

Maternal and burial environment determine the physical dormancy release in tropical *Senna auriculata* (Fabaceae) seeds

Ganesh K. Jaganathan¹ · Yingying Han¹ · Danping Song¹ · Panner Selvam² · Baolin Liu¹

Received: 28 February 2017 / Accepted: 21 April 2017 / Published online: 19 May 2018
© Northeast Forestry University and Springer-Verlag GmbH Germany, part of Springer Nature 2018

Abstract In tropical ecosystems, species with an impermeable seed coat, i.e. physical dormancy (PY), are large in number and their seed coat is considered to be an adaptive trait for species persistence and colonization. However, only little is known about their mechanisms for breaking dormancy. The objective of this study was to understand the importance of seed maturation site and burial location in determining the PY release of *Senna auriculata*. Freshly collected seeds of *S. auriculata* from Vellore and Coimbatore, Tamil Nadu, India, germinated to $11 \pm 1.5\%$ and $19 \pm 2.5\%$ respectively and remaining seeds did not imbibe water, thus had PY. Germination of seeds from both sites following hot-water treatment for 30 s and mechanical scarification increased significantly and seeds were able to germinate at a wide-range of temperatures (5–35 °C) both in light and darkness. When incubated at 15/60 °C for 3 months, dormancy release for seeds collected from Coimbatore (72%) was greater than seeds matured in

Vellore (53%). Following 1 year of burial at three different locations, seeds from Coimbatore germinated to higher percentage than Vellore seeds at all locations. In particular, the higher temperature sites released dormancy to greater extent than the lower temperature site. Our results suggest that summer temperatures (> 60 °C) prevailing in the tropics provide appropriate cues for breaking PY, but this could be greatly affected by the initial state of seeds and the burial environment.

Keywords Artificial burial · Germination ecology · Impermeable seed coat · Summer temperature

Introduction

Physical dormancy (PY) occurs in seeds of many genera belonging to 18 angiosperm families due to the palisade layer present in the seed coat becoming impermeable to water during maturation drying (Baskin and Baskin 2014; Baskin et al. 2000). Although this form of dormancy is documented in numerous species world-wide, this trait is more predominant in the species of tropical deciduous forests and Mediterranean ecosystems (Bargali and Bargali 2016; Jaganathan et al. 2017; Moreira and Pausas 2012;). For example, in a survey of 100 Fabaceae species from Sri Lanka, Jayasuriya et al. (2013) demonstrated that 86 species had PY, indicating this trait is widespread in this family, which is adapted to tropical environments. A wide-range of cues, including fire, passage through animal intestine, high summer temperature, wet heat, nocturnal and diurnal fluctuating summer temperatures have been identified to break dormancy (Baskin and Baskin 2014; Baskin et al. 2004; Jaganathan 2015; Jaganathan and Liu 2014; Jaganathan et al. 2016b). After PY is broken, the

Project funding: This study is supported by Chinese Government Grant Number 2016M601620 and NSFC (Grant Number 31750110474).

The online version is available at <http://www.springerlink.com>

Corresponding editor: Zhu Hong.

✉ Ganesh K. Jaganathan
jganeshcbe@gmail.com

✉ Baolin Liu
blliuk@163.com

¹ Institute of Biothermal Technology, University of Shanghai for Science and Technology, Shanghai 200093, People's Republic of China

² Agro Climate Research Centre, Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu 641019, India

seeds germinate immediately if suitable environmental conditions exist, unless the seeds have physiological dormancy (PD), i.e. combinational dormancy (PY + PD) (*sensu* Baskin and Baskin 2004), which also requires additional environmental cues to alleviate PD.

Seeds with PY have the ability to persist in soil for decades (Baskin and Baskin 2014). During persistence, the seeds experience heterogeneous environmental conditions over a number of years resulting from various ecological changes such as tree uprooting and clearing of standing vegetation by fire (Jaganathan 2015; Vázquez-Yanes and Orozco-Segovia 1993). Many previous studies focusing on PY alleviation under natural conditions have suggested that breaking of PY is affected by conditions present in a particular environment (Mott et al. 1981; Taylor 1996; Taylor and Ewing 1992; van Klinken and Goulier 2013). However, few studies have documented site-to-site variation in dormancy loss. For example, Quinlivan (1967) found that the seeds of *Lupinus varius* matured and persisted in Perth released dormancy over a 5-year period with about 15–20% of seeds germinating every year, whereas all the seeds buried at Chapman became non-dormant and germinated within 2 years. Van Klinken et al. (2008) also reported that the *Parkinsonia aculeata* seeds buried at various locations in Australia from wet to dry, displayed different requirements for dormancy release. Thus, in their natural environment, PY seeds can be dispersed to other sites where the conditions for breaking dormancy are different. Consequently, increased understanding of dormancy release mechanisms under various ecological conditions could provide important information on the germination ecology of PY species.

Senna auriculata (Fabaceae) is endemic to Sri Lanka (Jayasuriya et al. 2013; Jayaweera 1981) but has become naturalized in many regions of India, growing up to 2 m in height. It has the ability to colonize a range of environmental conditions from complete drylands to moist forests. The genus *Senna* belonging to the subfamily Caesalpinioideae includes nearly 240 species occurring in many ecosystems world-wide (Teketay 1996). Many species of *Senna* including *S. auriculata* have PY at maturity and germination requires softening of the seed coat (Baskin et al. 1998; de Paula et al. 2012; Delachiave and De Pinho 2003; Jayasuriya et al. 2013; Lacerda et al. 2004; Rodrigues-Junior et al. 2014; Teketay 1996; Vijayakumar and Selvaraju 2013). In most cases, seeds have been made permeable by dipping in hot water or by mechanical scarification (but see Baskin et al. 1998), thus the mechanism of dormancy-break in *Senna* seeds persisting in soil remains unknown.

In the present study, we examined the effects of maternal environment and burial site in determining dormancy loss of *S. auriculata* seeds. Our specific objectives

were to (1) determine the pattern of dormancy loss in soil; (2) document whether seeds collected from different maternal sites vary in their initial dormancy status; (3) understand the importance of summer temperature fluctuations in breaking dormancy and (3) identify if the burial site is an important factor determining dormancy loss.

Materials and methods

Seed materials

Mature pods of *S. auriculata* were collected either from Vellore or Coimbatore in Tamil Nadu, India (Table 1). These two sites are about 450 km apart. The temperature difference between two sites is approximately 2 °C during the cool season between September and February; and 3–5 °C in the warmest months (April–July) (Fig. 1). Throughout the year, relative humidity is higher in Coimbatore compared with Vellore (Fig. 1). Both sites received most of the rainfall following summer, i.e., from September to December (Fig. 1). Thus, Vellore is warmer and drier than Coimbatore.

In the field, seed maturation of *S. auriculata* began during the rainy season and maturation drying occurred during January after seeds were dispersed naturally during late-January or February. At each site, pods were collected directly from 10 to 15 healthy plants at the time of natural dispersal. Pods maturing in Vellore completed maturation drying 2 weeks earlier than in Coimbatore. Each pod contained 4–8 seeds. Seeds were removed from the pods, cleaned, air dried and stored in a glass jar at room temperature (approx. 24 °C and 60% RH). Seed mass was calculated using four replicates of 100 air-dried seeds. Laboratory and field experiments were conducted within 2 months after seed collection.

Moisture content of seeds

The moisture content of the freshly collected seeds from two sites was determined by oven drying. Three replicates of 60 seeds were weighted and dried at (103 ± 1) °C for 17 h to determine their dry weight. Moisture content was calculated as the difference in the weight before and after drying and expressed as a percentage of fresh weight.

Imbibition

Three replicates of 25 freshly collected or mechanically scarified (by cutting the seed coat using a scalpel) seeds were weighted in a digital balance to the nearest 0.001 g and placed on moistened filter paper in Petri dishes kept at room conditions. The seeds were re-weighed every hour for

Table 1 Characteristics of *S. auriculata* seeds (mass and moisture content) collected from two locations in Tamil Nadu, India

Seed maturation location	Seed characteristics and collection information			
	Location	Date collected	Seed mass (g)	Moisture content (%)
Vellore	12.92°N, 79.13°E	29/1/2013	1.9 ± 0.2 ^a	7.5 ± 1.3 ^a
Coimbatore	11.10°N, 76.74°E	15/2/2013	2.2 ± 0.1 ^b	11.1 ± 0.5 ^b

Different lower-case letters indicate significant difference between locations

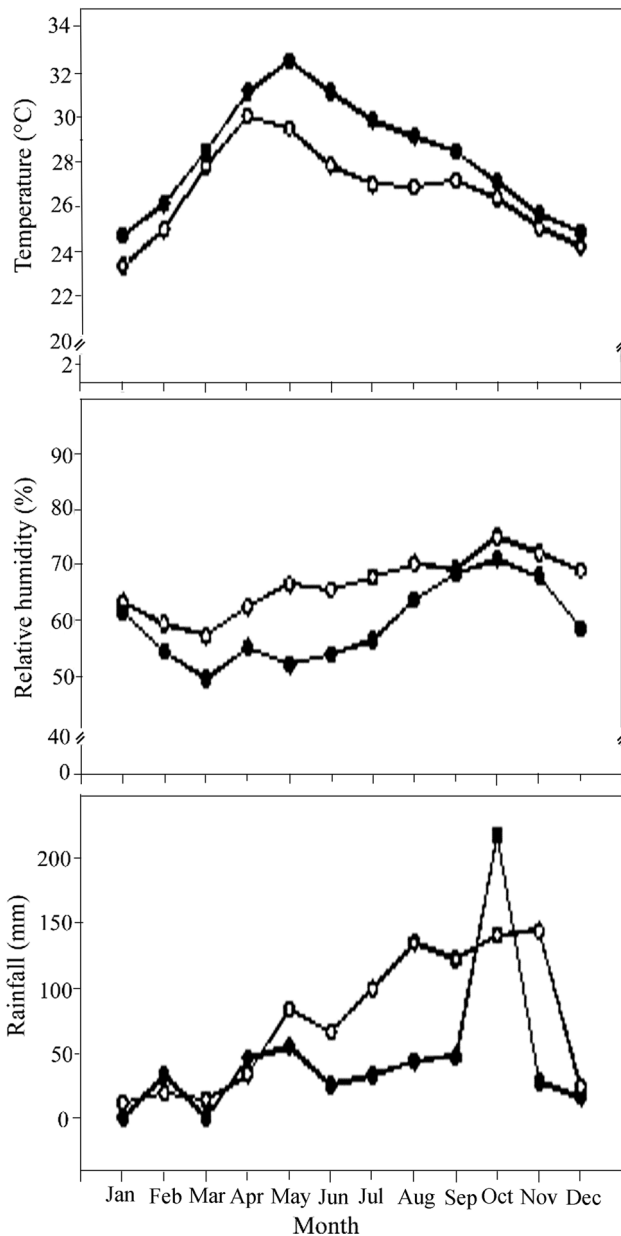


Fig. 1 Average air temperature, relative humidity and rainfall of the seed maturation sites recorded between 2012 and 2014

the initial 8 h and then weighed again at 16 h after blotting the surface water dry by placing them between soft tissue pads. Seeds were then returned to Petri dishes. The amount of water that entered seeds was converted to a percentage

using the method described by Baskin et al. (2004) and plotted against time.

Germination

Germination trials were conducted using three replicates of 25 freshly collected or mechanically scarified seeds sown on 1% agar in water in 175 × 115 × 70 mm clear plastic boxes at 5/15, 20/10, 20/25 and 20/35 °C or at 20/25 °C temperature regimes. These tests were conducted with a 14-h photoperiod provided by white fluorescent lights (approx. 40 μmol m⁻² s⁻¹, 400–700 nm). Seeds were also germinated in dark at 20/25 °C. Darkness was achieved by wrapping the plastic boxes with aluminum foil. Seeds with radicle emergence of 2 mm were scored as germinated. Germination counts were made at 2-day intervals until no seeds germinated for 5 days or after 25–28 days for dark samples.

Dormancy breaking treatments

To test the effect of hot water on dormancy break, seeds from both sites were immersed in boiling water (100 ± 3 °C) for 30 s and subsequently germinated. Three replicates of 25 seeds were used for each site.

The effect of diurnal temperature fluctuation in breaking dormancy was determined by incubating the seeds in Petri dishes at 15/60 °C (lower/upper limit daily temperature range) for 3 months. Thus, on each 24 h cycle seeds were exposed to 15 °C for 10 h, 35 °C for 4 h, 60 °C for 6 h, 20 °C for 4 h. This temperature range occurs during summer in the study region (Jaganathan and Liu 2014, 2015) and also in other tropical and Mediterranean soil during summer months (Turner et al. 2009; Jaganathan 2015). To mimic the rainfall days in the natural environment, we sprayed about 100 ml water after rain fell in the burial site. During the 3 months, we sprayed Coimbatore seeds four times and Vellore seeds seven times. At the end of every month, three replicates of 25 seeds were removed and germinated at 20/25 °C in 14-h photoperiod. The seeds remaining ungerminated at the end of germination tests were dipped in hot water for 30 s and germinated under conditions described above.

Seeds from both sites were also stored in Petri dishes for 1 year at room temperature (approx. 25 °C and 60% RH)

and germinated at the end of storage period. Three replicates of 25 seeds each collected from Coimbatore and Vellore were held for 1 year.

All the germination experiments following dormancy breaking treatments were carried out in 1% agar-water at 20/25 °C in 14 h light as above.

Seed burial experiments

In order to understand the importance of seed burial site in breaking dormancy, we performed the following experiment. Seeds from Coimbatore and Vellore were buried in three locations with contrasting climate. For burial experiments, fifty seeds each collected in Coimbatore and Vellore were placed in each of 12 nylon mesh bags. A total of 24 nylon mesh bags (12 for seeds collected at each site) were used. Three bags (replicates) were buried at the same site and three more bags each (replicates) were buried at the other sites, i.e. Coimbatore seeds were buried in Coimbatore, Vellore and Nilgiri. The average temperature of Nilgiri situated on the Western Ghats, Tamil Nadu is low throughout the year, April being the warmest month with mean temperature of 25 °C and January is the coolest month with a mean temperature of 5 °C (Indian Meteorological Department weather data; also see Caner et al. 2000). The rainfall pattern in Nilgiri also varied and most of the rain fell during June through October. To prevent the risk of predation, all the nylon bags were placed in separate trays (15 cm × 8 cm × 4 cm) with drainage holes for water movement and buried at a depth of 3 cm on February 2013 before the onset of summer. These bags were retrieved at the end of March 2014 and germination tests were conducted.

Statistical analyses

All germination results were analyzed using ANOVA in SPSS 21.0 software. A General Linear Model (GLM) was conducted by taking maturation site and burial locations as fixed factors to quantify the interaction between these factors. Data were arcsine-transformed to achieve normality whenever this assumption of ANOVA was not met. Between-group significance was tested using least significant difference (LSD) *post-hoc* analysis. All the tests were conducted with significance level of $P = 0.05$.

Results

Seed characteristics

Initial moisture content and size of the seeds collected at the two sites varied significantly (Table 1). Seeds from

Vellore had significantly less moisture content and weighed less compared with the seeds from Coimbatore (Table 1). Seeds from both sites were dark brown in color.

Imbibition

The percentage of freshly collected seeds imbibing water was significantly lower compared to mechanically scarified seeds ($P < 0.05$; Fig. 2). Eight and 15% of the non-scarified seeds from Vellore and Coimbatore respectively imbibed water at the time of collection. However, one hundred percentage of seeds from both sites imbibed water following mechanical scarification. Seeds reached one hundred percent moisture level within 16 h of scarification (Fig. 2).

Germination

Seeds tested for germination at the time of collection germinated to lower levels at all the temperatures tested (Fig. 3). Number of seeds germinated without any treatment also varied between sites. Overall, seeds collected from Coimbatore germinated at higher rates than did those from Vellore (Fig. 3). Following mechanical scarification, > 90% of the seeds germinated at all temperatures tested. Light was not a requirement for germination, as both non-scarified and mechanically scarified seeds germinated in dark (Fig. 3).

Effect of hot-water on dormancy break

Seeds from Vellore and Coimbatore germinated to $89 \pm 1.5\%$ and $95 \pm 1.5\%$ respectively; when dipped in boiling water for 30 s and incubated at 20/25 °C. Germination of hot-water seeds was usually slow compared to mechanically scarified seeds (data not shown).

Effect of laboratory storage on dormancy break

Germination percentages of seeds stored in Petri dishes at ambient condition were low when tested after 1 year. There was a moderate increase in germination percentage of seeds collected from Coimbatore ($32 \pm 2.6\%$ compared to 19% at the time of collection). Seeds from Vellore did not show any sign of dormancy break during dry storage ($14 \pm 1.7\%$ compared to 12% germination at the time of collection).

Effect of temperature fluctuation on dormancy break

Germination of seeds from both sites significantly improved when incubated at 15/60 °C. One-month storage

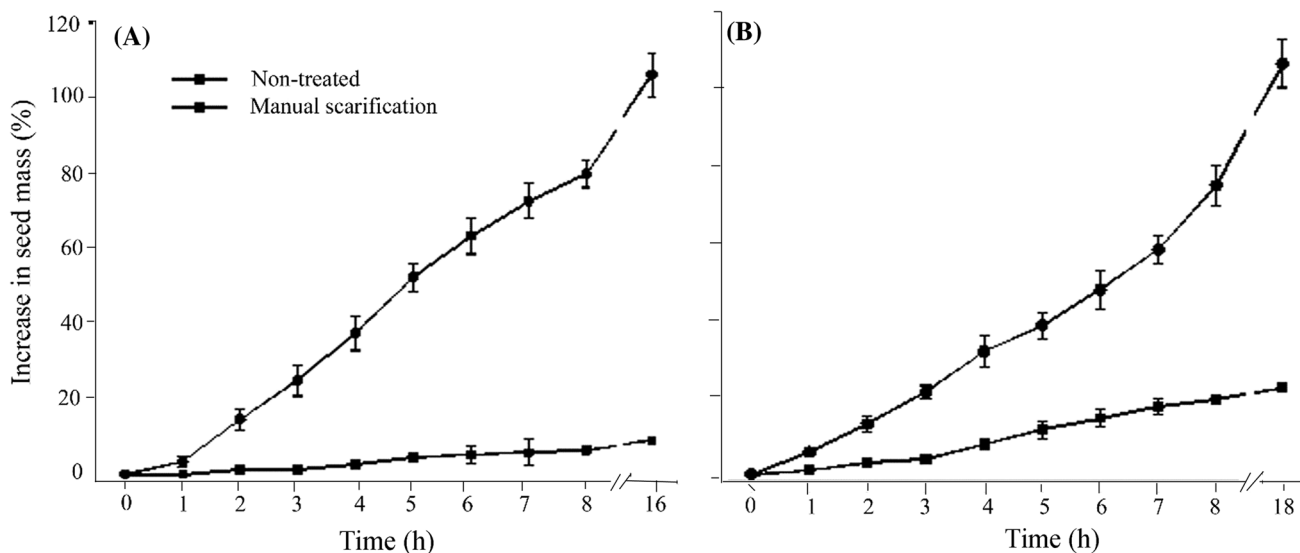
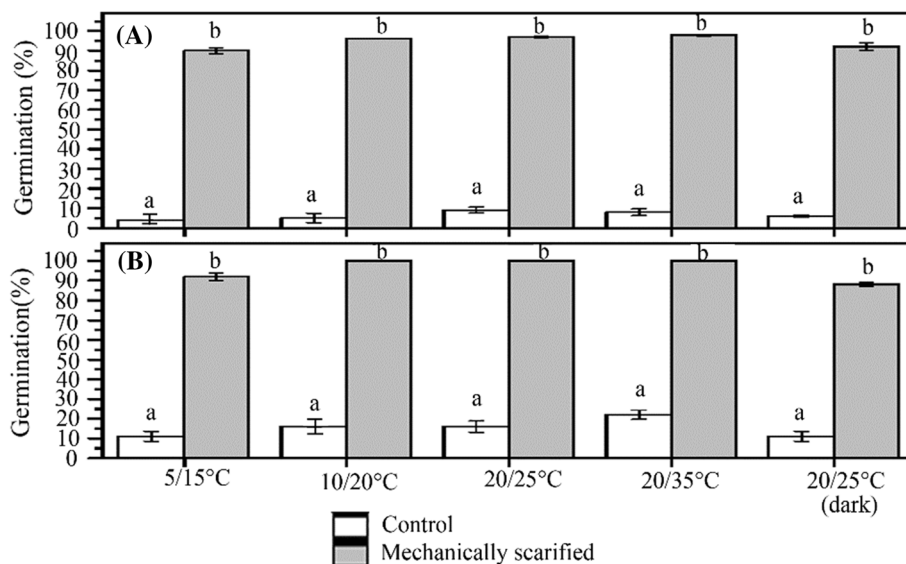


Fig. 2 Percentage of mass increase in non-treated and mechanically scarified *S. auriculata* seeds collected from a Vellore and b Coimbatore when incubated on moist filter paper in Petri dishes at laboratory temperature (20–25 °C)

Fig. 3 Germination percentage of control and mechanically scarified *S. auriculata* seeds collected from (a) Vellore (site A) and (b) Coimbatore (site B) at various temperatures. Different lower-case letters above columns indicate significant differences in final germination percentages between control and scarified seeds



was less effective for seeds from Vellore, whereas dormancy was broken in a significantly greater percentage of seeds collected from Coimbatore at the end of the first month ($P < 0.05$; Fig. 4). During the second month, more seeds from Vellore broke dormancy compared with those collected from Coimbatore. In general, percentages of seeds breaking dormancy increased with increase in duration (Fig. 3). After 3 months storage, $71 \pm 2.3\%$ of Coimbatore seeds germinated compared to $52 \pm 2.4\%$ of Vellore seeds ($P < 0.05$; Fig. 4). When non-germinated seeds at the end of each month were treated with hot-water, $> 85\%$ of these seeds germinated (data not shown).

Germination of buried seeds

Prior to burial, germination of seeds from both sites was low (Fig. 3). Burial of seeds in soil increased germination. Burial site affected germination percentage ($F_{2, 12} = 4.99$, $P = 0.02$) but seed maturation location did not ($F_{1, 12} = 3.19$, $P = 0.09$). Interaction between maturation location and burial site had no effect on overall germination percentage ($F_{2, 12} = 0.23$, $P = 0.79$). More seeds from Coimbatore, with a moderate climate, germinated at all burial sites compared to seeds collected from Vellore (Fig. 5). A small proportion of seeds (16% in Coimbatore and 24% in Vellore) germinated in the soil during burial. When the non-germinated seeds were incubated at

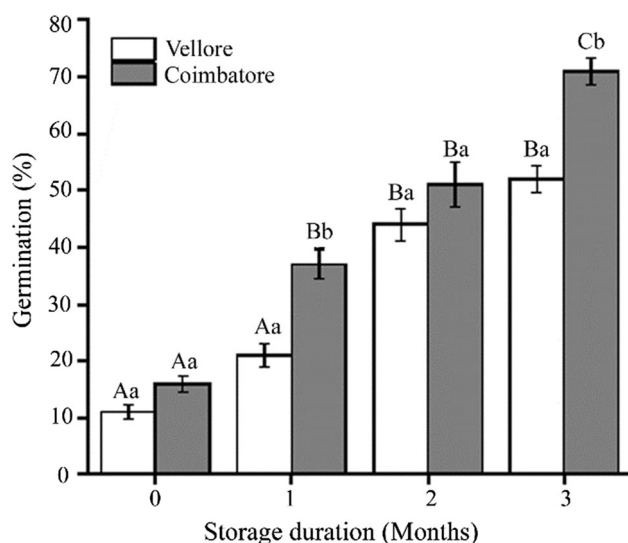


Fig. 4 Effect of diurnal temperature fluctuation (15/60 °C) on germination of *S. auriculata* seeds after various period. Different upper-case letters indicate significant difference ($P < 0.05$) observed over various duration of storage. Different lower-case letters indicate significant difference ($P < 0.05$) between seeds collected from different sites at each month

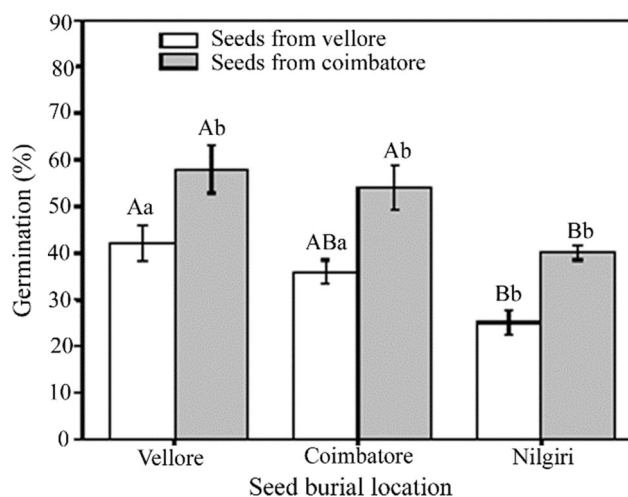


Fig. 5 Germination percentage of *S. auriculata* seeds collected from Vellore and Coimbatore and buried in three different locations for 1 year. Different upper-case letters indicate significant difference ($P < 0.05$) observed between the seeds matured from one location and buried at three different locations. Different lower-case letters indicate significant difference ($P < 0.05$) between seed collection site and particular burial site

germinating conditions, a few more germinated in the laboratory. The remaining non-imbibed seeds were dipped in boiling water for 30 s before placing them again in germination conditions. This treatment resulted in 85% of them germinating normally indicating those were dormant, despite 1 year of burial (data not shown).

Discussion

Freshly collected seeds of *S. auriculata* from Vellore and Coimbatore contained a small proportion of seeds that imbibed water. Seeds immersed in hot-water for 30 s or mechanically scarified germinated to $> 95\%$ at 20/25 °C. Immediate germination of mechanically scarified and hot-water treated seeds suggests that the embryo of *S. auriculata* does not have any physiological dormancy. Thus, seeds of *S. auriculata* collected at both localities had only PY and no combinational dormancy, as reported previously for seeds maturing in Sri Lanka (Jayasuriya et al. 2013). The absence of combinational dormancy appears to be a common trait in other *Senna* species including *S. occidentalis* (Delachiave and De Pinho 2003), *S. multijuga* (Lacerda et al. 2004; Rodrigues-Junior et al. 2014), *S. bicapsularis* (Teketay 1996), *S. didymobotrya* (Teketay 1996), *S. multiglandulosa* (Teketay 1996), *S. occidentalis* (Teketay 1996), *S. septemtrionalis* (Teketay 1996), *S. obtusifolia* (Baskin et al. 1998), *S. macranthera* (de Paula et al. 2012) and *S. marilandica* (Baskin et al. 1998).

Variation in the number of PY seeds produced by plants maturing in different environmental conditions has been documented for a number of species (Hu et al. 2009; Lacerda et al. 2004; Masaka and Yamada 2009; Meisert 2002; Nichols et al. 2009). The maternal environmental conditions, including temperature, rainfall and relative humidity, during maturation drying have been identified as important factors leading to this variation (Baskin and Baskin 2014; Jaganathan 2016). Because seeds matured at the warmer and drier Vellore site had lower moisture content and fewer permeable seeds (Fig. 1; Fig. 2), we accept that the site-to-site variation in the proportion of *S. auriculata* seeds with PY was due to conditions that prevailed during maturation drying (Fig. 1). One plausible reason for this seems to be the ability of seeds to establish long-term seed banks in drier sites because of the hotter summers. Further, some studies have highlighted that the proportion of hard seeds increases with declining seed mass (Yaklich et al. 1986) and this was also seen in the present study on *S. auriculata* (Table 1).

Because seeds of *S. auriculata* collected from both sites were able to break dormancy when incubated at 15/60 °C (Fig. 3), we suggest that diurnal summer temperature fluctuations warming soil surfaces in canopy gaps or other open microsites in the tropics could be an appropriate cue for breaking dormancy (Jaganathan and Liu 2014). Our results show that the pattern of dormancy loss in seeds when exposed these conditions varied among seeds maturing at different locations (Fig. 4). In particular, seeds of *S. auriculata* collected from Coimbatore showed a significantly higher germination percentage at the end of

1 month, whereas 1-month at 15/60 °C had little effect on seeds matured at Vellore (Fig. 3). Despite significant improvement in germination percentage of seeds from Vellore after two and 3 months, seeds from Coimbatore germinated to significantly higher percentages. This implies that seed maturation site could have an important role in determining PY loss, as described in previous studies (Mott et al. 1981; Norman et al. 2006; Taylor 1996; van Klinken and Goulier 2013).

In addition to the seed maturation environment, our burial experiments revealed that the burial site could also have a remarkable effect on PY loss in *S. auriculata* (Fig. 4). The number of seeds becoming permeable after 1 year of burial varied significantly between sites (Fig. 4). Seeds matured at Vellore and Coimbatore germinated to significantly higher percentages when buried at Vellore as compared to Coimbatore, which has a slightly lower temperature (Fig. 1). However, the seeds from Vellore required a higher temperature to break dormancy. This explains the lower germination percentage when buried at Coimbatore. Further, it was clear that the germination percentage of seeds matured and buried at Coimbatore was significantly higher compared with seeds matured and buried at Vellore (Fig. 5). More seeds buried in the soil at the high-temperature site (both Vellore and Coimbatore) came out of dormancy, compared with fewer seeds germinating after 1 year at Nilgiri, a site of relatively low temperature (Fig. 5), supporting the hypothesis that moderate temperatures are less effective in making *Senna* seeds permeable (Baskin et al. 1998; de Paula et al. 2012). These observations reinforce the contention that number of seeds germinating every year in soil is controlled by the prevailing climatic conditions (Lodge et al. 1990; Quinlivan 1967; van Klinken and Goulier 2013).

In the natural environment, however, many seeds are buried under canopy shade or deep in the soil. These seeds buried deep in the soil or those present under canopy shade do not experience temperature fluctuations as extreme as experienced by seeds present near the soil surface or in open environments. These seeds possibly wait for soil disturbance or clearing of standing vegetation to break dormancy. Our laboratory storage experiments showed that *S. auriculata* seeds stored at constant temperature (~25 °C) for 1 year remained dormant. Most of the PY species studied hitherto from various families remained dormant for long periods (Jaganathan and Liu 2014; Meisert 2002; Quinlivan 1968). It appears that PY breaks only when suitable cues occur, which provides fitness benefits to synchronize the germination timing with that of the growing season (Baskin and Baskin, 2014; Van Assche et al. 2003). Seeds of *Senna marilandica* and *S. obtusifolia* from Wilson County, Tennessee did not break dormancy when exposed to seasonal temperatures [15/6

(1 month) → 20/10 (1 month) → 25/15 (1 month) → 30/15 (1 month) → 35/20 (1 month) → 40/25 °C) prevailing at that site (Baskin et al. 1998). Consequently, we believe more efforts are required to bury seeds at different depths to determine the pattern of dormancy loss in soil.

Seed burial sites chosen for this experiment had distinct characteristics with warm (Vellore), moderate/warm (Coimbatore) and cold (Nilgiri) conditions (Fig. 1; Indian Meteorological Department weather data). Rainfall provides a moist environment for seeds in soil seed banks. When combined with higher temperature or temperature fluctuations, many PY species can break dormancy (Hu et al. 2009; Van Klinken et al. 2006). From our data, it was not possible to clearly show which of these conditions made *S. auriculata* seeds permeable to water, thus the exact dormancy loss mechanism remains to be tested in detail. In particular, the effects of constant temperature and fluctuating temperature in moist and dry conditions must be investigated.

Moreira and Pausas (2012) concluded that summer conditions in a Mediterranean climate would have no effect on breaking PY. They argued that temperature fluctuations between 18 and 43 °C for 1 month did not break dormancy in *Fumana thymifolia*, *Cistus salvifolius*, *C. albidus*, *C. parviflorus*, *C. creticus*, but some seeds of *U. parviflorus* broke dormancy. However, it is clear that summer season in the tropics is longer and probably warmer than were the temperatures reported by those authors. The results of the present research demonstrate that buried *S. auriculata* seeds break dormancy between one and 3 months (Fig. 4). In support of this finding, evidence from burial and laboratory experiments show that PY seeds break dormancy after 1 month at tropical or Mediterranean summer temperatures (Hagon 1971; Jaganathan et al. 2016a; Lodge et al. 1990; Moreno-Casasola et al. 1994; Quinlivan 1968; Quinlivan and Millington 1962). Given the limitation of 1-month duration of burial in some previous studies (Jaganathan 2015), we believe that the lower germination percentage reported in those studies is an artefact of experimental design. Thus, we emphasize that any future studies must consider using longer burial periods and ecologically meaningful summer temperatures.

As noted in other PY species, e.g. *Dodonea viscosa* (Baskin et al. 2004), light was not a prerequisite for germination of *S. auriculata*. Because PY break is an irreversible event and germination in dormancy-broken seeds occurs at a wide range of temperatures with or without light, the seed coat becoming permeable is a haphazard event in nature (Baskin and Baskin 2014). In the case of falsified dormancy loss, the resulting seedlings may die. However, a small volume of work demonstrates that PY break occurs in two-steps: (1) a pre-conditioning step where seeds are conditioned, which can be reversed if the

conditions for dormancy break are not met; and (2) an actual dormancy-break step, where the seeds become permeable to water, i.e., a 'water-gap' opens (Gama-Arachchige et al. 2012; Jayasuriya et al. 2008). These mechanisms possibly hold dormancy in check until a specific set of cues occurs in sequence. Although we did not specifically investigate the step-wise dormancy breaking mechanism in *S. auriculata*, this should become a subject of future study.

Conclusions

Our results show that both the maternal and burial environment can affect seed persistence and the dormancy-breaking ability of PY species. More importantly, during persistence, there are, at the very least, two possible factors contributing to the variation in the PY alleviation mechanism. The first is temperature experienced by seeds in soil. There appear to be specific temperature thresholds required to break dormancy in seeds maturing at different locations. Thus, the initial state of the seeds and the soil temperature experienced in a particular environment might explain the difference in the proportion of seeds becoming non-dormant in different environments. The second factor is the amount of rainfall received by seeds during burial. Rainfall increases soil moisture and provides a wet medium for the seeds requiring wet conditions. However, the interaction between these factors requires further detailed studies.

Acknowledgements We thank Ms Xiao Qun for her help in the preparation of manuscript. Financial support by Chinese Government Grant Numbers 2016M601620 and NSFC (Grant Number 31750110474) for part of this study are gratefully acknowledged.

References

- Bargali K, Bargali S (2016) Germination capacity of seeds of leguminous plants under water deficit conditions: implication for restoration of degraded lands in Kumaun Himalaya. *Trop Ecol* 57(3):444–445
- Baskin JM, Baskin CC (2004) A classification system for seed dormancy. *Seed Sci Res* 14(1):1–16
- Baskin CC, Baskin JM (2014) *Seeds: ecology, biogeography, and evolution of dormancy and germination*, 2nd edn. Elsevier, San Diego
- Baskin JM, Nan X, Baskin CC (1998) A comparative study of seed dormancy and germination in an annual and a perennial species of *Senna* (Fabaceae). *Seed Sci Res* 8(4):501–512
- Baskin JM, Baskin CC, Li X (2000) Taxonomy, anatomy and evolution of physical dormancy in seeds. *Plant Species Biol* 15(2):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(1):81–90
- Caner L, Bourgeon G, Toutain F, Herbillion A (2000) Characteristics of non-allophanic Andisols derived from low-activity clay regoliths in the Nilgiri Hills (Southern India). *Eur J Soil Sci* 51(4):553–563
- de Paula AS, Delgado CML, Paulilo MTS, Santos M (2012) Breaking physical dormancy of *Cassia leptophylla* and *Senna macranthera* (Fabaceae: Caesalpinioideae) seeds: water absorption and alternating temperatures. *Seed Sci Res* 22(4):259–267
- Delachiave M, De Pinho S (2003) Scarification, temperature and light in germination of *Senna occidentalis* seed (Caesalpinaceae). *Seed Sci Technol* 31(2):225–230
- Gama-Arachchige N, Baskin J, Geneve R, Baskin C (2012) The autumn effect: timing of physical dormancy break in seeds of two winter annual species of *Geraniaceae* by a stepwise process. *Ann Bot* 110(3):637–651
- Hagon M (1971) The action of temperature fluctuations on hard seeds of subterranean clover. *Aust J Exp Agric* 11(51):440–443
- 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(5):1051–1056
- Jaganathan GK (2015) Are wildfires an adapted ecological cue breaking physical dormancy in the Mediterranean basin? *Seed Sci Res* 25(2):120–126
- Jaganathan GK (2016) Influence of maternal environment in developing different levels of physical dormancy and its ecological significance. *Plant Ecol* 217(1):71–79
- Jaganathan GK, Liu B (2014) Seasonal influence on dormancy alleviation in *Dodonaea viscosa* (Sapindaceae) seeds. *Seed Sci Res* 24(3):229–237
- Jaganathan GK, Liu B (2015) 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(1):23–29
- Jaganathan GK, Wu GR, Han YY, Liu BL (2016a) Role of the lens in controlling physical dormancy break and germination of *Delonix regia* (Fabaceae: Caesalpinioideae). *Plant Biol* 19(1):53–60
- Jaganathan GK, Yule K, Liu B (2016b) On the evolutionary and ecological value of breaking physical dormancy by endozoochory. *Perspect Plant Ecol Evol* 22:11–22
- Jaganathan GK, Song D, Liu B (2017) Diversity and distribution of physical dormant species in relation to ecosystem and life-forms. *Plant Sci Today* 4(2):55–63
- Jayasuriya KG, Baskin JM, Baskin CC (2008) Cycling of sensitivity to physical dormancy-break in seeds of *Ipomoea lacunosa* (Convolvulaceae) and ecological significance. *Ann Bot* 101(3):341–352
- Jayasuriya KG, 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(4):257–269
- Jayaweera D (1981) Medicinal plants used in Ceylon. The National Science Council of Sri Lanka, Colombo 2:214–215
- Lacerda DR, Lemos Filho JP, Goulart MF, Ribeiro RA, Lovato MB (2004) Seed-dormancy variation in natural populations of two tropical leguminous tree species: *Senna multijuga* (Caesalpinioideae) and *Plathymenia reticulata* (Mimosoideae). *Seed Sci Res* 14(1):127–135
- Lodge G, Murison R, 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(5):941–955
- Masaka K, Yamada K (2009) Variation in germination character of *Robinia pseudoacacia* L. (Leguminosae) seeds at individual tree level. *J For Res* 14(3):167–177
- Meisert A (2002) Physical dormancy in Geraniaceae seeds. *Seed Sci Res* 12(2):121–128

- Moreira B, Pausas JG (2012) Tanned or burned: the role of fire in shaping physical seed dormancy. *PLoS ONE* 7(12):e51523
- Moreno-Casasola P, Grime JP, Martinez ML (1994) A comparative study of the effects of fluctuations in temperature and moisture supply on hard coat dormancy in seeds of coastal tropical legumes in Mexico. *J Trop Ecol* 10(01):67–86
- Mott J, McKeon G, Gardener C, Lt Mannelje (1981) Geographic variation in the reduction of hard seed content of *Stylosanthes* seeds in the tropics and subtropics of northern Australia. *Ausi J Agric Res* 32(6):861–869
- Nichols P, Cocks P, Francis C (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(1):31–48
- Norman H, Smith F, Nichols P, Si P, Galwey N (2006) Variation in seed softening patterns and impact of seed production environment on hardseededness in early-maturing genotypes of subterranean clover. *Aust J Agric Res* 57(1):65–74
- Quinlivan B (1967) Environmental variation in the long term pattern of germination from hard seeds of *Lupinus varius* animal production science. *Aust J Exp Agric* 7(26):263–265
- Quinlivan B (1968) Seed coat impermeability in the common annual legume pasture species of Western Australia animal production science. *Aust J Exp Agric* 8(35):695–701
- Quinlivan B, Millington A (1962) The effect of a Mediterranean summer environment on the permeability of hard seeds of subterranean clover. *Crop Pasture Sci* 13(3):377–387
- Rodrigues-Junior AG, Faria JM, Vaz TA, Nakamura AT, José AC (2014) Physical dormancy in *Senna multijuga* (Fabaceae: Caesalpinioideae) seeds: the role of seed structures in water uptake. *Seed Sci Res* 24(2):147–157
- Taylor G (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. *Crop Pasture Sci* 47(1):141–159
- Taylor G, Ewing M (1992) Long-term patterns of seed softening in some annual pasture legumes in a low rainfall environment. *Aust J Exp Agric* 32(3):331–337
- Teketay D (1996) The effect of different pre-sowing seed treatments, temperature and light on the germination of five *Senna* species from Ethiopia. *New For* 11(2):155–171
- Turner S, Cook A, Baskin J, Baskin C, Tuckett R, Steadman K, Dixon K (2009) Identification and characterization of the water gap in the physically dormant seeds of *Dodonaea petiolaris*: a first report for Sapindaceae. *Ann Bot* 104(5):833–844
- Van Assche JA, Debucquoy KL, Rommens WA (2003) Seasonal cycles in the germination capacity of buried seeds of some Leguminosae (Fabaceae). *New Phytol* 158(2):315–323
- Van Klinken RD, Goulier J-B (2013) Habitat-specific seed dormancy-release mechanisms in four legume species. *Seed Sci Res* 23(3):181–188
- 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(4):875–883
- Van Klinken RD, Lukitsch B, Cook C (2008) Interaction between seed dormancy-release mechanism, environment and seed bank strategy for a widely distributed perennial legume, *Parkinsonia aculeata* (Caesalpinaceae). *Ann Bot* 102(2):255–264
- Vázquez-Yanes C, Orozco-Segovia A (1993) Patterns of seed longevity and germination in the tropical rainforest. *Annu Rev Ecol Evol Syst* 24(24):69–87
- Vijayakumar A, Selvaraju P (2013) Standardization of seed dormancy breaking treatment in *Senna (Cassia auriculata)*. *J Plant Breed Crop Sci* 5(11):220–223
- Yaklich R, Vigil E, Wergin W (1986) Pore development and seed coat permeability in soybean. *Crop Sci* 26(3):616–624