Seed Science Research

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Seed dormancy diversity of the mangrove plant community in Sri Lanka to assist in direct seeding and seedling transplanting restoration

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Research Paper

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Abstract

Mangroves are one of the most important ecosystems in the world being found in the tropical–subtropical belt. Despite their significance, they have been highly disturbed due to many anthropogenic and natural causes. A significant effort has been made to restore mangroves around the world. However, a lack of information on the seed biology of mangrove species has impeded restoration. Thus, this study aimed to produce a seed dormancy profile for selected plant species of mangroves in Sri Lanka. This profile would allow restoration ecologists to better understand what kinds of dormancy are present, how to alleviate dormancy and how to best stimulate germination to generate seedlings for nursery stock or out-planting. Mature fruits/seeds were collected from coastal zone mangroves in Sri Lanka. Germination and imbibition of non-scarified and manually scarified seeds and embryo:seed length (E:S) ratio of fresh and radicle-emerged seeds were evaluated to assess the class of dormancy. Of the 30 species, seeds from 12 (40%) were non-dormant and 18 (60%) were dormant. Three dormancy classes [physiological (PD), physical (PY) and morphophysiological (MPD)] and presence of epicotyl dormancy were identified. Among species producing dormant seeds, most of them showed PD (44%). PY, MPD and presence of epicotyl dormancy were represented by 28, 17 and 11% of the species, respectively. These findings aid practitioners to craft strategies to effectively break dormancy and germinate seeds for conservation and restoration activities of mangroves.

Introduction

The extent of mangroves in Sri Lanka is about 15,981 ha, covering only about 0.24% of the land in the coastal districts (Arulnayagam et al., 2021). Mangrove distribution in Sri Lanka is usually limited to narrow belts along the coastline because of the low (75 cm) tidal amplitude (Ranawana, 2017). However, mangroves provide invaluable ecosystem services to the human community by economic and environmental means (Lee et al., 2014; Carugati et al., 2018; Getzner and Islam, 2020; Takahashi et al., 2022), especially for the people in coastal communities that heavily depend on the ecosystem services provided by mangroves directly or indirectly (Katupotha, 2016). Despite their significance, mangrove ecosystems are at the brink of deterioration in Sri Lanka similar to many other locations in the world (Wickramasinghe, 2017; Leal and Spalding, 2022). Furthermore, natural regeneration of mangroves is hampered when they experience unfavourable conditions for their seed dispersal, germination and seedling growth and establishment due to natural (climate change and natural disasters) and anthropogenic activities (urban development, encroachment). For instance, after the 2004 tsunami in the Indian Ocean, 1200 km of coastline in Sri Lanka was damaged, as a consequence the natural habitat of the mangroves was altered and did not recover well (Kodikara et al., 2017).

Thus, assisting in mangrove regeneration and rehabilitation is important to continuously receive their ecosystem services. As such, a large number of restoration attempts have been conducted in Sri Lanka to conserve mangrove ecosystems. Unfortunately, most of these attempts have failed (Kodikara et al., 2017). Furthermore, most of these restoration attempts have used only few mangrove species, especially targeting those with readily available propagules (Kodikara et al., 2017). However, restoring monoculture mangroves or mangroves with few species does not support restoration of the dynamic nature of mangroves to provide ecosystem services to the same extent as diverse mangroves.

Selection of plant species or species composition is very important in restoration when returning wetlands to their previous non-disturbed state and this can be done in two ways:

native species can be selected that historically existed on the site or native species can be selected that occur in nearby ecosystems with similar environmental conditions as the targeted mangrove that needs restoration (Allen et al., 2001; Kettenring and Tarsa, 2020). However, reintroduction of historical species at a site does not guarantee that they will succeed there again if the environmental degradation has exceeded the level of the species' tolerance. In general, a sound knowledge on the major ecological components of the restoration sites, scientific understanding on mangrove ecosystem and selection of suitable plant species composition are some of the important factors that need consideration in the restoration of mangroves.

Information on seed germination behaviour (dormancy, dormancy-breaking requirements and germination requirements) for a particular mangrove species is essential for their restoration in both direct seeding and seedling transplanting methods (Baskin and Baskin, 2004). Even though the direct seeding in the field is the most cost-effective method of restoration over transplanting juvenile plants to the site, seeds with dormancy might cause a negative impact on restoration. For instance, direct seeding mixtures of species might contain species with dormant seeds and others with non-dormant seeds, in which case non-dormant seeds will germinate quickly and dominate the restoration site (Baskin and Baskin, 2020). This might be the same scenario in mangrove nurseries developed for restoration purposes. Therefore, information on seed dormancy and germination of species in mangrove ecosystems is crucial for restoration practitioners when conducting restoration projects (Duke et al., 2007; Polidoro et al., 2010; Van Lavieren et al., 2012; Baskin and Baskin, 2014).

In addition to restoration, seed dormancy studies are important in comparing the relative importance of seed dormancy classes in species in a particular ecosystem (Baskin and Baskin, 2010) and ultimately elucidating the dynamics of ecosystems (Skoglund, 1992). However, many studies on dormancy and germination have been conducted at the species level and only a few studies have been done to evaluate seed dormancy and germination at the community level (Sautu et al., 2007; Athugala et al., 2021; Samarasinghe et al., 2022). Although several other scientists have studied seed dormancy at the plant community level (Ng, 1975, 1980; Ng and Asri, 1979; Garwood, 1983; Murali, 1997; Thapliyal and Phartyal, 2005), these studies have not been carried out in a way to allow standard comparisons using the current dormancy classification system (*sensu* Baskin and Baskin, 2004). Furthermore, no community-level study has been focused on seed dormancy and germination in species in mangrove ecosystems.

Seed germination and dormancy studies have mainly been conducted on viviparous (i.e. germination and subsequent development of the propagule take place while the fruit is still attached to the mother plant) mangrove species, while only a few studies have been reported on non-viviparous (i.e. germination and subsequent development of the seeds/diaspore take place after seed dispersal) species (Tomlinson, 1994; Baskin and Baskin, 2014; Wijayasinghe et al., 2019). Thus, the main objective of this study was to evaluate the seed dormancy of selected plant species in mangrove plant communities in Sri Lanka. The information gathered was used to construct a dormancy profile for the mangrove plant community and to evaluate the relative importance of the different dormancy classes found in the community in relation to other communities. Baskin and Baskin (2004, 2014) developed a dichotomous key to identify the class of seed dormancy for a particular seed lot for a plant species. For that key, we need information on embryo morphology, whether or not embryo grows prior to germination, water permeability of the dispersal unit, ability of seeds to germinate within about 4 weeks and time duration of radicle and shoot emergence. Using aforesaid information, seeds can be categorized into five dormancy classes: physical dormancy (PY), physiological dormancy (PD), morphological dormancy (MD), morphophysiological dormancy (MPD) and combinational dormancy (PY + PD).

Materials and methods

Study species

Thirty true-mangroves and mangrove associates, excluding true-viviparous species, were included in this study (Table 1). Scientific names of the species were checked with 'Plants of the world online' website (POWO, 2023). We purposely selected a broad diversity of species to construct a representative profile for seed dormancy of plants that closely match most mangrove communities in Sri Lanka.

Seed collection

Mature ripened dispersal-ready fruits of the study species were collected in 2012, 2013 and 2014 from at least five individuals (except for *Xylocarpus rumphii*) of each species at mangrove sites in Sri Lanka. Fruits were stored in labelled polythene bags in the field and brought to the Department of Botany, University of Peradeniya, Sri Lanka. Diaspores (i.e. seeds or fruits depending on the species, hereafter referred to as seeds) and seeds were extracted from fruits, and air-dried for about 2–3 h. Afterwards, they were stored in plastic bottles at ambient room temperature (28°C) until used in experiments which were initiated at least within a week after collection.

Standard germination test

A standard germination test was conducted on intact seeds to identify the presence of non-dormancy (ND) or dormancy (D). Three replicates of 15–25 intact-fresh seeds of each species were placed on tissue papers moistened with distilled water in 9-cm diameter Petri dishes and incubated in light/dark (14 h/10 h) at 25°C. Seeds were monitored for germination (radicle emergence to >1 mm) and cotyledon emergence at 3-d intervals for 30 d. Seeds that germinated to high percentages were considered as non-dormant, while those that did so to low or moderate percentages (or did not germinate at all) were considered as dormant. Non-germinated seeds were dissected to check viability of the embryo at the end of the experiment and presence of white firm embryo was considered to be potentially viable. Seeds classified as dormant were manually scarified (individually with a razor blade) and the same standard germination test was done on them, as described above.

Imbibition test

An imbibition test was conducted to identify the species with physical dormancy (PY). If seeds have PY, intact seeds will not imbibe water, while scarified seeds will imbibe water and germinate within 30 d. To test for PY in seeds, two samples of 15 non-scarified (intact-fresh) seeds and 15 manually scarified

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Table 1. Germination behaviour of non-scarified (NS) and manually scarified (MS) seeds on distilled water or on GA_3, imbibition of NS seeds on distilled water, embryo types and the suggested seed dormancy class for mangrove species in Sri Lanka

Species name (Family)	Germination %		Distilled water imbibition (NS seeds)	GA_3-treated NS seeds germination % (mean ± SE)	Embryo type[h]	Suggested dormancy type[f]
	Mean ± SE (NS)	Mean ± SE (MS)				
Acanthus ilicifolius L. (Acanthaceae)	86 ± 5	[d]	Imbibed	[e]	Investing	ND
Aegiceras corniculatum (L.) Blanco (Primulaceae)	96 ± 4	[d]	Imbibed	[e]	Cryptovivipary	Epicotyl dormancy
Allophylus cobbe (L.) Forsyth f. (Sapindaceae)	92 ± 9	[d]	Imbibed	[e]	Bent^{FD}	ND
Annona glabra L. (Annonaceae)	0	0	Imbibed	13 ± 8	Linear^{UD}	MPD
Ardisia elliptica Thunb. (Primulaceae)	89 ± 12	[d]	Imbibed	[e]	Linear^{FD}	Epicotyl dormancy
Canavalia cathartica Thouars (Fabaceae)	0	81 ± 9	Non-imbibed	[e]	Bent^{FD}	PY
Cynometra iripa Kostel. (Fabaceae)	98 ± 4	[d]	[b]	[e]	Investing^{FD}	ND
Cayratia trifolia (L.) Domin (Vitaceae)	0	0	[c]	[g]	Spatulate^{UD}	MPD[a]
Clerodendrum inerme (L.) Gaertn. (Lamiaceae)	9 ± 12	18 ± 9	Imbibed	80 ± 20	Investing^{FD}	PD
Dalbergia candenatensis (Dennst.) Prain (Fabaceae)	89 ± 22	[d]	Imbibed	[e]	Bent^{FD}	ND
Dendrolobium umbellatum (L.) Benth. (Fabaceae)	42 ± 17	91 ± 12	No	[e]	Bent^{FD}	PY
Dolichandrone spathacea (L.f.) K.Schum. (Bignoniaceae)	56 ± 16	51 ± 21	Imbibed	62 ± 12	Spatulate^{FD}	ND
Excoecaria agallocha L. (Euphorbiaceae)	87 ± 13	[d]	Imbibed	[e]	Spatulate^{FD}	ND
Heritiera littoralis Aiton (Malvaceae)	0	67 ± 21	Imbibed	[e]	Investing^{FD}	PD
Hibiscus tiliaceus L. (Malvaceae)	2 ± 4	73 ± 0	No	[e]	Folded^{FD}	PY
Ipomoea violacea L. (Convolvulaceae)	23 ± 7	87 ± 17	No	[e]	Folded^{FD}	PY
Lumnitzera racemosa Willd. (Combretaceae)	0	0	Imbibed	[g]	Linear^{FD}	PD[a]
Parsonsia alboflavescens (Dennst.) Mabb. (Apocynaceae)	58 ± 16	[d]	Imbibed	[e]	Spatulate^{FD}	ND
Pemphis acidula J.R.Forst. & G.Forst. (Lythraceae)	60 ± 21	[d]	Imbibed	[e]	Linear^{FD}	ND
Phoenix pusilla Gaertn. (Arecaceae)	0	0	[c]	[e]	Linear^{UD}	MPD[a]
Phyla nodiflora (L.) Greene (Verbenaceae)	0	[d]	[c]	60 ± 13	Spatulate^{FD}	PD
Pongamia pinnata (L.) Pierre (Fabaceae)	97 ± 7	[d]	Imbibed	[e]	Bent^{FD}	ND
Premna serratifolia L. (Lamiaceae)	20 ± 15	18 ± 16	Imbibed	89 ± 16	Spatualate^{FD}	PD
Suaeda vermiculata Forssk. ex J.F.Gmel. (Amaranthaceae)	36 ± 12	24 ± 16	[c]	64 ± 31	Peripheral^{FD}	PD

(*Continued*)

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Table 1. (*Continued.*)

Species name (Family)	Germination %		Distilled water imbibition (NS seeds)	GA_3-treated NS seeds germination % (mean ± SE)	Embryo type[h]	Suggested dormancy type[f]
	Mean ± SE (NS)	Mean ± SE (MS)				
Scaevola taccada (Gaertn.) Roxb. (Goodeniaceae)	0	25 ± 4	Imbibed	[g]	Spatulate^{FD}	PD[a]
Sesuvium portulacastrum (L.) L. (Aizoaceae)	0	24 ± 19	[c]	[g]	Peripheral^{FD}	PD[a]
Sonneratia caseolaris (L.) Engl. (Lythraceae)	96 ± 4	[d]	Imbibed	[e]	Linear^{FD}	ND
Thespesia populnea (L.) Sol. ex Corrêa (Malvaceae)	0.1 ± 0.04	78 ± 16	No	[e]	Folded^{FD}	PY
Xylocarpus granatum J.Koenig (Meliaceae)	83 ± 9	[d]	[b]	[e]	Investing^{FD}	ND
Xylocarpus rumphii (Kostel.) Mabb. (Meliaceae)	81 ± 14	[d]	[b]	[e]	Investing^{FD}	ND

[a]Speculated from available previous literature [(*Scaevola taccada* – Liang et al., 2020); (*Phoenix* sp – Baskin and Baskin, 2014); (*Lumnitzera racemosa* – Perera et al., 2019); (*Cayratia trifolia* – Baskin and Baskin, 2014); (*Sesuvium portulacastrum* – Baskin and Baskin, 2014; Martinez and Casasolai, 1992)].
[b]Imbibition test was not conducted since a high percentage of NS seeds germinated on distilled water.
[c]Imbibition test was not conducted because of a limited number of seeds or due to the very small size of the seed.
[d]Germination test was not conducted since a high percentage of NS seeds germinated on distilled water.
[e]Germination test was not conducted since a high percentage of NS/MS seeds germinated on distilled water.
[f]ND, non-dormant; MPD, morphophysiological dormancy; PD, physiological dormancy; PY, physical dormancy.
[g]GA_3 test was not conducted due to the limited number of seeds.
[h]Superscript ^{FD} – Fully developed embryo; Superscript ^{UD} – Underdeveloped embryo.

(individually with a razor blade) seeds were weighed individually with a digital analytical balance to nearest 0.0001 g, and placed individually on tissue papers moistened with distilled water in Petri dishes at 25°C. Seeds were retrieved, reweighed and returned to the Petri dishes after 2, 5, 7, and 24 h and then at 1-d intervals until all the scarified seeds were fully imbibed. Imbibition tests were not conducted for five species because of a limited number of seeds or due to the very small size of the seed (Table 1).

Gibberellic acid treatment

For seed lots that showed dormancy under the standard germination test, gibberellic acid (GA_3) was applied to them to test whether GA_3 could overcome dormancy. A sample of three replicates with 15 or 25 seeds each were placed on tissue papers moistened with 100 ppm GA_3 solution in 9-cm diameter Petri dishes and incubated in light/dark (14 h/10 h) at 25°C. Seeds were observed for germination (radicle emergence to >1 mm) at 3-d intervals for 30 d.

Embryo type and embryo (E)/seed (S) length ratio

Fresh seeds of each species were cut longitudinally in half and the embryo was observed. The type of embryo in each species was identified according to a modified version of Martin's (1946) classification system (Baskin and Baskin, 2007). Ten fresh seeds were selected randomly from each species and dissected. Length of the embryos and length of the seeds were measured to nearest 0.01 mm using a Vernier caliper. Embryo (E):seed (S) length ratio was determined for each species.

Since *Annona glabra* seeds had a low E:S ratio, embryo development was monitored during germination. Two samples of 20 non-scarified seeds each of *A. glabra* were placed on tissue paper moistened with distilled water or 100 ppm GA_3 solution in Petri dishes separately at ambient laboratory conditions. Five seeds were retrieved after 7, 30, 52 and 60 d from each treatment (distilled water, GA_3) and were dissected; E:S ratio was determined at each time.

Data analysis

All of the experiments were conducted in a completely randomized design. The equation to calculate the germination percentage (GP) was: GP = (number of seeds germinated/number of total viable seeds) × 100. Germination data were analysed using a binary logistic regression. Epicotyl dormancy experiments (time difference between root and shoot emergence) were analysed using non-parametric Moods' median test. Minitab 14.1 (Minitab Inc., State College, PA, USA) statistical software was used to analyse the data. Regression lines were fitted for the data taken from the water imbibition test for each tested species.

Results

Germination of seeds on distilled water

Non-scarified seeds of 11 species germinated >80% within 30 d (Table 1) and the remaining (non-germinated) seeds of these species were viable. Non-scarified seeds of *Dolichandron spathaceae*, *Parsonsonia alboflavescens* and *Pemphis acidula* germinated to 55–60%. Less than 25% of non-scarified *Canavalia cathertica*, *Heritiera littoralis*, *Hibiscus tiliaceus*, *Ipomoea violacea* and *Thespesia populnea* seeds germinated, while the manually scarified seeds of these species germinated >65%. Moreover, germination of *Dendrolobium umbellatum* seeds was 91% after manual scarification (compared to 42% in non-scarified seeds) (Table 1). Non-scarified as well as manually scarified seeds of *A. glabra*, *Cayratia trifolia*, *Luminitzera racemosa*, *Suaeda*

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vermiculata, *Scaveola taccada*, *Sesuvium portulacastrum* and *Premna serratifolia* germinated to <30%. Non-scarified seeds of *Phoenix pusilla* and *Phyla nodiflora* germinated to <5%, while the germination test of manually scarified seeds of these species was not conducted due to the limited number of seeds or due to their small size.

Shoot emergence

Non-scarified seeds of *Aegiceras corniculatum* placed on tissue papers moistened with distilled water took 115.7 ± 17.3 d between radicle and shoot emergence, and those of *Ardisia elliptica* took 45.8 ± 10.0 d. Radicle-emerged seeds of all the other tested species had an emerged epicotyl within <7 d.

Imbibition test

A mass increase of manually scarified seeds of *Canavalia cathertica*, *Hibiscus tiliaceus*, *Thespesia populnea*, *Dendrolobium umbellatum* and *Ipomoea violacea*, was significantly higher than that of non-scarified seeds ($P < 0.05$) during imbibition. Furthermore, manually scarified seeds of these five species had a mass increase of >100%, while non-scarified seeds of these species showed a wide range of mass increase. For instance, a mass increase of non-scarified seeds of *C. cathertica*, *H. tiliaceus* and *T. populnea* was <10% (Fig. 1A), while those of *D. umbellatum* and *I. violacea* was ~50% (Fig. 1B). Eighteen species showed a similar water imbibition pattern in both manually and non-scarified seeds (Fig. 1C, D).

Gibberellic acid treatment

Non-scarified seeds of *Premna serratifolia* and *Clerodendrum inerme* germinated to >80% on tissue papers moistened with 100 ppm GA_3 (Table 1). Seed germination of non-scarified *Phyla nodiflora* and *Saueda vermiculata* seeds on GA_3 was >60%, whereas that of *A. glabra* seeds was 13%. Germination of seeds of all these species was significantly higher on GA_3 than on distilled water (<0.05, data not shown).

Embryo type and embryo/seed length ratio (E/S)

Eight types of differentiated embryos were identified among the seeds of the study species (Table 1). None of the study species

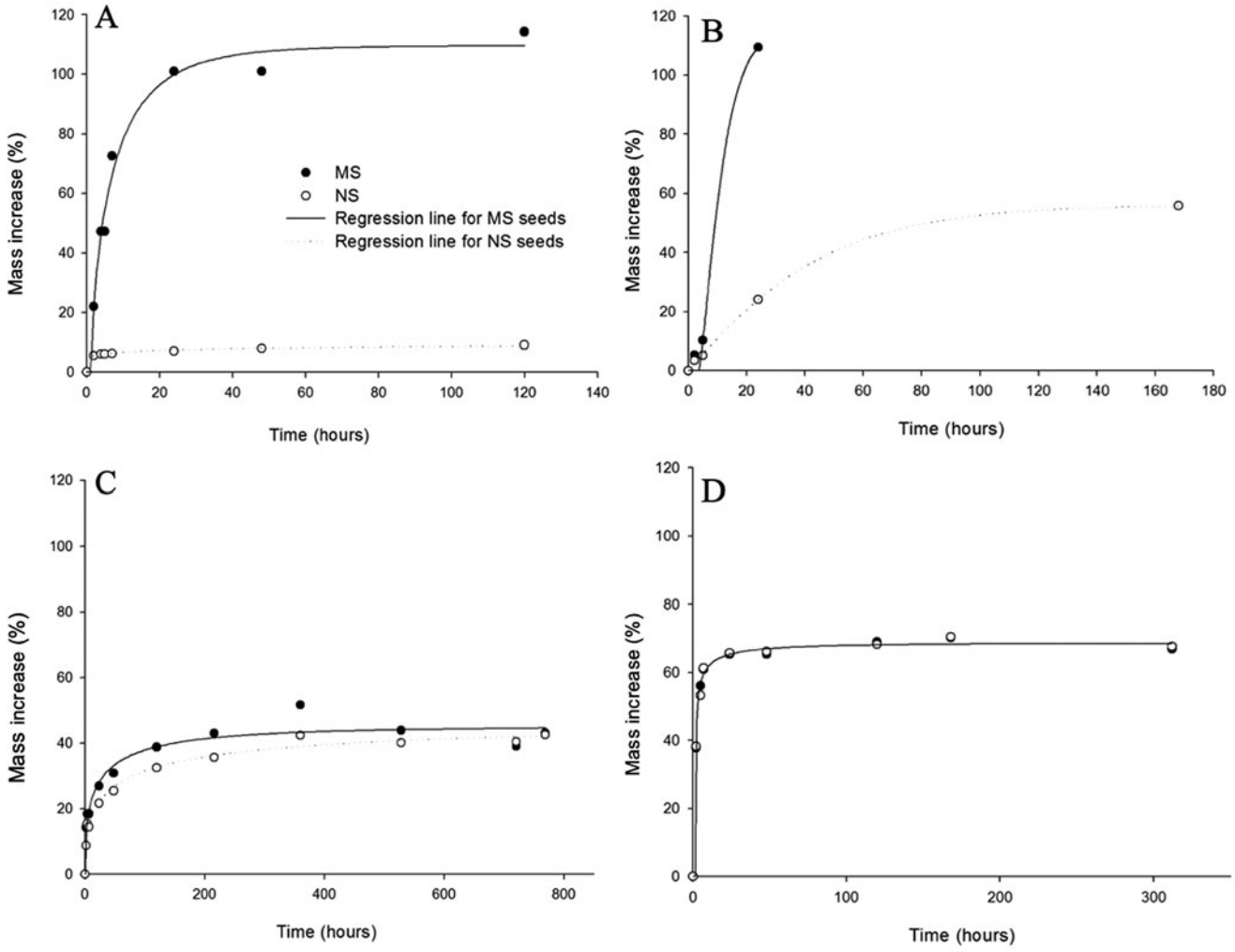

Figure 1. Mass increase of manually scarified (MS) and non-scarified (NS) seeds of representative mangrove species having (A, B) seeds that are physically dormant and (C, D) seeds that are not. Seeds of (A) *Thespesia populnea*, (B) *Ipomoea violacea*, (C) *Premna serratifolia* and (D) *Sonneratia caseolaris* were tested at ambient room temperature in light/dark (14/10 h) condition on filter paper moistened with distilled water.

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showed undifferentiated embryos. Seeds of *A. glabra* had a small underdeveloped, but differentiated embryo at the time of seed dispersal. Mean (±SE) initial E:S length ratio of non-scarified seeds was 0.22 ± 0.01. It increased to 0.70 ± 0.01 in seeds incubated for 2 months on GA_3 and to 0.33 ± 0.01 on distilled water. Growth on GA_3 was significantly greater than that in seeds on distilled water (Figs. 2, 3, $F = 489.29$, $P < 0.001$).

Discussion

Class of seed dormancy

As revealed in the imbibition test, manually scarified seeds of five species (*Canavalia cathertica, Hibiscus tiliaceus*, *Thespesia populnea*, *Dendrolobium umbellatum* and *Ipomoea violacea*) imbibed a significantly high amount of water compared to non-scarified seeds, revealing that intact seeds of these species have impermeable seed coats, i.e. their seeds have physical dormancy (PY). This conclusion was confirmed by the germination test, where manually scarified seeds of these species germinated to a significantly higher percentage than non-scarified seeds. Furthermore, manually scarified seeds of these species germinated to a high percentage (>73) indicating that their embryos did not have a physiological component to dormancy, i.e. seeds of these species only have PY. Our observations confirmed the previous reports in the scientific literature that these species produce seeds with PY [*T. populnea*, Gupta et al. (2004) and Gagare and Mate (2009); *H. tiliaceus*, Francis and Rodrguez (1993); *I. violacea,* Jayasuriya et al. (2009) and *D. umbellatum*, Jayasuriya et al. (2013)].

On the other hand, only <5% of non-scarified seeds of *C. cathertica, H. tiliaceus* and *T. populinea* germinated at 25°C, while about 25 and 45% of *I. violacea* and *D. umbellatum*, respectively, did so. This finding revealed that these two groups of species have different germination strategies even though both groups have PY. Most of the seeds produced by *C. cathertica, H. tiliaceus* and *T. populinea* had PY, while a considerably large portion of seeds from *I. violacea* and *D. umbellatum* were non-dormant within the physically dormant seed lots. Producing dormant and non-dormant seeds in the same seed lot has been proposed to be an adaptation to survival in unpredictable environments (Venable, 1985; Mandák, 1997). However, Paulsen et al. (2013, 2014) suggested that producing non-dormant seeds in a seed lot with PY is an adaptation for dispersal through rodents who depend on olfactory cues to detect seeds. The production of non-dormant seeds among physically dormant seed lots of *I. violacea* and *D. umbellatum* may be an adaptation for the species survival by both germinating a fraction of seeds soon after dispersal and depositing the remainder seeds in the soil seed bank for future germination. Although manual scarification promoted the germination of these species producing seeds with PY, natural cues for breaking dormancy are still to be identified.

According to the results of the germination tests, *Acanthus ilicifolius*, *Aegiceras corniculatum*, *Allophylus cobbe*, *Ardisia elliptica*, *Cynometra iripa*, *Dalbergia candenatensis*, *Excoecaria agallocha*, *Pongamia pinnata*, *Sonneratia caseolaris*, *Xylocarpus granatum* and *Xylocarpus rumphii* seeds showed non-dormancy (ND; Table 1). Although another three species (*Parsonsia alboflavescens*, *Pemphis acidula* and *Dolichandrone spathacea*) can be categorized as non-dormant since their germination was between 56 and 60%, the rest of the seeds in their seed lot had PD (40–44%).

Although both non-scarified and manually scarified seeds of *Premna serratifolia*, *Clerodendrum inerme*, *Phyla nodiflora* and *Suaeda vermiculata* germinated to <40% within 30 d on distilled water, seeds of these species germinated to higher percentages when incubated on GA_3 (Table 1), revealing that these seeds have physiological dormancy (PD). Moreover, embryos in seeds of these species were fully developed, and thus, there is no morphological component to dormancy. Apparently, there have been less or no previous studies on germination/dormancy of *P. serratifolia*, *P. nodiflora* or *S. vermiculata* seeds. However, studies done on seeds of the other species in the same genera revealed that they have PD or ND (Baskin and Baskin, 2014). None of the non-treated seeds of *Heritiera littoralis* germinated on distilled water. However, excised embryos of *H. littoralis* germinated to >67% under similar temperature and light conditions. Moreover, it was observed that *H. littoralis* seeds imbibed (i.e. they did not have PY) when kept in distilled water (data not shown). Hence, the fruit coat of the diaspore apparently acted as a barrier for radicle emergence, and thus, seed dormancy of *H. littoralis* can be categorized as PD. Ye et al. (2004) reported that >90% of the *H. littoralis* (from southern China) seeds germinated without any treatment within 1–2 months which contradicted our observation. This difference may be due to geographic variation in dormancy.

None of the non-scarified or manually scarified *A. glabra* seeds germinated within 30 d on distilled water or on GA_3 and it took

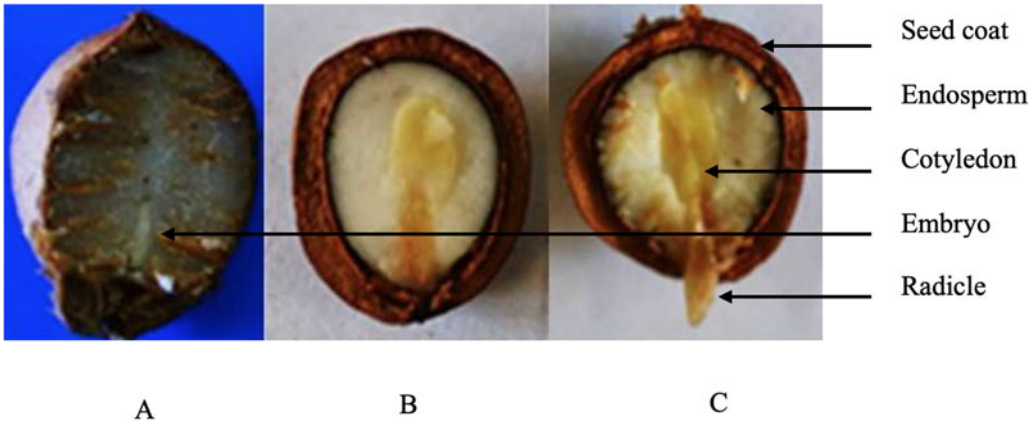

Figure 2. Embryo developmental stages inside *A. glabra* seeds: (A) fresh intact mature seed showing the small embryo, (B) embryo elongation within the seed and (C) radicle emergence. Seeds were incubated on tissue papers moistened with GA_3 (100 ppm) solution at ambient laboratory temperature under light/dark (14/10 h) condition.

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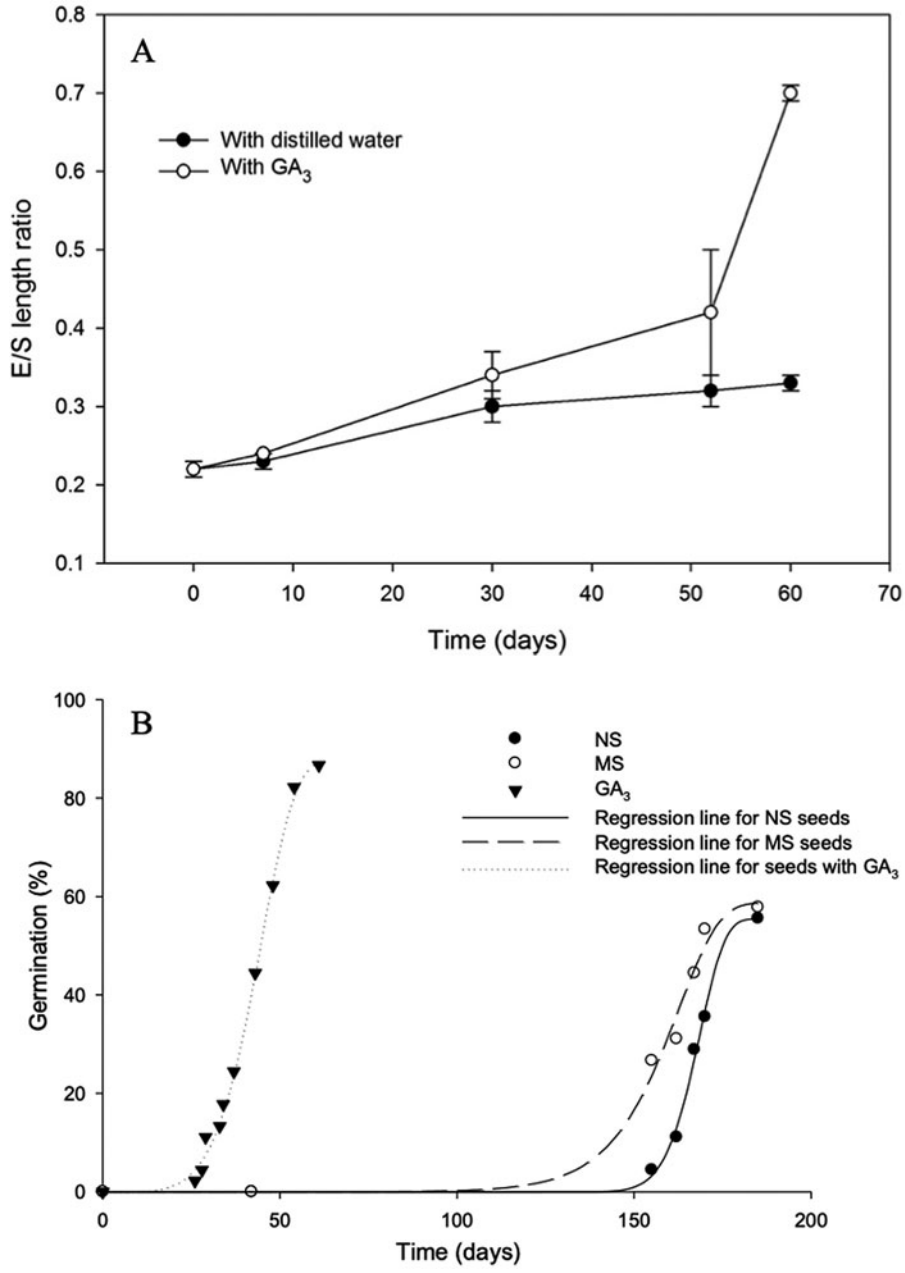

Figure 3. Embryo development in *A. glabra* seeds as measured by (A) embryo/seed length ratio and (B) germination. Non-scarified (NS) or manually scarified (MS) seeds were placed on tissue papers moistened with distilled water in light/dark (14/10 h) condition at ambient laboratory temperature; NS seeds also were tested on 100 ppm gibberellic acid (GA_3) solution.

more than 5 months to germinate on distilled water. However, non-scarified seeds of *A. glabra* germinated >85% on GA_3 within 2 months, indicating that there is a physiological component to dormancy. Moreover, fresh *A. glabra* seeds have a linear, differentiated underdeveloped embryo with E:S ratio of 0.22. The E:S ratio increased up by 0.71 and 0.33 when seeds were placed on GA_3 and on distilled water, respectively, for 60 d. The E:S ratio of *A. glabra* seeds just after the seed coat ruptured was ~0.71. Thus, the embryo in *A. glabra* seeds elongated within the seed prior to radicle emergence showing that there was a morphological component to seed dormancy. Moreover, the rate of embryo growth and germination increased with GA_3 confirming a physiological component to dormancy as well. Thus, seeds of *A. glabra* have morphophysiological dormancy (MPD).

Although all *Aegiceras corniculatum* and *Ardisia elliptica* seeds germinated within 30 d, a substantial time delay was observed between radicle emergence and shoot emergence indicating epicotyl dormancy. Interestingly, our study is the first report of epicotyl dormancy in seeds of mangrove species.

Less than 5% of the non-scarified seeds of *Phoenix pusilla*, *Cayratia trifolia*, *Lumnitzera racemosa*, *Scaevola taccada* and *Sesuvium portulacastrum* germinated on distilled water revealing that they are dormant. Imbibition test was not conducted on seeds of *S. portulacastrum* as seeds of this species are very small. Both non-scarified and manually scarified seeds of the other four species imbibed at a similar rate, revealing that they did not have PY. Moreover, none of the tested treatments improved germination of their seeds except manual scarification which increased germination of *S. taccada* from 0 to 25%. Furthermore, embryos of *L. racemosa*, *S. taccada* and *S. portulacastrum* were fully developed and thus, they do not have a morphological component to their dormancy. Thus, seeds of

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Table 2. Possible seed dormancy breaking treatments and suggested propagation methods for mangrove restoration in Sri Lanka

Species name	Possible seed dormancy breaking treatment(s)	Suggested propagation method in restoration under a suitable hydrological and topological setting	Special remarks
Acanthus ilicifolius	No dormancy present in most of the seeds; hence, no dormancy breaking treatments required.	Both direct seeding and seedling transplanting.	
Aegiceras corniculatum	No dormancy present in seeds for radicle emergence; hence, seeds will germinate within 30 d. Epicotyl dormancy can be broken by treating fruits with GA_3 (250–500 ppm) or removing fruit coat.	Both direct seeding and seedling transplanting. Plant nursery should be established to acquire seedlings and saplings.	Seeds have epicotyl dormancy without a treatment, but seeds require about 60 d for shoot emergence.
Allophylus cobbe	No dormancy present in seeds; hence, no dormancy breaking treatments required.	Both direct seeding and seedling transplanting.	
Annona glabra	GA_3 can be used to break the physiological part of the dormancy. However, it will take around 2 months to germinate even with GA_3.	Not recommended to plant this species in species-rich mangrove forests due to the presence of highly invasive characteristics. This species may be suitable to restore bare lands or abandoned salt pans. However, future experiments should be done to ascertain the suitability of the species for a particular restoration site.	This species is considered as an invasive species. As shown here, seeds can stay dormant for long periods and probably form a substantial soil seed bank. As such, it may be necessary to conduct regular eradication of the plant to deplete the seed bank and prevent the species from becoming too abundant at a site.
Ardisia elliptica	No dormancy present in seeds for radicle emergence; hence, seeds will germinate well. Presence of epicotyl dormancy can be broken by treating fruits with GA_3 (250–500 ppm).	Direct seeding. Direct seedling can also be used after breaking epicotyl dormancy by treating seeds with GA_3. Polythene bags can be used to raise this species in a nursery; however, seeds should be exposed to direct sunlight.	
Canavalia cathartica	Mechanical scarification can alleviate seed dormancy.	Direct seeding after scarification. However, non-treated dormant seeds can also be used to improve the soil seed bank.	Fabaceae species will also contribute to improved soil conditions since they have root nodules.
Cynometra iripa	No dormancy present in seeds; hence, no dormancy breaking treatments required.	Both direct seeding and seedling transplanting.	
Cayratia trifolia	Seeds should be incubated on moist filter papers or any moist substrate for about 2–3 months at around 30°C to break dormancy.	Seedling transplanting.	Speculated from Baskin and Baskin (2014).
Clerodendrum inerme	GA_3 (100 ppm) can be used to break the physiological dormancy.	Direct seeding after exposing them to 500 ppm GA_3 solution for 1 d.	As it is an associated mangrove and could grow in other places, this species can be used as a horticultural plant for live fencing.
Dalbergia candenatensis	No dormancy present in seeds; hence, no dormancy breaking treatments required.	Both direct seeding and seedling transplanting.	Fabaceae species will also contribute to improved soil conditions since they have root nodules.
Dendrolobium umbellatum	Seeds should be manually scarified carefully without damaging the embryo.	About 1/3 of the seeds in a sample is non-dormant. Therefore, direct seeding without pretreatment also is suitable. This method will provide opportunity to make a soil seed bank.	Fabaceae species will also contribute to improved soil conditions since they have root nodules.
Dolichandrone spathacea	Majority of the seeds do not have dormant seeds. However, around 1/3 of the seeds are dormant.	Direct seeding is suitable as 1/3 of the seeds will make soil bank. Seedling transplanting also is suitable when a small number of plants is needed for the restoration.	
Excoecaria agallocha	No dormancy present in seeds; hence, no dormancy breaking treatments required.	Direct seeding.	

(*Continued*)

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Table 2. (*Continued.*)

Species name	Possible seed dormancy breaking treatment(s)	Suggested propagation method in restoration under a suitable hydrological and topological setting	Special remarks
Heritiera littoralis	Fruit coat should be removed to increase the germinability of the seeds.	Both direct seeding and seedling transplanting.	
Hibiscus tiliaceus	Seeds should be manually scarified carefully without damaging the embryo.	Direct seeding is suitable after breaking seed dormancy. Non-treated seeds can be used to establish a soil seed bank.	Used as an ornamental plant.
Ipomoea violacea	Seeds should be manually scarified carefully without damaging the embryo.	Direct seeding is suitable after breaking seed dormancy. Non-treated seeds can be used to establish soil seed bank.	High potential to be used as an ornamental plant.
Lumnitzera racemosa	Uninfected (by a moth) fruits should carefully select prior to germination.	Seedling transplanting is suitable over direct seeding if the restoration site is highly degraded.	Speculated from Perera et al. (2019).
Parsonsia alboflavescens	No dormancy present in most of the seeds; hence, no dormancy breaking treatments required.	Direct seeding.	
Pemphis acidula	No dormancy present in most of the seeds; hence, no dormancy breaking treatments required.	Both direct seeding and seedling transplanting.	Herbaceous plant and could be used in restoring the whole community.
Phoenix pusilla	Seeds should be moistened with water for around 2–3 months to induce germination.	Seedling transplanting.	
Phyla nodiflora	Seeds should be treated with GA_3 to break the dormancy.	Direct seeding after GA_3 treatment.	Herbaceous plant and could be used in restoring the whole community.
Pongamia pinnata	No dormancy present in most of the seeds; hence, no dormancy breaking treatments required.	Direct seeding and seedling transplanting.	
Premna serratifolia	Seeds should be treated with GA_3 to break the dormancy.	Direct seeding after GA_3 treatment.	
Suaeda vermiculata	Seeds should be treated with GA_3 to break the dormancy.	Direct seeding after GA_3 treatment.	
Scaevola taccada	Seeds should be treated with salt water or GA_3 to break the dormancy.	Direct seeding after GA_3 or salt water treatment.	Speculated from Liang et al. (2020).
Sesuvium portulacastrum	Seeds should be treated with GA_3 to break the dormancy.	Direct seeding after GA_3.	Speculated from Baskin and Baskin (2014).
Sonneratia caseolaris	No dormancy present in most of the seeds; hence, no dormancy breaking treatments required.	Direct seeding is suitable over a seedling transplanting if the restoration site contains other mangrove species. Seedling transplanting.	
Thespesia populnea	Seeds should be manually scarified carefully without damaging the embryo.	Direct seeding and seedling transplanting. Non-treated seeds can be used to establish soil seed bank.	Used as an ornamental plant in a coastal setting.
Xylocarpus granatum	No dormancy present in most of the seeds; hence, no dormancy breaking treatments required. However, about 30 d are required to produce leaves after radicle emergence.	Both direct seeding and seedling transplanting. If the restoration site is a bare land, seedling transplanting is more suitable over direct seeding.	
Xylocarpus rumphii	No dormancy present in most of the seeds; hence, no dormancy breaking treatments required. However, about 30 d are required to produce leaves after radicle emergence.	Both direct seeding and seedling transplanting. If the restoration site is a bare land, seedling transplanting is more suitable over direct seeding.	Species occurs in a restricted location and is used as a medicinal plant. Thus, important to utilize this plant for restoration activities.

L. racemosa, *S. taccada* and *S. portulacastrum* may have PD. This conclusion was supported by similar observations reported by Ye et al. (2004) and Martinez and Casasolai (1992); Ye et al. (2004) reported that no fresh *L. racemosa* seeds germinated, while ~30% of 2-month dry-stored (after-ripened) seeds did so. Martinez and Casasolai (1992) found that *S. portulacastrum* seeds required after-ripening or incubation at fluctuating temperatures for germination. E:S ratio in fresh seeds of *P. pusilla* and *C. trifolia* was low, and thus, it could be speculated that seeds of these species have MPD. Furthermore, *P. pusilla* (Arecaceae) and *C. trifolia*

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(Vitaceae) belong to families known to contain species with MPD (Baskin and Baskin, 2014). However, other *Phoenix* species have been reported to produce seeds with PD only (Baskin and Baskin, 2014). Further studies are needed to clearly identify the dormancy classes of these five species.

Ecological implications

Heretofore, seed dormancy of mangroves has not been studied at a community level, and this study is the first attempt to categorize dormancy (*sensu* Baskin and Baskin, 2004) of mangrove plants at a community level. Most of the investigated species (18 species – 60%) had dormant seeds, while the rest had non-dormant seeds (12 species – 40%) (Table 1). Among species producing dormant seeds, most of them showed PD (44%). PY, MPD and presence of epicotyl dormancy are represented by 28, 17 and 11% of the species, respectively. For the tropics, Samarasinghe et al. (2022) conducted a community-level study on seed dormancy of lowland rainforest tree species in Sri Lanka. They found that the identified MPD, PD, MD and PY dormancy classes among the species were related to the forest strata and dispersal time. In contrast to our mangrove ecosystem, the majority of lowland rainforest trees had non-dormant seeds (62%) and 14.3, 14.3, 7.0 and 2.3% had MPD, PD, MD and PY, respectively (Samarasinghe et al., 2022). Thus, stronger selection pressures must be present for dormancy in mangrove ecosystems than in a lowland rainforest. All of the different dormancy classes represented in our mangrove community show that various germination strategies are present enabling species to survive in this harsh environment. The different kinds of dormancy classes shown by species in the mangrove plant community are crucial for their survival as a community because they provide mechanisms for coping with the environmental challenges they face, including saltwater inundation, drought, low temperatures and low-oxygen soils. Dormancy allows mangroves to avoid or tolerate adverse conditions, conserve energy, and ensure their long-term survival, thus enabling the persistence and resilience of the entire mangrove plant community.

Two mangrove species produced seeds with epicotyl dormancy, which represented the first report of this kind of dormancy in a mangrove ecosystem and more investigations should be done to identify the type of epicotyl dormancy. Athugala et al. (2018) suggested that after initiating and establishing a root system, the timing of shoot emergence can be flexible for a seed with epicotyl dormancy. Although Athugala et al.'s (2018) study focused on tropical montane forest species, the same reasoning might be true for mangrove ecosystems. In mangroves, establishing a root system and becoming stationary in the muddy substrate with fluctuating tides, is difficult and the timing of such would be very important for the seedling to start obtaining water and nutrients for growth. To this end, shoot emergence could be delayed until the plant is firmly established.

A relatively high SE (standard error) in germination percentages was observed among our study species. This variation suggests that germination would be spread-out temporally. Since seeds of mangrove species experience highly fluctuating environmental conditions such as water, salinity and temperature, after seed dispersal, the probability of seeds germination and seedlings becoming established would be increased by having this large variation instead of a narrow window for germination and establishment. This high-temporal variation may be critical for the continuation and survival of species in mangrove environments.

Implications for restoration

Mangrove rehabilitation and restoration is considered as one of the most effective management options globally for dealing with degradation of mangrove forests. In Sri Lanka, 80% of the restoration sites of mangroves were unsuccessful according to the study done by Kodikara et al. (2017). In most of the restoration sites in Sri Lanka, a single species (mainly Rhizophoraceae species) is planted (direct seedling) without considering the biotic and abiotic factors in the site, because of ease of access to plant material as well as handling both during the nursery and planting stages. Kodikara et al. (2017) recommended that direct planting practice (mainly for monospecific cultivation) should be avoided, and mixed species planting should be promoted to enhance the effectiveness of the restoration. To this end, our dormancy profile gives necessary information on seed germination and dormancy of plant species in a mangrove community so that restoration practitioners can identify the kind of dormancy (or non-dormancy) and the level of dormancy to manage nursery stock to be outplanted for restoration and conserve genetic diversity of species having deep dormancies (Table 2).

Conclusion

Three dormancy classes (PY, PD and MPD) and presence of epicotyl dormancy were identified among mangrove species showing that mangrove plants have diverse germination strategies. Furthermore, our study is the first to report the presence of epicotyl dormancy in seeds of mangroves. These findings can assist practitioners in crafting strategies to effectively break dormancy and germinate seeds in conservation and restoration activities of mangroves because failure of germination due to seed dormancy can be a major impediment in producing these plants.

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Competing interest. The authors declare no conflict of interest.

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