Seed dormancy and germination behaviour of tropical rainforest tree species from Sri Lanka

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Abstract

Plant community-level studies on seed dormancy traits are important to understand and determine the significance of seed dormancy in different ecosystems. Hence, we studied seed dormancy and other related seed biological traits of 42 selected tropical lowland rainforest tree species from Sri Lanka, aiming to address seed dormancy class(es) for a biodiverse tropical lowland wet zone forest community and the relationship between dormancy classes, forest strata and seed dispersal mechanisms. Seed germination, imbibition, embryo length: seed length ratio, embryo morphology and the effect of gibberrelic acid on seed germination were determined. Sixty-two percent of the species with $T_{50} < 30$ days were identified as having fast-germinating seeds and the remaining 38% with $T_{50} > 30$ possessed slow-germinating seeds. Seeds of 33 species had fully developed embryos, while nine species had underdeveloped embryos; three had morphological dormancy (MD) and six morphophysiological dormancy (MPD). Treatment with gibberellic acid revealed physiological dormancy (PD) in seeds of six species, and the response to manual scarification confirmed physical dormancy (PY) in seeds of *Pericopsis moonina*. The majority of tropical lowland rainforests had non-dormant (ND) species (62%), and 14.3, 14.3, 7 and 2.3% of the species had MPD, PD, MD, and PY, respectively. Non-dormancy decreased for taxa from the upper strata to the lower strata of the forest. ND seeds were dispersed during the rainy season. Thus, non-dormancy seems to be the most dominant germination behaviour among the tree species in the lowland rainforest of Sri Lanka with the class of dormancy related to forest strata and dispersal time.

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Introduction

Tropical lowland rainforests are one of the ecosystems that habour the highest plant biodiversity on earth, and they provide many valuable ecosystem services. However, these forests are under severe threat due to human impact throughout the world (Morris, 2010). Sri Lankan rainforests are similarly under anthropogenic pressure and are facing the threat of destruction due to increased consumer demands for timber and cropping (Sarathchandra et al., 2021). There is a greater need to conserve and restore these pristine ecosystems to ensure future ecosystem services (Corlett and Primack, 2008). Direct seeding and seedling planting are two of the key methods used in the restoration of degraded areas in tropical regions. Knowledge of seed biology of native species used in such seed-based restoration is, therefore, essential for restoration success (Hamilton et al., 2013; Miller et al., 2017). Most direct seeding and seedling planting activities throughout the world have insufficient seed biological information of the species used for these activities leading to failure of many restoration attempts (Baskin and Baskin, 2005). When dormancy is not considered in seeding programmes, there is a likelihood of restoration failures (Merritt and Dixon, 2011).

Baskin and Baskin (2014) have compiled information on seed dormancy of 1430 tropical rainforest species and found that 48% of the species have non-dormant (ND) seeds. Furthermore, they recorded that 25, 3, 14, 9 and 1% of the species have seeds with physiological dormancy (PD), morphological dormancy (MD), morphophysiological dormancy (MPD), physical dormancy (PY) and PY + PD, respectively. However, this key study does not relate dormancy to biomes such as lowland rainforests.

Although there is information available on the seed biology of tropical rainforest species in many other parts of the world [Malaysia (Ng, 1973, 1980), Mexico (Vázquez-Yanes and Orozco-Segovia, 1993), India (Murali, 1997) and Brazil (Valio and Scarpa, 2001; de Souza et al., 2015; Daibes et al., 2019)], published information on seed dormancy of South Asian

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tropical rainforest species is scant. The available information from other regions of the tropics suggests that seeds of many rainforest species are ND. However, a considerable percentage of these species can also produce dormant seeds (Marques and Oliveira, 2008). Furthermore, many studies have shown that proportions of ND to dormant seed-producing species vary within a tropical rainforest biome depending on local habitat conditions (Lan et al., 2018).

Moreover, seed dormancy and other seed biological traits at the plant community level are important in understanding the dynamics of these plant communities (Tweddle et al., 2003). Community-level information on seed traits enables us to answer key ecological questions that underpin restoration planning decisions when seed is involved such as the relative proportion of different dormancy classes and how these relate to vegetation strata. Although there are many studies of plant community structure for tropical ecosystems (Sautu et al., 2007), there are no studies available on community-level seed dormancy in lowland tropical rainforest plant communities.

Thus, we studied seed dormancy and other related seed biology traits of 42 tropical lowland rainforest tree species from Sri Lanka. This covers about 20% of the dominant tree species in this ecosystem. The study mainly aimed to provide seed dormancy information to assist the restoration of rainforest on degraded lands in southwestern Sri Lanka, which is, together with the Western Ghats of India, a biodiversity hotspot (Gunawardene et al., 2007). The specific aims are to determine: (1) what seed dormancy class(es) is/are important for tropical lowland wet zone rainforest community in Sri Lanka and (2) what dormancy classes are present in species representing the different forest strata and seed dispersal modes under different climatic conditions. Moreover, the dormancy profile constructed for the tree species in Sri Lankan lowland tropical rainforest species was compared with the dormancy profile constructed by Baskin and Baskin (2014) for tree species of the tropical rainforest biome to test the hypothesis that seed dormancy profiles for different plant communities of the same biome can be different from the generalized seed dormancy profile constructed for the biome due to variations in climate.

Materials and methods

Study species and collection of seeds

The studied tree species (Supplementary Table S1) were selected from the tropical lowland rainforests in Sri Lanka based on their ecological significance, threatened status, the availability of seeds and endemicity. Fruits were collected at least from six individuals from each species located in five rainforests in Sri Lanka, such as Sinharaja, Kanneliya, Yagirala, Kottawa, Pituwala and Dombagaskanda forest reserves, from October 2017 to September 2019 during the peak fruiting season of each species. Mature ripened fruits were collected from trees whenever possible. When fruits were inaccessible and less number of fruits were available on trees, fruits fallen on the ground were collected. Additional care was taken to collect healthy non-predated freshly fallen fruits when they were collected from the ground. Collected fruits were stored in labelled paper or polythene bags and transported to the seed biology laboratory, Department of Botany, University of Peradeniya, where laboratory experiments were conducted. Seeds were extracted from fruits and air-dried to remove surface water if seeds were extracted by soaking in water.

Extracted seeds were stored in closed plastic bottles until experiments were initiated within 2–3 d from seed collection, as literature indicates that species may have recalcitrant or very short-lived seeds (Umarani et al., 2015). The stratum (canopy, subcanopy, understory trees and understory shrubs) was identified by using the height information of plants based on Ashton et al. (1997) and field observations. Month of seed collection was used to determine the time of seed dispersal, which was further divided into three sessions according to rainfall data: wet (100–200 mm), super wet (200–400 mm) and peak (400–500 mm) rainy season.

Seed germination

To determine whether seeds are dormant or not, four replicates, each of at least ten seeds were incubated on moistened tissue papers in Petri dishes at 25°C in light/dark (12 h/12 h) conditions. Seeds were observed for germination at 3-d intervals for 100 d or until all the viable seeds germinated. Radicle emergence (>1 mm) was the criterion for germination. At the end of the experiments, non-germinated seeds were dissected to determine the viability (white firm viable embryos vs grey soft non-viable embryos). Seed germination progression curves were prepared, and T_{50} was determined using the curves. Species with $T_{50} < 30$ d were categorized as fast-germinating seeds, while remaining species with $T_{50} > 30$ were categorized as slow-germinating seeds (as suggested by Athugala et al., 2021).

Imbibition of seeds

To determine whether the seeds of the studied species have water permeable seed coat or not, seeds incubated at 25°C under conditions mentioned under 'seed germination' were observed for changes due to water imbibition (seed coat rupture and seed size increase) in 1-d intervals for consequent 5 d. If the seeds show seed coat rupture and the increment of seed size, they were considered to have a permeable seed coat. Other species with no sign of imbibition were subjected to an imbibition test. Initial mass of 15 fresh intact and manually scarified seeds was measured to the nearest 0.001 g using a digital analytical balance (GR 200, A&D Company Pvt. Ltd.). These seeds were placed on moistened tissue papers in Petri dishes separately and retrieved 2, 5, 8, 24 and 48 h after incubation, blotted dry, reweighed and returned to the Petri dish. Imbibition curves of intact and scarified seeds were prepared and compared.

Embryo length:seed length ratio

Studies were conducted to determine the presence or absence of MD or MPD of seeds (developed vs underdeveloped embryo). If slow-germinating seeds have underdeveloped embryos they can be categorized as seeds with MPD, while fast-germinating seeds with underdeveloped embryos can be categorized as seeds with MD. Eight samples of ten seeds were placed on filter papers moistened with distilled water in 9-cm diameter Petri dishes and incubated at 25°C. Seven samples were retrieved after 12 h, and then after 2-week intervals until germination of seeds was complete. The eighth sample was retrieved soon after the seed coat rupture for radicle protrusion. Seeds were dissected, and seed length and embryo length were measured using a Vernier caliper (AVM Scientific, India). Embryo length:seed length ratio (E:S ratio) was calculated for each seed. Embryo development at the

time of radicle emergence was calculated using the equation given below:

Percentage embryo development =

$$\frac{\text{E:S ratio at the time of radicle protrusion} - \text{E:S ratio of fresh seed}}{\text{E:S ratio of fresh seed}}$$

$$\times \, 100\%$$

Seeds with an E:S ratio of >0.5 or if the E:S ratio did not increase prior to germination were considered to have fully developed embryos, while seeds having an E:S ratio of <0.5 and the E:S ratio increased significantly prior to germination were considered to have underdeveloped embryos. Embryo growth studies were not conducted on species with seeds <1 mm in diameter.

Embryo morphology

Five seeds of each species (except the minute seeds) were cut into half using a razor blade. The embryo shape was observed and categorized according to the modified Martins classification system (Baskin and Baskin, 2007). Embryos were observed under a light microscope if seeds were <5 mm in length.

Effect of GA$_3$ on germination

This experiment was conducted for the species that had $T_{50} > 30$ d to confirm the physiological dormancy of seeds. Four replicates each of at least ten seeds were placed on Whatman No. 1 filter paper moistened with 500 ppm GA$_3$ solution and incubated at 25°C under light/dark (12 h/12 h) condition. Seeds were observed for radicle and shoot emergence at 3-d intervals for at least 30 consecutive days. Radical emergence (>1 mm) was recorded as

the criterion for germination. Non-germinated seeds were dissected to check the viability of the embryo as explained above.

Analysis of data

Four-parameter logistic sigmoidal curves were fitted to the germination data of all species to identify the germination pattern (as suggested by Brown and Mayer, 1988). T_{50} values were determined from the graphs. The relationship between strata and the time of dispersal was analysed with a nominal regression analysis using the dormancy class as the dependant variable and other variables as independent variables. Dormancy profiles created during the present study were compared with that constructed for the tropical rainforest biome (Baskin and Baskin, 2014) using the χ^2 test.

Results

Seed germination

Five types of germination behaviour were identified among the 42 studied species based on the cumulative germination curves (Fig. 1) and other germination parameters (Table 1). Seeds showing A and B types of germination behaviour could be described as 'fast-germinating seeds' and seeds with C, D and E types of germination behaviour could be grouped as 'slow-germinating seeds'. Species showing germination behaviour type A had seeds that reached >90% germination (of the seeds which were viable till the end of the experiment) within 30 d (Table 1). Type A was represented by 46% of the study species. Type B germination behaviour was shown by 16% of the study species with $T_{50} < 30$ d and >90% germination after 30 d (Table 1). However, seeds of type B species reached 100%
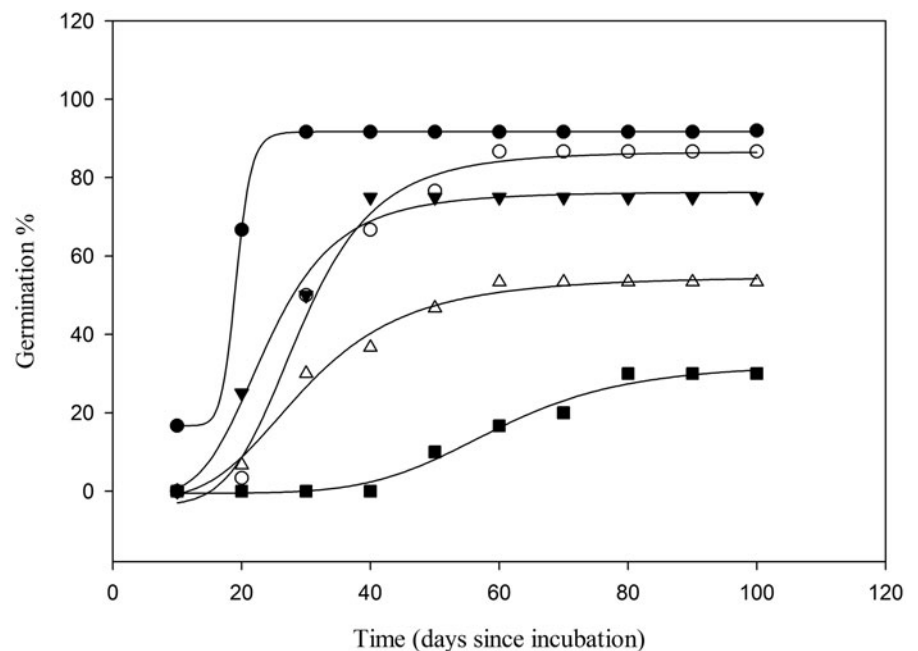
Fig. 1. Cumulative germination of *Isonandra lanceolata* (type A), *Horsfieldia iryaghedhi* (type B), *Canarium zeylanicum* (type C), *Fagraea ceilanica* (type D) and *Margaritaria cyanospermus* (type E). Four-parameter logistic sigmodial curves were fitted to identify the germination behaviour.

● Type A (*Isonandra lanceolata*)
○ Type B (*Horsfieldia iryaghedhi*)
▼ Type C (*Canarium zeylanicum*)
△ Type D (*Fagraea ceilanica*)
■ Type E (*Margaritaria cyanospermus*)

Table 1. Characteristics of the study species having different germination behaviour types A, B, C, D and E

Species name	Final germination (%)	Days to achieve final germination	Germination % after 30 d	MC (%)	Median germination time (days)
Type A					
Gomphia serrata	83.3	6	83.3 (100)	9.5	5
Mesua thwaitesii	84	14	84.0 (100)	7.7	7
Syzygium nervosum	80	8	80 (100)	66.34	7
Mesua ferrea	92.5	15	92.5 (100)	8.5	8
Gaertnera vaginans	88.5	30	88.5 (100)	44.2	9
Artocarpus nobilis	76.7	22	76.6 (99)	42	10
Bhesa ceylanica	80	21	80 (100)	56.3	10
Shorea affinis	100	30	100 (100)	42	12
Pericopsis mooniana (MS)	82.4	26	82.4 (100)	12.9	13
Shorea trapezifolia	80	30	80 (100)	34.6	13
Dichapetalum gelonioides	90	29	90 (100)	10.2	14
Diospyros acuminata	80	27	80 (100)	22.3	14
Glochidion nemorale	64.3	30	64.3 (100)	38.7	15
Isonandra lanceolata	91.7	30	91.7 (100)	40.8	15
Eurya ceylanica	86.6	30	86.6 (100)	11.8	16
Strychnos benthamii	90	22	90 (100)	45.9	16
Semecarpus walkeri	70	40	70 (100)	33.8	17
Bridelia moonii	97.5	30	97.5 (100)	29	18
Hortonia angustifolia	88.2	39	82.8 (94)	33.1	18
Bhesa nitidissima	80	34	78 (98)	41.4	19
Humboldtia laurifolia	87	45	75 (86)	56.6	19
Syzygium lanceolatum	76.9	30	76.9 (100)	53.5	19
Dipterocarpus zeylanicus	50	30	50 (100)	47	30
Type B					
Myristica dactyloides	86.7	42	66.6 (77)	24.5	27
Palaquium thwaitesii	80	50	50 (63)	35.96	28
Mangifera zeylanica	63.33	48	29.3	47.27	29
Horsfieldia iryaghedhi	76.7	44	49.1 (64)	30.2	30
Type C					
Timonius flavescens	80	41	46.6 (58)	14.5	31
Canarium zeylanicum	70	40	44.6 (64)	6.3	35
Dillenia indica	97.4	50	0 (0)	6.2	46
Type D					
Fagraea ceilanica	53.3	90	25.8 (48)	11.4	60
Stemonurus apicalis	80	90	0 (0)	57.2	60
Garcinia terpnophylla	75	70	3.7 (5)	38.5	62
Mesua stylosa (T)	40	70	23 (50)	35.3	62
Type E					
Turpinia malabarica	60	98	0 (0)	43.7	90
Madhuca longifolia	50	100	0 (0)	47.5	>90
Margariiaria cyanospermus	30	100	0 (0)	15.1	>100

(*Continued*)

Table 1. (*Continued.*)

Species name	Final germination (%)	Days to achieve final germination	Germination % after 30 d	MC (%)	Median germination time (days)
Glochidion zeylanicum	–	–	–	–	–
Urophyllum ceylanicum	–	–	–	–	–
Elaeocarpus subvillosus	–	–	–	–	–
Hydnocarpus octandra	–	–	–	–	–
Unknown sp.	–	–	–	–	–

germination within at least ∼55 d. Species with type C germination behaviour consisted of seeds having T_{50} between 30 and 50 d represented by 9% of the study species. Species with seeds that had T_{50} between 50 and 65 d were grouped into germination behaviour type D. This type contained 7% of the study species. Finally, type E germination behaviour was seen in species having seeds with T_{50} >80 d. This type was observed in only 21% of the studied species.

Imbibition of seeds

Visual signs of imbibition (rupturing of seed coat and increasing seed size, Supplementary Fig. S2) were observed in all the studied species, except in seeds of *Pericopsis mooniana* when incubated on water alone. When non-scarified *P. mooniana* seeds were incubated on distilled water at 25°C, a negligible amount of mass increment was observed within 4 d (Supplementary Fig. S3). In contrast, scarified seeds showed a >100% mass increase followed by the enlargement of the seed and the rupturing of the seed coat. The mass increment of manually scarified seeds was significantly higher than that of the intact seeds ($F = 54.73$, $P < 0.001$).

Embryo length:seed length ratio

Among the 42 study species, 31 species (Table 2) such as *Elaeocarpus subvillosus*, *Hydnocarpus octandra*, *Palaquium thwaitesii* and *Bhesa ceylanica* had an E:S ratio of >0.5 (Fig. 2). They were categorized as seeds with fully developed embryos. The remaining 11 species had an E:S ratio of <0.5. However, although the initial E:S ratio of *Myristica dactyloides* and *Horsfieldia iryaghedhi* was <0.5, it did not increased >0.5 prior to radicle emergence (15% embryo development). Their cotyledons also did not develop into a functioning leaf, instead leaves developed from the shoot meristem separately and hence, cotyledons act as haustoria to supply nutrients to the developing seedling from the shoot meristem after germination. They were also categorized as seeds with developed embryos. The E:S ratio of the seeds of remaining species (10 species) developed prior to radicle emergence, while at the time of radicle emergence the E:S ratio was >0.5 (Tables 2 and 3), and this group was represented by *Stemonurus apicalis* and *Hortonia angustifolia* (Fig. 3). They were categorized as seeds with underdeveloped embryos.

Embryo morphology

Seeds of most of the study species have FA1: spatulate axile (13 species); LA: linear axile (10 species) and FA2: bent axile (10 species) embryos. In addition, FA4: investing and B1: rudimentary embryo types were also observed (Table 2). Among the spatulate and linear embryos, fully developed and underdeveloped types were observed. However, seeds of *Urophyllum ceylanicum* were categorized as dwarf seeds as they were very tiny (>1 mm in length) seeds.

Effect of GA_3 on germination

As majority of the species germinated well with distilled water, this treatment was only conducted for *Glochidion zeylanicum*, *Urophyllum ceylanicum*, *Elaeocarpus subvillosus*, *Madhuca longifolia*, *Mesua stylosa*, *Hydnocarpus octandra* and unknown sp. as none of their seeds germinated with distilled water within 100 d. Seeds of *G. zeylanicum* and *E. subvillosus* germinated >50% within 30 d on tissue papers moistened with GA_3 solution, while *U. ceylanicum* and *H. octandra* germinated to 50% after 30 d. Although seeds of *Mesua stylosa* germinated to 40% without any treatment, there was a significant increase in germination (69%) after treatment with 500 ppm GA_3.

Diversity of seed dormancy types of studied rainforest species

Dormancy types of the studied species were categorized based on their T_{50} value, embryo development during radicle emergence and imbibition studies (Table 2). Embryos of nine study species were underdeveloped, while 33 species had developed embryos. The seeds with underdeveloped embryos have morphological or MPD. Thus, among the studied species, 26 species were identified as ND (62% from the total species), while 16 species (38%) were identified as dormant. Dormant species included one physically dormant species, three morphologically dormant species, six physiologically dormant species and six morphophysiologically dormant species.

Seed dormancy distribution among forest strata

A significant association was discovered between the dormancy type and forest stratification ($\chi^2 = 11.93$, $P = 0.003$). Non-dormancy was abundant among all the tree species. However, the number of ND species decreased when moving from the upper strata towards the lower strata. Three quarters of the canopy species produced ND seeds. MD and PD were not found among canopy species, while PY and MPD were represented by 12.5% of species in each class. Sixty seven percent of the subcanopy species produced ND seeds, whereas PD and MPD were represented by 25 and 8.3% species, respectively. Fifty two percent of ND species were observed in the tree layer, while MPD, PD and MD were represented by 21, 13 and 13% of species, respectively.

Table 2. Classification of embryo type, embryo shape and dormancy type of studied species

Species name	Embryo type	Embryo shape	Germination behaviour type	Imbibition	Dormancy type
Artocarpus nobilis	D	FA2	A	VS	ND
Bhesa ceylanica	D	FA1	A	VS	ND
Bhesa nitidissima	D	FA1	A	VS	ND
Bridelia moonii	D	FA1	A	VS	ND
Canarium zeylanicum	D	LA	C	VS	ND
Dichapetalum gelonioides	D	LA	A	VS	ND
Dillenia indica	UD	LA	C	VS	MPD
Diospyros acuminata	D	FA1	A	VS	ND
Dipterocarpus zeylanicus	D	FA2	A	VS	ND
Elaeocarpus subvillosus	D	FA1	E	VS	PD
Eurya ceylanica	D	FA2	A	VS	ND
Fagraea ceilanica	UD	LA	D	VS	MPD
Gaertnera vaginans	UD	LA	A	VS	MD
Garcinia terpnophylla	UD	FA4	D	VS	MPD
Glochidion nemorale	D	FA1	A	VS	ND
Glochidion zeylanicum	D	FA1	E	VS	PD
Gomphia serrata	D	FA4	E	VS	ND
Horsfieldia iryaghedhi	D	B1	B	VS	ND
Hortonia angustifolia	UD	FA1	A	VS	MD
Humboldtia laurifolia	D	FA2	A	VS	ND
Hydnocarpus octandra	D	FA1	E	VS	PD
Isonandra lanceolata	D	FA1	A	VS	ND
Madhuca longifolia	D	FA2	E	VS	PD
Mangifera zeylanica	D	FA2	B	VS	ND
Margaritaria cyanospermus	UD	LA	E	VS	MPD
Mesua ferrea	D	FA4	A	VS	ND
Mesua stylosa	D	FA4	E	VS	PD
Mesua thwaitesii	D	FA4	A	VS	ND
Myristica dactyloides	D	B1	B	VS	ND
Palaquium thwaitesii	D	FA1	B	VS	ND
Pericopsis mooniana	D	FA2	A	VSA	PY
Semecarpus walkeri	D	FA2	A	VS	ND
Shorea affinis	D	FA2	A	VS	ND
Shorea trapezifolia	D	FA2	A	VS	ND
Stemonurus apicalis	UD	LA	D	VS	MPD
Strychnos benthamii	D	FA1	A	VS	MD
Syzygium nervosum	D	LA	A	VS	ND
Syzygium lanceolatum	D	LA	A	VS	ND
Timonius flavescens	D	LA	C	VS	ND
Turpinia malabarica	UD	FA1	E	VS	ND
Urophyllum ceylanicum	UD	Df	E	VS	MPD
Unknown sp.	D	FA4	E	VS	PD

D, developed embryo; UD, underdeveloped embryo; B1, rudimentary; FA1, spatulate axile; FA2, bent axile; FA4, investing axile; LA, linear axile; VS, visual signs present; VSA, visual signs absent
MD, morphological dormancy; MPD, morphophysiological dormancy; ND, no dormancy.
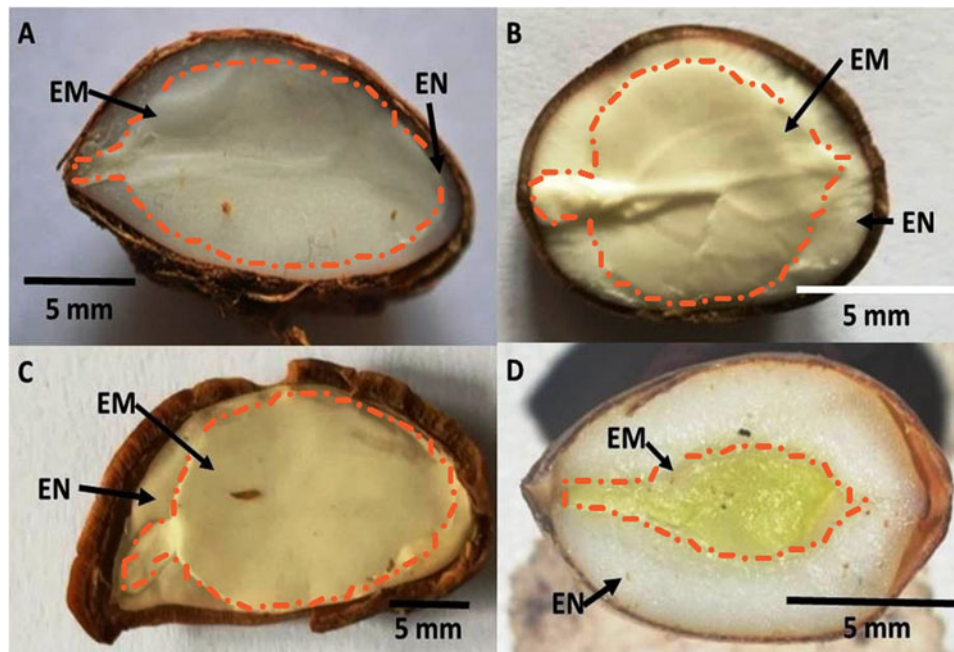
Fig. 2. Developed embryos of fresh seeds of *Elaeocarpus subvillosus* (A), *Hydnocarpus octandra* (B), *Palaquium thwaitesii* (C) and *Bhesa ceylanica* (D). EM, embryo; EN, endosperm.

Seed dormancy versus non-dormancy during different seed dispersal seasons

A significant association was found between the seed dormancy type and seed dispersal time ($\chi^2 = 128.61$, $P < 0.001$). All the seeds (100%) dispersed during the peak rainy season (>500 mm monthly rainfall) during May were ND. The majority of the species (73%) dispersed during other less wet parts of the rainy season (200–500 mm) during April, June, September, October and November were also ND, and 27% of them were dormant. In contrast, 75% of the seeds dispersed during the wet season (100–

200 mm) during February and March were dormant, while only 25% of them were ND. See Supplementary Fig. S1 for the generalized climatic profiles for the wet zone of Sri Lanka.

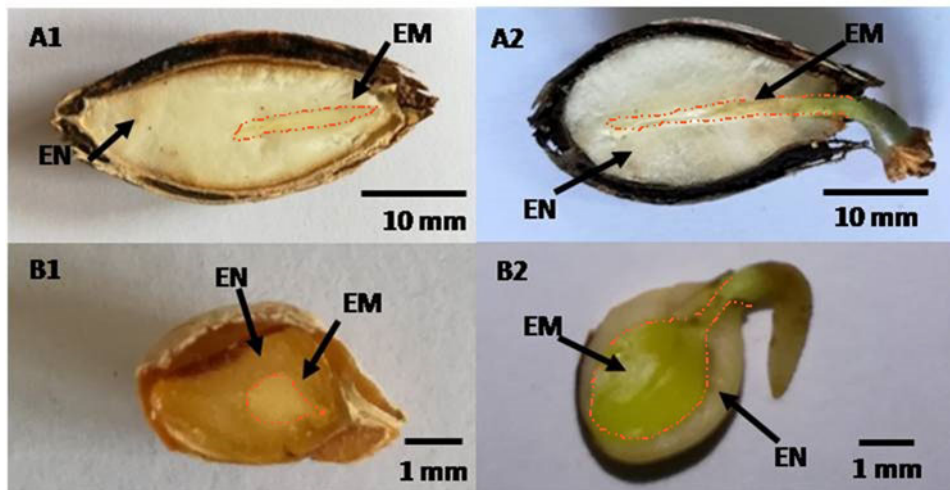### Dormancy profiles for Sri Lankan rainforests versus rainforests in the world biome

Results of the χ^2 test revealed that the dormancy profile constructed for Sri Lankan rainforest tree species during the present study was significantly different ($\chi^2 = 9.85$, $P = 0.043$) from that created for global rainforest by Baskin and Baskin (2014). The percentage of ND (62%) and morphologically (7%) dormant seed-producing species in the dormancy profile constructed for Sri Lanka was higher than that for the world (49 and 3%, respectively). Consequently, the percentage of PD (14.3%) and PY (2.3%) seed-producing species of the local profile was less than that of reported in the world tropical rainforest biome (25 and 8.5%, respectively).

Discussion

In this study of Sri Lankan lowland rainforest, there was considerable variability in the dominance of different dormancy types across rainforest strata. Most of the species that represent the upper strata of Sri Lankan rainforests produced ND seeds, while most of the species in the lower strata produced seeds with PD or MPD. Similar trends have been identified by Athugala et al. (2021) from montane forest species of Sri Lanka. They suggested that the species from the upper strata produce fast-germinating seeds as they have a higher chance of long distance dispersal than seeds of species in lower strata. Thus, seeds of species occupying lower strata may depend on secondary dispersal that, in turn, would require additional time for dispersal to occur. Therefore, species in lower strata produce seeds that have a high proportion of dormancy. This study found that the same principal

Table 3. E:S ratio of some studied species

Species	E:S ratio		% Embryo development
	Fresh	After radical Emergence	
Mesua ferrea	0.98 ± 0.00	0.99 ± 0.00	1
Shorea affinis	0.89 ± 0.1	0.9 ± 0.08	1.12
Elaeocarpus subvillosus	0.9 ± 0.03	0.92 ± 0.02	2.22
Pericopsis mooniana	0.9 ± 0.01	0.92 ± 0.02	2.22
Bhesa ceylanica	0.76 ± 0.07	0.78 ± 0.05	2.66
Canarium ceylanicum	0.79 ± 0.01	0.82 ± 0.03	3.77
Hydnocarpus octandra	0.76 ± 0.0	0.8 ± 0.0	5.26
Palaquium thwaitesii	0.88 ± 0.00	0.96 ± 0.01	8
Myristica dactyloides	0.25 ± 0.01	0.28 ± 0.01	12
Horsfieldia iryaghedhi	0.20 ± 0.00	0.23 ± 0.03	15
Hortonia angustifolia	0.43 ± 0.08	0.7 ± 0.03	62.79
Stemonurus apicalis	0.38 ± 0.15	0.73 ± 0.00	92.1

Fig. 3. Underdeveloped embryos of fresh (1) and developed embryo of the germinating (2) seeds of *Stemonurus apicalis* (A) and *Hortonia angustifolia* (B). EM, embryo; EN, endosperm.

applies to the lowland rain forests in Sri Lanka. Species in the upper strata of tropical rainforest are much taller (>30 m) than species in the montane forest upper strata (>20 m). Thus, these species have even higher opportunities to disperse seeds a longer distance with the aid of animals and wind. However, more studies are needed to determine the ecological significance of this phenomenon.

Furthermore, our research showed that the seed dormancy of species seems to be more dependent on the peak seed dispersal period of these species, which was directly linked with rainfall. Species-dispersing seeds in the peak and other wet periods produce ND seeds. Similar results were reported by Garwood (1983) where Garwood described that the time of germination is controlled by dispersal time. Furthermore, Garwood stated that seeds dispersed in the early rainy season were ND seeds, while seeds dispersed in the late rainy season and in the dry season were dormant. Peak and wet periods provide favourable conditions for seedlings to grow in the forest floor. During these periods, the forest floor is more humid, and thus, pathogenicity and predation pressure is higher for newly dispersed seeds (Dalling et al., 2011, 2020), which can be more easily overcome if seeds have rapid germination and establishment syndromes (Green and Juniper, 2004; Dalling et al., 2011, 2020). Species producing dormant seeds dispersed their seeds during the relatively dry period, which is somewhat less favourable for seedling development and also less favourable for pathogens and predators, and thus, these seeds can stay in the soil seed bank until the peak of the super wet period in the region initiates germination following dormancy release.

Our research also identified, for the first time, the dormancy classes of 27 rainforest species. Among these 27 species, dormancy information is not available for *Hortonia angustifolia*, *Timonius flavescens*, *Isonandra lanceolata* and *Stemonurus apicalis* even at the genus level. Only genus-level information is available for the remaining 23 species. However, for 12 of the above species, available genus-level information suggested two or more dormancy classes (Baskin and Baskin, 2014). The dormancy classes identified for 8 of the remaining 12 species were different from those reported in the literature at the genus level (Baskin and Baskin, 2014). Our study confirmed the dormancy class previous

identified or speculated at the genus level for 4 of the above 12 species [ND in genus *Artocarpus* (Beniwal and Singh, 1989; Elliott et al., 1996), PD in genus *Elaeocarpus* (Chien et al., 1998; Iralu and Upadhaya, 2018), MD in genus *Gaertnera* (Athugala et al., 2021) and PD in genus *Glochidian* (Athugala et al., 2021)]. Fourteen of the study species have been previously studied and dormancy classes were identified or speculated. Six of the above 14 species have previously been studied in different ecosystems [*Urophyllum ceylanicum*, *Turpinia malabarica*, *Bhesa nitidissima* and *Eurya ceylanica* in tropical mountain forests (Athugala et al., 2021), and *Messua ferrea* (Troup, 1921; Joshi et al., 2015) and *Dillenia indica* (Thapliyal et al., 2008) in tropical semi-evergreen forests], while the rest of the species (eight) have been studied in the same ecosystem [*Mangifera zeylanica* and *Dipterocarpus zeylanicus* (Holmes, 1954), *Shorea affinis* (Tompsett, 1998) *S. trapezifolia* (de Zoysa, 1986) *Strychnos benthamii* (Muthuthanthirige et al., 2020) *Humboldtia laurifolia* (Jayasuriya et al., 2010), *Gomphia serrata* (Ng, 1992) and *P. mooniana* (Jayasuriya et al., 2013)]. The previously reported dormancy class (PD) of *Bheasa nitidissima*, *Eurya ceylanica* and *Gomphia serrata* are identified as ND in the present study. However, seed dormancy, of eight species that have been previously studied from the same ecosystem, matched the outcomes of this study. Our study confirmed the class of dormancy for some but not all previously studied species. This information is a valuable addition to understanding the seed conservation of these important endemic and threatened species from tropical lowland rain forest species.

The differences in dormancy classes between the present study and previously published works at the genus level may be a result of: firstly, as Baskin and Baskin (2004) suggested some of these studies did not specifically aim to identify the dormancy class, and thus, the identified or speculated dormancy class through these studies may not be accurate. Secondly, dormancy can vary between species within the same genus (Finch-Savage and Leubner-Metzger, 2006) and may even vary within the species between populations inhabiting different ecosystems (Tseng et al., 2013).

Our study also showed that the dormancy profile created for the Sri Lankan rainforest tree species was significantly different from that created for the tropical rainforests worldwide by Baskin and

Baskin (2014). This is a similar observation to Athugala et al. (2021) and Lan et al. (2018) where they also found that dormancy profiles of Sri Lankan montane forests and seasonal tropical semi-evergreen rainforests in China were different from dormancy profiles constructed for tropical montane forest and seasonal tropical rainforest biomes of the world, respectively. The percentage of ND seed-producing species was higher in Sri Lankan rainforests compared to the world rainforest biome.

In addition, species that produce seeds having MD were often fast germinating with >50% of viable seeds germinating within 30 d. This can be expected as Sri Lankan rainforests are more aseasonal and more humid than most of the other tropical regions (Gunawardene et al., 2007). Fast germination is a sound adaptation for overcoming mortality issues (Dalling et al., 2011) associated with humid aseasonal tropical climates (Vázquez-Yanes and Segovia, 1984). Fast-germinating seeds can outgrow high predation and high pathogenicity through fast germination (Daws et al., 2005). Thus, non-dormancy is the most dominant type of germination behaviour among the tree species in the lowland rainforest of Sri Lanka.

Conservation and restoration implications

This study shows that tests of seed dormancy may require independent validation when extended to other parts of a biome. Simply relying on published sources from other regions or other biome types may lead to seed being inappropriately treated with subsequent loss of germination capacity for translocation or restoration programmes. In addition, the study demonstrated that the speed of germination can vary greatly within the same biome and therefore customizing seed pre-treatments such as priming may be necessary to ensure all seeds are in a readily germinable state.

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