum elatius* collected prior to maturation drying and subsequently dried over $CaCl_2$ became impermeable only if they were dried in air or oxygen, but all the seeds remained permeable if dried in a vacuum with nitrogen. In contrast, all *Robinia pseudoacacia* seeds dried in any of the above conditions developed permeable seed coats when collected early in the maturation drying stage, but seeds collected late developed impermeable seed coats when dried in air and oxygen, but only a few in vacuum with nitrogen.

The season in which the PY seeds mature greatly affects the proportion of impermeable seeds developed. In general, seeds maturing in wet seasons are less impermeable than those that mature during dry seasons. For instance, Quinlivan (1965) found that the seeds of *Trifolium subterraneum* growing in environments with a long spring growing period developed more impermeable seeds than those matured where there was a short growing period. Similarly, seeds of *Centrosema virginianum* and *Macroptilium atropurpureum* produced higher number of impermeable seeds in the spring than in autumn (Clements 1977). In the case of *Prosopis juliflora*, there were significantly fewer impermeable seeds when seeds matured in autumn compared with winter and spring (El-Keblawy and Al-Rawai 2006). The number of dormant seeds produced by *Fumana ericoides* matured in winter was 1.7 % compared with 100 % dormant seeds matured in late spring/early summer (Llorens et al. 2008). In addition, the variation in the length of the growing period during seed maturation also seems to be a crucial factor in the development of various levels of hardseededness (Collins 1981; Lodge et al. 1990; Revell et al. 1999).

Evidence also indicates that the amount of rainfall received by the parent plant site plays a vital role in whether an impermeable seed coat develops. One possible reason for the variation in development of impermeable seed coats can be ascribed to water stress resulting from varied rainfall (Argel and Humphreys 1983b; Cameron 1967; Hill et al. 1986; Smith et al. 1998). Less rainfall results in exposure to higher water stress, which leads to development of a high proportion of water impermeable seed, but in the years with high rainfall, the proportion impermeable seed is low. Even within the same site, variation in rainfall can produce various numbers of permeable and non-permeable seed coat within the same plant in seeds maturing at different years (Nichols et al. 2009).

Many detailed investigations agree that species with a known history of PY can maintain or lose the dormancy state depending upon the environmental conditions under which the descendent populations are grown. Development of an impermeable seed coat in *Phaseolus vulgaris* is heritable from the parent plant, but the next generation plants growing in a different set of environments compared with that of the mother plant can result in different proportions seeds with impermeable coats. Generally, there are more impermeable seeds in dry environments (Lebedeff 1947). The only detailed study that has shown environmental conditions as selective force in the development of an impermeable seed coat (Nichols et al. 2009) revealed that plants that migrated to where the growing season was short generally developed seeds with high proportion of impermeable coats, whereas in sites with a long growing season, the proportion of impermeable seed was low. In addition to the length of growing season, other factors, such as low rainfall and harsh environmental conditions prevalent during a short growing season, act as driving forces for developing high proportions of impermeable seeds (Nichols et al. 2009). Because this change in the proportion of impermeability in response to the prevailing environment occurred within 2 years, climate might possibly be the important driving force contributed to the evolution of PY in seeds. Thus, as proposed by Baskin et al. (2000), climatic drying could be the important selective force for the evolution of PY, and natural selection fine-tunes the species with PY to fit the environment.

The literature available on environmental factors controlling the extent of PY development has been reviewed thus far. However, it is worth noting that apart from the external environmental factors, there are some maternal effects such as age of the mother plant (reviewed by Baskin and Baskin 2014), seed size produced (Calero et al. 1981; Jaganathan et al. submitted; Yaklich et al. 1986), composition of seed coat (Egley et al. 1983; Saio 1976; Stabell et al. 1996), and position of seed on plant and inflorescence (Pérez-García 1997; Taylor and Palmer 1979) that can also potentially affect the PY status of seeds. Nevertheless, almost nothing is known about the relationship (if any) between the environmental factors and maternal effects. The studies concluding that maternal effects play an important role in determining the development of PY did not consider the effect of maternal environment at different maturation sites. Given the fact that environmental conditions around the mother plant varies significantly at different positions on the mother plant, it is not clear whether maternal effects per se influence the PY development, or the influence is from the environmental conditions or a combination of both. For example, seeds in the inflorescence exposed to direct sunlight presumably dry to lower moisture level compared with the seeds developing in shade, and this scenario is particularly true for plants in wild (Hay et al. 2010). Thus, this area warrants detailed studies.

Ecological considerations

The ability of plants to produce seeds with different levels of PY offers extensive ecological benefit for species colonization (Venable 1985). Indeed, variation in the number of PY seeds produced by plants growing in different environmental conditions is likely to be advantageous for persistence in diverse ecosystems. Given that species producing PY seeds occur in many types of the ecosystems from alpine to warm deserts (Baskin and Baskin 2014; Jaganathan et al. 2015), the environmental control of PY development has several ecological implications. Based on the evidence presented above, it is safe to assume that species with a known history of developing an impermeable seed coat growing in arid and dry environments could produce higher percentage of PY seeds. All the environmental conditions reviewed above affect not only the number of impermeable seeds that develop but also the level of hardseededness within impermeable proportion of the seed population. Under conditions of low relative humidity, high temperature, and low rainfall during seed maturation, seeds persist in soil for a long time, forming persistent seed banks, and spread the risk of germination over many years. High summer temperatures in these environments favor dormancy loss and synchronize germination with the wet season (Jaganathan and Liu 2014b). Even seeds that break dormancy before the wet season do not germinate, as the seedling mortality would be high (Baskin et al. 2004; Jaganathan and Liu 2014a; Leck et al. 2008).

Although strong empirical evidence to validate that maternal environmental conditions affect the seed persistence and dormancy-breaking requirements of PY seeds is scarce, several studies provide evidence (Bolland 1985; Taylor 1996). Taylor (1996) found that seeds of *Medicago polymorpha* and *M. truncatula*, collected from three sites, showed different dormancy loss responses when buried in four seed softening sites. Thus, Taylor (1996) unequivocally concluded that '*seed growing environments were more important than seed softening environments in determining rates of seed softening in all cultivars*.' Quinlivan (1967) also presented evidence to show that PY seeds maturing in different environments would have different dormancy-breaking requirements, and this would essentially determine the loss of seeds from soil seed banks. It was shown that *L. varius* plants grown in a low moisture environment persisted in soil for 5 years, with 15–20 % of propagules broke dormancy every summer and germinated during the rain in autumn. However, seeds from drier site germinated within 2 years. The difference in the level of hardseededness in seeds matured at different sites along with different environmental conditions (moist vs. dry) can explain this variation in persistence capacity. Similarly, Michael et al. (2006) reported that more than 80 % of *Malva parviflora* seeds collected at higher rainfall site lost dormancy in 3 months (100 % in 6 months) when incubated at 50/20 °C, but dormancy in seeds collected from a lower rainfall area only germinated to about 60 % even after 2 years of incubation at 50/20 °C. In addition, when batches of seeds from four different sites (two with high rainfall, two with low rainfall) were buried in a site different from the seed maturation site, about 50 % of the seeds from lower rainfall sites broke dormancy in 3 months compared with <5 % germination from seeds matured in the higher rainfall sites. Various levels of coat impermeability and different dormancy-breaking requirements have also been reported for Fabaceae (Taylor et al. 1991), indicating that this pattern might be common to all PY species. Norman et al. (2002) showed the level of hardseededness in *Trifolium* (Fabaceae) seeds produced in the same year differs between sites and also demonstrated that the softening pattern varies in accordance with the level of coat impermeability.

Laboratory studies have shown that seed coat of PY species becomes impermeable to water only when the moisture content of the seeds drop below particular species-specific threshold value, e.g., 15 % in *Peltophorum pterocarpum* (Mai-Hong et al. 2003) and *Lupinus varius* (Quinlivan 1968); 12 % in *Gleditsia triacanthos* (Geneve 2009), *G. aquatica* (Geneve 2009), *Gymnocladus dioicus* (Geneve 2009), *L. arboreus* (Hyde 1954), *Pisum sativum* (Ellis and Roberts 1982), *Trifolium ambiguum* (Hay et al. 2010), *T. pretense* (Hyde 1954), and *T. repens* (Hyde 1954); 11 % in *Lupinus digitatus* (Gladstones 1958). However, in the field seeds are likely to lose more moisture

(Jaganathan and Liu 2014b; Jayasuriya et al. 2013). Thus, based on the available evidence, it is proposed that two levels of PY might result from the moisture content attained during maturation drying or continued drying after seed dispersal: (1) shallow and (2) absolute. Seeds with 'shallow' PY have higher moisture content, whereas those with 'absolute' PY have much lower water content. It is not clear from the previous studies whether there is also an 'intermediate' level of PY. In addition, the reversing of PY in seeds with shallow dormancy reported in *Lupinus digitatus* (Gladstones 1958) and *Trifolium ambiguum* (Hay et al. 2010) must be investigated in a wide range of species.

Interestingly, Quinlivan (1968) found that seeds of *Lupinus varius* with moisture content above 10 % (but below 15 %) had an impermeable seed coat and that dormancy was broken in moist or high humidity atmosphere by diffusion of water in the form of vapor only through testa. On the other hand, for the seeds with a moisture content below 10 %, moist conditions did not break dormancy, but temperature fluctuations between 15 and 65 °C had fractured seed coat at the strophiole region and allowed seeds to imbibe water. This study confirmed that the germination pattern of PY species largely depends on the degree to which the summer temperature and/or ambient RH desiccates the seeds. Thus, if the moisture content remains above 10 %, a large proportion of seeds will germinate over several months, and only a smaller proportion remains as part of the seed bank, but with moisture content below 8.5 %, only appropriate summer temperature fluctuations can break dormancy and these seeds would begin to germinate at the onset of the wet season.

Many studies have documented that under natural conditions, the dormancy break in PY species occurs in two steps (1) a pre-conditioning step that softens and makes the seeds sensitive to dormancy breaking and (2) the actual dormancy-breaking step, during which seeds imbibe water (Jayasuriya et al. 2008a, b, 2009; Taylor 2005; Taylor and Revell 1999; Van Assche et al. 2003). These studies also displayed a relationship between the RH and dormancy breaking. In *Ipomoea lacunose*, for example, seeds generally became sensitive to dormancy break under wet conditions (Jayasuriya et al. 2008a). However, dormancy is only alleviated in sensitive seeds when the seeds experience higher temperature (35 °C) in moist soil. In contrast, in sensitive seeds exposed to dry conditions at ≤5 °C or ≥30 °C, the sensitive stage was reversed, i.e., seeds became insensitive to dormancy break. Interestingly, some samples collected at a different time showed alleviation of dormancy when subjected to 35 °C wet treatment even in the absence of prior dry storage to make seeds sensitive. In contrast, seeds of *Cuscuta australis* required dry storage to become sensitive and then wet conditions combined with high temperature to break dormancy (Jayasuriya et al. 2008b). Unfortunately, the moisture content of the seeds was not measured at the time of maturity and it is likely that variation in lower level of moisture content attained during seed maturation could have led to production of 'shallow' and 'absolutely' dormant seeds matured at different times. As such, this would have affected the dormancy release process.

Seeds with PY generally persist in soil for a long time before they germinate (Baskin and Baskin 2014). In their natural environment, the ability of seeds to respond to the humid and dry conditions during dormancy break can also be influenced by the position of seeds in the soil. In general, PY seeds present in the surface soil layers are released from dormancy more quickly than seeds buried deeper. This is presumably due to temperature fluctuations at the surface (Loi et al. 1999; Taylor and Ewing 1988). However, Hu et al. (2009) found that seeds of *Sophora alopecuroides* matured at higher and lower rainfall site differed in the initial level of hardseededness, and this difference contributed to two distinct patterns of dormancy loss when buried at two different depths. Dormancy release rate in seeds from the lower rainfall site decreased as burial depth increased, but only 9 % of the seeds matured from higher rainfall site showed alleviation of dormancy when left on the soil surface (compared with 73 % of seeds from lower rainfall site and left on soil surface), although 71 % of the seeds from the high rainfall site became non-dormant when buried at 2 cm depth.

None of the studies that illustrated a two-step dormancy break in PY seeds (see references above) measured the initial moisture content of seeds. There are at least three difficulties in understanding the dormancy break of PY seeds without this information. Firstly, the pre-conditioning step in seeds dried to lower moisture content (absolute dormant seeds) may be different from that of seeds maintaining higher water content as an equilibration to surrounding RH and temperature (shallow dormant seeds). It is not clearly known, if this difference is the reason for mixed results with some studies claiming wet heat is effective in breaking dormancy compared with dry heat and others concluding the opposite (Martin et al. 1975; Van Klinken et al. 2006). Nevertheless, the findings reported by Hu et al. (2009) suggest that variation in dormancy levels resulting from different maturation sites could be the important factor in this disparity. Those authors reported wet heat released dormancy in *S. alopecuroides* seeds matured in both high and low rainfall sites; however, dry heat was less effective in breaking dormancy of seeds collected from the high rainfall site. Perhaps, this difference determines the time and duration required by high temperature, e.g., during fire to break dormancy (Jaganathan 2015). Secondly, it remains unclear whether shallow and absolute dormant seeds have any specific pre-conditioning and dormancy-breaking requirements. Thirdly, the rate of completion of each step could also vary between seeds with different moisture levels. Moist or dry conditions and the temperature at which these treatments are applied might affect dormancy loss mechanisms. Thus, future studies should place special emphasis on understanding the dormancy-breaking mechanisms in PY seeds with different moisture contents, i.e., shallow and absolute dormant seeds.

Conclusions

Environmental factors play an important role in the development of the number of impermeable seeds and various levels of hardseededness within impermeable seeds. Available literature strongly suggests that maternal environment during seed development affects the level of hardseededness, resulting in two levels of PY, i.e., shallow and absolute. This notion helps explain the year-to-year variation in dormancy of PY seeds growing in the same site or within year variation of seeds from different sites and the difference in pattern of dormancy loss. This also partly supports the proposal that climate drying would have acted as the selective force for the development of hard seed coat in seeds. Thus, depending on environmental conditions, PY seeds dispersed to different locations could develop all or no dormant seeds. Although the data are not conclusive, it is believed that the variation in moisture level reached during seed maturation and subsequent soil drying can affect the dormancy loss mechanism. Nevertheless, almost nothing is known about the ecological significance of this process. Understanding how PY seeds having shallow or absolute dormancy germinate in natural environments will greatly increase our knowledge of the mechanism(s) underlying large-scale ecological patterns of PY species.

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References

Argel PJ, Humphreys LR (1983a) Environmental effects on seed development and hardseededness in *Stylosanthes hamata* cv. Verano. I. Temperature. Aust J Agric Res 34:261–270

Argel PJ, Humphreys LR (1983b) Environmental effects on seed development and hardseededness in *Stylosanthes hamata* cv. Verano. II. Moisture supply and illuminance. Aust J Agric Res 34:271–277

Argel PJ, Paton CJ (1999) Overcoming Legume 14 hardseededness. In: Loch DS, Ferguson JE (eds) Forage seed production: Tropical and subtropical species, vol 2. CAB International, Wallingford, pp 247–256

Barrett-Lennard RA, Gladstones JS (1964) Dormancy and hardseededness in Western Australian serradella (*Ornithopus compressus* L.). Aust J Agric Res 15:895–904

Baskin JM, Baskin CC (2004) A classification system for seed dormancy. Seed Sci Res 14:1–16

Baskin CC, Baskin JM (2014) Seeds: ecology, biogeography, and evolution of dormancy and germination, 2nd edn. Elsevier, San Diego

Baskin JM, Baskin CC, Li X (2000) Taxonomy, anatomy and evolution of physical dormancy in seeds. Plant Species Biol 15:139–152

Baskin JM, Davis BH, Baskin CC, Gleason SM, Cordell S (2004) Physical dormancy in seeds of *Dodonaea viscosa* (Sapindales, Sapindaceae) from Hawaii. Seed Sci Res 14:81–90

Biasutti Owen E (1956) The storage of seeds for maintenance of viability, Commonwealth Bureaux Pastures Field Crops (Bulletin 43). Commonwealth Agricultural Bureaux, Hurley, p 81

Bolland MDA (1985) Serradella (*Ornithopus* sp.): maturity range and hard seed studies of some strains of five species. Aust J Exp Agric 25:580–587

Calero E, West SH, Hinson K (1981) Water absorption of soybean seeds and associated causal factors. Crop Sci 21:926–933

Cameron DF (1967) Hardseededness and seed dormancy of Townsville lucerne (*Stylosanthes humilis)* selections. Aust J Exp Agric 7:237–240

Clements RJ (1977) Agronomic variation in *Centrosema virginianum* in relation to its use as a sub-tropical pasture plant. Aust J Exp Agric 17:435–444

Collins WJ (1981) The effects of length of growing season, with and without defoliation, on seed yield and hard-seededness in swards of subterranean clover. Aust J Agric Res 32:783–792

Corner EJH (1951) The leguminous seed. Phytomorphology 1:117–150

D'hondt B, Brys R, Hoffmann M (2010) The incidence, field performance and heritability of non-dormant seeds in white clover (*Trifolium repens* L.). Seed Sci Res 20:169–177

Egley GH (1979) Seed coat impermeability and germination of showy crotalaria (*Crotalaria spectabilis*) seeds. Weed Sci 27:355–361

Egley GH, Paul RN Jr, Vaughn KC, Duke SO (1983) Role of peroxidase in the development of water-impermeable seed coats in *Sida spinosa* L. Planta 157:224–232

El-Keblawy A, Al-Rawai A (2006) Effects of seed maturation time and dry storage on light and temperature requirements during germination in invasive *Prosopis juliflora*. Flora Morphol Distrib Funct Ecol Plants 201:135–143

Ellis RH, Roberts EH (1982) Desiccation, rehydration, germination, imbibition injury and longevity of pea seeds (*Pisum sativum*). Seed Sci Technol 10:501–508

Gama-Arachchige NS, Baskin JM, Geneve RL, Baskin CC (2011) Acquisition of physical dormancy and ontogeny of the micropyle–water-gap complex in developing seeds of *Geranium carolinianum* (Geraniaceae). Ann Bot 108:51–64

Geneve RL (2009) Physical seed dormancy in selected Caesalpinioid legumes from eastern North America. Propag Ornam Plants 9:129–134

Gladstones JS (1958) The influence of temperature and humidity in storage on seed viability and hard-seededness in the west Australian, Blue Lupin, *Lupinus digitatus* Forsk. Aust J Agric Res 9:171–181

Hay FR, Smith RD, Ellis RH, Butler LH (2010) Developmental changes in the germinability, desiccation tolerance, hardseededness, and longevity of individual seeds of *Trifolium ambiguum*. Ann Bot 105:1035–1052

Helgeson EA (1932) Impermeability in mature and immature sweet clover seeds as affected by conditions of storage. Trans Wis Acad Sci Arts Lett 27:193–206

Hill HJ, West SH, Hinson K (1986) Effect of water stress during seedfill on impermeable seed expression in soybean. Crop Sci 26:807–812

Hills LK (1942) Dormancy and hardseededness in *Trifolium subterraneum*. 1. The effect of time of harvest and of certain seed storage conditions. J Counc Sci Ind Res 15:275–284

Hopkins EF, Silva JR, Pagan V, Villafane AG (1947) Investigations on the storage and preservation of seed in Puerto Rico. Puerto Rico Exp Sta Bull 72:47

Hu XW, Wu YP, Wang YR (2009) Different requirements for physical dormancy release in two populations of *Sophora alopecuroides* relation to burial depth. Ecol Res 24:1051–1056

Hudson AR, Ayre DJ, Ooi MKJ (2015) Physical dormancy in a changing climate. Seed Sci Res 25:66–81

Hurwitz S, Gabrielith-Gelmond H (1952) Hardening of sweet lupin seeds. Ktavim 2:57–64

Hyde EOC (1954) The function of the hilum in some Papilionaceae in relation to the ripening of the seed and the permeability of the testa. Ann Bot 18:241–256

Jaganathan GK (2015) Are wildfires an adapted ecological cue breaking physical dormancy in the Mediterranean basin? Seed Sci Res 25:120–126

Jaganathan GK, Liu B (2014a) Role of seed sowing time and microclimate on germination and seedling establishment of *Dodonaea viscosa* (Sapindaceae) in a seasonal dry tropical environment—a special insight to restoration efforts. Botany 93:23–29

Jaganathan GK, Liu B (2014b) Seasonal influence on dormancy alleviation in *Dodonaea viscosa* (Sapindaceae) seeds. Seed Sci Res 24:229–237

Jaganathan GK, Dalrymple SE, Liu B (2015) Towards an understanding of factors controlling seed bank composition and longevity in the alpine environment. Bot Rev 81:70–103

Jayasuriya KMGG, Baskin JM, Baskin CC (2008a) Cycling of sensitivity to physical dormancy-break in seeds of *Ipomoea lacunosa* (Convolvulaceae) and ecological significance. Ann Bot 101:341–352

Jayasuriya KMGG, Baskin JM, Geneve RL, Baskin CC, Chien C-T (2008b) Physical dormancy in seeds of the holoparasitic angiosperm *Cuscuta australis* (Convolvulaceae, Cuscuteae): dormancy-breaking requirements, anatomy of the water gap and sensitivity cycling. Ann Bot 102:39–48

Jayasuriya KMGG, Baskin JM, Geneve RL, Baskin CC (2009) Sensitivity cycling and mechanism of physical dormancy break in seeds of *Ipomoea hederacea* (Convolvulaceae). Int J Plant Sci 170:429–443

Jayasuriya KMGG, Wijetunga AS, Baskin JM, Baskin CC (2013) Seed dormancy and storage behaviour in tropical Fabaceae: a study of 100 species from Sri Lanka. Seed Sci Res 23:257–269

Lebedeff GA (1947) Studies on the inheritance of hard seeds in beans. J Agric Res 74:205

Leck MA, Parker VT, Simpson RL (2008) Seedling ecology and evolution. Cambridge University Press, Cambridge

Llorens L, Pons M, Gil L, Boira H (2008) Seasonality of seed production and germination trends of *Fumana ericoides* (Cistaceae) in the west semiarid Mediterranean region. J Arid Environ 72:121–126

Lodge GM, Murison RD, Heap EW (1990) The effect of temperature on the hardseed content of some annual legumes grown on the northern slopes of New South Wales. Aust J Agric Res 41:941–955

Loi A, Cocks PS, Howieson JG, Carr SJ (1999) Hardseededness and the pattern of softening in *Biserrula pelecinus* L., *Ornithopus compressus* L., and *Trifolium subterraneum* L. seeds. Aust J Agric Res 50:1073–1082

Mai-Hong T, Hong TD, Hien NT, Ellis RH (2003) Onset of germinability, desiccation tolerance and hardseededness in developing seeds of *Peltophorum pterocarpum* (DC) K. Heyne (Caesalpinioideae). Seed Sci Res 13:323–327

Marbach I, Mayer AM (1974) Permeability of seed coats to water as related to drying conditions and metabolism of phenolics. Plant Physiol 54:817–820

Martin RE, Miller RL, Cushwa CT (1975) Germination response of legume seeds subjected to moist and dry heat. Ecology 56:1441–1445

Michael PJ, Steadman KJ, Plummer JA (2006) Climatic regulation of seed dormancy and emergence of diverse *Malva parviflora* populations from a Mediterranean-type environment. Seed Sci Res 16:273–281

Nichols PGH, Cocks PS, Francis CM (2009) Evolution over 16 years in a bulk-hybrid population of subterranean clover (*Trifolium subterraneum* L.) at two contrasting sites in south-western Australia. Euphytica 169:31–48

Norman HC, Cocks PS, Galwey NW (2002) Hardseededness in annual clovers: variation between populations from wet and dry environments. Aust J Agric Res 53:821–829

Nutile, G, Nutile, LC (1947) Effect of relative humidity on hard seeds in garden beans. In Proceedings of the Association of Official Seed Analysts, pp 106–114

Pérez-García F (1997) Germination of *Cistus ladanifer* seeds in relation to parent material. Plant Ecol 133:57–62

Piano E, Pecetti L, Carroni AM (1996) Climatic adaptation in subterranean clover populations. Euphytica 92:39–44

Quinlivan BN (1965) The influence of the growing season and the following dry season on the hardseeedness of subterranean clover in different environments. Aust J Agric Res 16:277–291

Quinlivan BJ (1967) Environmental variation in the long term pattern of germination from hard seeds of *Lupinus varius*. Aust J Exp Agric 7:263–265

Quinlivan BJ (1968) The softening of hard seeds of san-plain lupin (*Lupinus varius*). Aust J Agric Res 19:507–515

Quinlivan BJ (1971) Seed coat impermeability in legumes. J Aust Inst Agric Sci 37:283–295

Quinlivan BJ, Millington AJ (1962) The effect of a Mediterranean summer environment on the permeability of hard seeds of subterranean clover. Aust J Agric Res 13:377–387

Revell CK, Taylor GB, Cocks PS (1999) Effect of length of growing season on development of hard seeds in yellow serradella and their subsequent softening at various depths of burial. Aust J Agric Res 50:1211–1223

Rolston MP (1978) Water impermeable seed dormancy. Bot Rev 44:365–396

Saio K (1976) Soybeans resistant to water absorption. Cereal Foods World 21:168–173

Smith F, Cocks P, Ewing M (1998) Seed production in cluster clover (*Trifolium glomeratum* L.). 1. Flowering time, abortion, seed size, and hardseededness along branches. Aust J Agric Res 49:961–964

Souza FH, Marcos-Filho J (2001) The seed coat as a modulator of seed-environment relationships in Fabaceae. Braz J Bot 24:365–375

Stabell E, Upadhyaya MK, Ellis BE (1996) Development of seed coat-imposed dormancy during seed maturation in *Cynoglossum officinale*. Physiol Plant 97:28–34

Taylor GB (1996) Effect of the environment in which seeds are grown and softened on the incidence of autumn seed softening in two species of annual medics. Aust J Agric Res 47:141–159

Taylor GB (2005) Hardseededness in Mediterranean annual pasture legumes in Australia: a review. Aust J Agric Res 56:645–661

Taylor GB, Ewing MA (1988) Effect of depth of burial on the longevity of hard seeds of subterranean clover and annual medics. Aust J Exp Agric 28:77–81

Taylor GB, Palmer MJ (1979) The effect of some environmental conditions on seed development and hard-seededness in subterranean clover (*Trifolium subterraneum* L.). Aust J Agric Res 30:65–76

Taylor GB, Revell CK (1999) Effect of pod burial, light, and temperature on seed softening in yellow serradella. Aus J Agr Res 50:1203–1209

Taylor GB, Maller RA, Rossiter RC (1991) A model describing the influence of hard seededness on the persistance of an annual forage legume, in a ley farming system, in a mediterranean-type environment. Agric Ecosyst Environ 37:275–301

Tozer MG, Ooi MK (2014) Humidity-regulated dormancy onset in the Fabaceae: a conceptual model and its ecological implications for the Australian wattle *Acacia saligna*. Ann Bot 114:579–590

Van Assche JA, Debucquoy KL, Rommens WA (2003) Seasonal cycles in the germination capacity of buried seeds of some Leguminosae (Fabaceae). New Phytol 158:315–323

Van Klinken RD, Flack LK, Pettit W (2006) Wet-season dormancy release in seed banks of a tropical leguminous shrub is determined by wet heat. Ann Bot 98:875–883

Venable DL (1985) The evolutionary ecology of seed heteromorphism. Am Nat 126:577–595

Yaklich R, Vigil E, Wergin W (1986) Pore development and seed coat permeability in soybean. Crop Sci 26:616–624