Seed germination of coastal monsoon vine forest species in the Northern Territory, Australia, and contrasts with evergreen rainforest

Running title: Seed biology of coastal rainforest species in the NT.

Vidushi.Thusithana¹#, Sean M. Bellairs¹, Christine S. Bach²

¹ College of Engineering, IT and Environment, Research Institute of Environment and Livelihoods, Charles Darwin University, NT 0810
² Casuarina Senior College, Casuarina, Darwin, NT 0810

For correspondence, Vidushi Thusithana, +6146621002, Vidushi.Sarvananthar@cdu.edu.au

# College of Engineering, IT and Environment, Charles Darwin University, Darwin, NT 0810, Australia.

Abstract. Seed germination traits of seasonal rainforest species differ from permanently moist evergreen rainforest species due to the prolonged seasonal drought. We investigated whether seed germination traits used to categorize evergreen rainforest species into pioneer and climax guilds were applicable to seasonal rainforest species. Seed dormancy, light requirements for germination and seed storage types of five climax and thirteen pioneer species of a coastal vine thicket were studied. Results were compared to published studies of evergreen rainforest species. Evergreen rainforest pioneer species are typically dormant, require light to germinate and tolerate desiccation, whereas climax species are typically non-dormant, tolerate shade during germination and are sensitive to desiccation. In seasonal rainforest we found that a high proportion of pioneer species had seeds that were non-dormant (62%), and a high proportion of pioneer species germinated equally well in light and dark conditions. In seasonal rainforest, we found that the majority of climax species had desiccation tolerant seeds, whereas in evergreen rainforest the proportion of climax species producing desiccation sensitive seeds is equal to or greater than the proportion of species with desiccation tolerant seeds. In seasonal rainforest species physical, physiological and epicotyl dormancy types were found. Generally, for seasonal rainforest species, the prevalent form of dormancy in pioneer species was physical dormancy whereas physiological dormancy was most common in evergreen rainforest pioneer species with dormancy. Our results suggest that the contrasting seed biology traits that typically apply to pioneer and climax species of evergreen rainforest species don’t typically apply to seasonal rainforest species.

Additional keywords: Pioneer, climax, seed dormancy, seed storage, seasonal rainforest, evergreen rainforest
Introduction

Monsoon rainforests or seasonal rainforests are tropical rainforests with distinct wet and dry seasons. They occur between the equatorial region and the tropical dry areas south of the Tropic of Cancer in the northern hemisphere, and north of the Tropic of Capricorn in the southern hemisphere. During the summer monsoon they receive a high rainfall followed by a winter drought that lasts for several months. Unlike equatorial or continually moist evergreen rainforest, seasonal rainforests show a degree of deciduousness in the canopy (Walter 1979).

In northern Australia, seasonal rainforests in the Top End of the Northern Territory (NT) and the Kimberley of Western Australia occur as small, discrete patches within a vast expanse of eucalypt-dominated savanna (Russell-Smith 1991). Wet seasonal rainforest types are associated with sites where moisture is permanently available, such as rivers, small springs and seepages, whereas dry seasonal rainforest types are associated with seasonally dry substrates. Coastal vine forest is a dry seasonal rainforest type (Russell-Smith 1991) established along the coastal laterites and hind dunes in the NT. They experience a prolonged dry season from May to September and rely on the monsoon rain in the wet season to stimulate growth and allow seedling regeneration.

Seed germination of rainforest species is affected by seed viability, seed moisture, seed dormancy, and light. Evergreen tropical rainforest seeds typically have short viability in the wild because they generally lose viability quickly in a soil environment characterized by continuous high moisture and warm temperatures. As well as high soil moisture and warm temperatures directly affecting seed viability, these warm moist conditions throughout the year also promote continuous high levels of activity by fungi and invertebrate consumers of seeds (Myster 2015; Sarmiento et al. 2017). In contrast, many seasonal rainforest species lose viability due to desiccation during the dry season drought (Khurana and Singh 2001). Viability is also affected by pre-dispersal predation of rainforest fruits, which causes physical damage to the seeds and affects the seed fill (Tiansawat et al. 2017).

Seeds of most species tolerate desiccation in seasonal rainforest, whereas a higher proportion of species tend to be desiccation sensitive in evergreen rainforest (Daws et al. 2005; Tweddle et al.
Desiccation sensitive seeds, which are dispersed with greater than >15% moisture, are killed when moisture drops to 10-15% of the seed total fresh mass (Hong and Ellis 1996). Thus, they are susceptible to mortality due to water stress. In contrast, desiccation tolerant seeds tolerate seed moisture content falling to 10-15% and can be viable even when the moisture drops to 5% or below (Hong and Ellis 1996). Woody taxa which tolerate desiccation are frequent in the seasonal rainforest habitats (Khurana and Singh 2001; Tweddle et al. 2003; Galindo-Rodriguez and Roa-Fuentes 2017). Woody species which produce desiccation sensitive seeds are common in moist, evergreen rainforest, but are infrequent in seasonal rainforest. In their study of 225 species from a seasonal rainforest in Panama, Daws et al. (2005) found that 189 species are desiccation tolerant and only 36 species have desiccation sensitive seeds. In a comparative analysis of 886 trees and shrubs, Tweddle et al. (2003) reported that > 45% of species from evergreen rainforest are desiccation sensitive, whereas in seasonal rainforest < 25% of species are desiccation sensitive. However, Wyse and Dickie (2017) indicated that the proportion of desiccation sensitive species in evergreen rainforest drops to 18.5% when herbaceous species are included.

Seed dormancy occurs in about half of evergreen rainforest species (53% of 2563 species (Baskin and Baskin 2014)), whereas a greater proportion of species in seasonal rainforest produce dormant seeds. According to Baskin and Baskin (2014), a species is dormant if ≥ 50% of viable seeds take more than one month to germinate. From their compiled data set on seed dormancy of seasonal rainforest species, Baskin and Baskin (2014) report that 66% of the 221 seasonal rainforest species have dormant seeds. Dormancy is primarily found in species which disperse seeds in the dry season. This is to prevent germination during the infrequent early dry season rains which are unfavourable for seedling establishment and survival (Khurana and Singh 2001).

Light is an important abiotic factor affecting seed germination and establishment of rainforest species. Seeds of some rainforest species require light to germinate and their germination and establishment are associated with forest gaps (Swaine and Whitmore 1988). Gap creation causes an increase in irradiance and in the R:FR ratio (Lee 1987; Vazquez-Yanes et al. 1990; Orozco-Segovia et al. 1993). Often gap dependent species have seed dormancy that is broken by gap
conditions. An increase in irradiance causes an increase in temperature and in the magnitude of temperature fluctuations at the soil surface (Vazquez-Yanes and Orozco-Segovia, 1982). These changes can break seed dormancy of gap-demanding species, allowing them to germinate (Vazquez-Yanes and Orozco-Segovia, 1982; Pons 2000; Pearson et al. 2003).

Rainforest species are divided into pioneer and climax guilds based on the requirement of light for germination and for initial seedling establishment (Swaine and Whitmore 1988). In evergreen rainforest, pioneer species require higher light levels for germination, establishment and growth (Vazquez-Yanes and Smith 1982, Swaine and Whitmore 1988). Their seeds are commonly dormant, and their establishment is associated with tree fall gaps (Swaine and Whitmore 1988). Most rainforest pioneers have desiccation tolerant seeds to tolerate the elevated temperatures associated with gaps (Swaine and Whitmore 1988). Tweddle et al. (2003) reported that of 21 pioneer species from evergreen rainforest, 57% of species are dormant and 100% are desiccation tolerant. In contrast, climax species are shade tolerant and are able to germinate in lower light conditions associated with canopy cover. Their seeds are typically non-dormant and are sensitive to desiccation (Swaine and Whitmore 1988). Tweddle et al. (2003) reported that of 157 climax species from evergreen rainforest, only 24.8% of species are dormant and 64.8% are sensitive to desiccation.

In seasonal rainforest, the relative differences in seed biology characteristics of pioneer and climax species may differ from that of evergreen rainforest. This is due to the prolonged seasonal drought, which does not affect evergreen rainforest, but does affect the seed biology of seasonal rainforest. Prolonged seasonal drought may temporarily suspend the germination of climax species due to quiescence in the dry season (Yu et al. 2008) or it may promote the evolution of dormancy in species which shed seeds late in the wet season. A relatively high proportion of climax species in seasonal rainforest may exhibit a degree of desiccation tolerance.

In the Northern Territory of Australia, little is known about the seed biology of species that dominate seasonally dry rainforest. Bach (1998) studied the phenology, germination rate and the effect of pulp removal on the emergence of seedlings of eight dry seasonal rainforest species in the Northern Territory. She categorized the species as dormant if they did not germinate within six months. Baskin and Baskin (2014) class rainforest species as dormant if $\geq$ 50% of viable seeds take more than 30 days to germinate, so some species Bach (1998) categorised as non-
dormant may be dormant according to this classification. Russell-Smith (1991) scored the NT rainforest taxa as dormant if seeds retained viability in dry storage for at least six months, approximately the duration of the regional annual dry season. However, many non-dormant species that tolerate desiccation can remain viable and quiescent for six months. Thus, there is a clear need to understand the presence of dormancy in seeds of seasonally dry rainforest species based on the globally accepted dormancy classification system by Baskin and Baskin (2004; 2014). There are also knowledge gaps for seed storage behaviour, light requirements and suitable dormancy breaking treatments for seasonally dry rainforest species.

This study determined whether the seed biology of pioneer and climax species from a seasonal rainforest in northern Australia are similar to that of published studies of pioneer and climax species from permanently moist evergreen rainforest. Differences in seed biology were assessed by determining the seed viability, dormancy, seed moisture and the effect of light on germination. If dormancy was present, then the aim was to classify the seed dormancy type according to Baskin and Baskin (2004).

Materials and methods
Seed material
Mature seeds/fruits of 18 native species were collected from at least ten adult plants per species from coastal vine forest in East Point Reserve, Darwin, Northern Territory (12°24’39” S, 130°49’26” E). Seeds of nine species were collected between June and October during the dry season and another nine species were collected between November-March during the wet season (Table 1).

Fruits were checked fortnightly and were collected when they started to disperse. Seed/fruit morphology was assessed based on the presence or absence of: a fleshy or dry pericarp, grooves for dehiscence, stony mesocarp and hesperidium. The fruit type of each species was determined (Harris and Harris 2001). The number of seeds per fruit in at least 30 fruits were counted. Seeds were dissected to classify the embryo type based on Baskin and Baskin (2007). Studied species were classified as climax or pioneer by Jeremy Russell-Smith (pers.comm.) on the basis of unpublished field observations as to whether seedlings of the species established under a closed
canopy. Germination, imbibition, dormancy breaking treatments and assessment of seed storage behavior were started within one week of seed collection. Seed fresh weight was assessed within three days of collection.

**Seed viability**

Seed viability was determined using a cut test and with 2,3,5-triphenyl tetrazolium chloride (TTC). Three samples each with 25 seeds were subjected to the cut test and seeds with a missing embryo were scored as inviable. Seeds with an embryo were then tested with TTC. Seeds were mechanically scarified away from the embryo to ensure the uptake of TTC. Soft seeds had the seed testa pricked with a sterile needle. Hard coated seeds had the seed coat scarified using a scalpel blade. Seeds were then soaked in 1% TTC (Sigma-Aldrich, Australia) solution, in containers wrapped with aluminium foil to exclude light. After incubation at 30°C for 48h, seeds were inspected under a dissecting microscope. Seeds were scored as viable if vital tissues more or less uniformly stained to red (or to purple if the embryo was green).

**Seed germination and dormancy**

Germination testing was undertaken for each species using five replicates of 25 untreated seeds. Each replicate was placed on a 9 cm filter paper (Whatman No. 1) moistened with deionised water in a 9 cm diameter plastic Petri dish. All the samples were then incubated in a germination cabinet at 30°C in a 12 h light:12 h dark cycle, with light provided by three 30 W fluorescent bulbs (GRO-LUX). Samples were checked every two days for germination for 30 days and dead and germinated seeds were removed. Visible protrusion of the radicle was the criterion to score germination. Seeds were dead if they were no longer firm and offered no resistance if lightly pressed. Cumulative germination 30 days after imbibition was determined. Seed populations were considered non-dormant if more than 50% of viable seeds germinated within 30 days, or dormant if they took more than 30 days (Baskin and Baskin 2014). The mean number of days taken by each species to achieve the total germination percentage was calculated by using the following equation (Agyili et al. 2007; Chuanren et al. 2004; Tompsett and Pitchard 1998).
MTG = $\sum(nd)/N$

Where $n$ is the number of seeds germinated between scoring intervals; $d$ is the incubation period in days at that time point of the count and $N$ is the total number of seeds germinated in the treatment.

**Effect of light on seed germination**

Germination of seeds incubated in 12 h light/12 h dark conditions as above (hereafter referred to as light), was compared to germination of seeds incubated in darkness. For the dark treatment, five replicates each with 25 intact seeds were placed on a filter paper moistened with deionised water in a Petri dish inside a dark room illuminated by a green safe light (ILFORD 916). Each of the five Petri dishes was then wrapped with aluminium foil to exclude light and incubated in a germination cabinet at 30°C. Seeds incubated in the light treatment were observed every two days for germination, while seeds incubated in darkness were just observed after 30 days.

**Seed imbibition and physical dormancy**

Species which had significantly fewer seeds germinate within 30 days than the proportion of viable seeds, were assessed for physical dormancy (PY). Imbibition was assessed for 25 untreated seeds and 25 manually scarified seeds. Scarification techniques varied but removed a portion of the seed coat away from the micropyle region without piercing the embryo. *Abrus precatorius* and *Dodonaea platyptera* had very hard seed coats and were scarified by delicately drilling using a Dremel (MultiPro). For the rest of the species, the seed coat was manually nicked using a sterilized scalpel blade. Untreated seeds and scarified seeds were weighed individually to 0.00001 g using a digital balance, placed on moistened filter paper in Petri dishes, and reweighed after 168 h (Cook et al. 2008, Turner et al. 2009). For *Abrus precatorius*, treated seeds were weighed after 120 h because the seed coat had begun to split and radicle protrusion was about to start. Percent imbibition (I%) was calculated using the following formula:

$$I\% = \frac{(\text{Final weight of the seeds after imbibition} - \text{Initial weight of the seeds}) \times 100}{\text{Initial weight of the seeds}}$$
If a significant increase in percent imbibition of treated seeds compared to untreated seeds occurred PY was present (Baskin et al. 2006).

To assess the effect of treatments on PY, five replicates each with 25 seeds were subjected to treatments to rupture the seed coat. Seeds of *Alphitonia excelsa*, were manually nicked with a sterilized scalpel blade. For *Abras precatorius* and *Dodonaea platyptera* seeds were delicately drilled with the Dremel away from the micropyle region. Hot and boiling water treatments were also applied. Smaller *Dodonaea platyptera* seeds were placed in a hot water bath at 88°C for 30 sec as this was the optimum for other *Dodonaea* species (Turner et al. 2009). *Alphitonia excelsa* seeds were treated at 92°C for 3 min (Turner et al. 2005). Larger *Abras precatorius* seeds were treated at 100°C for 2 min. Treated seeds had germination tested as stated above.

**Physiological dormancy (PD)**

*Morinda citrifolia* and *Drypetes deplanchei*, which did not have all viable seeds germinate following scarification, were tested for PD. Five Petri dishes, each with twenty five seeds, were subjected to each of the following treatments: incubation of intact seeds on 5 ml of 500 ppm GA$_3$ (Sigma-Aldrich, Sydney, Australia) soaked filter paper; similarly on 1000 ppm GA$_3$ soaked filter paper; incubation of manually scarified seeds on 5 ml of 500 ppm GA$_3$ filter paper; manually scarified seeds on 1000 ppm GA$_3$ soaked filter paper; and manual scarification of the seed coat without GA$_3$.

All Petri dishes were incubated in 12 hour light/12 hour dark at 30°C in a germination cabinet. Germination was observed every three days for 30 days. Dead and germinated seeds were removed. Visible protrusion of the radicle was the criterion to score seed germination.

**Morphological dormancy (MD)**

Species that were not PY, and had endosperm, had seeds assessed for an underdeveloped or undifferentiated embryo, as indicated by the embryo not being differentiated into an embryonic
plumular-radicular axis and cotyledons (Baskin and Baskin 2014). Under-developed embryos were assessed by measuring the embryo-length (E):seed-length (S) ratio.

Twenty-five seeds were selected. The length of the embryo (E) and length of the seed (S) were measured to the nearest 0.01 mm using a Vernier caliper. A seed was considered morphologically dormant if it had E: S ratio ≤ 0.5 and if the embryo grew significantly before germination (Baskin and Baskin 2007). To confirm MD, another 25 seeds were measured for E:S ratio at the time of endocarp split (but before the length of the emerging radicle exceeded 0.5 mm). The embryo was measured excluding any portion of the radicle outside the seed coat. The E:S ratio of intact fresh seeds and germinating seeds were compared statistically to determine whether a significant difference in embryo growth occurred prior to germination to confirm the morphological dormancy.

Epicotyl dormancy (eD)

Species which had a delay in the epicotyl emergence was assessed for epicotyl dormancy. Five samples each with twenty-five germinated seeds (in 12 h light/12 h dark at 30°C) of *Strychnos lucida* were incubated on 24 layers of paper towelling moistened with distilled water in plastic seedling trays (34 x 28 x 5 cm) in 12 hour light/12 hour dark at 30°C in a germination cabinet. The time taken for the shoot (plumule) to emerge from each seed was recorded.

Seed moisture content

Sixteen species had their seed moisture content (MC) determined within three days after collection to assess their seed storage behaviour. Seeds were stored in an air-conditioned laboratory under 25°C in paper bags for up to three days. Other species were not assessed due to insufficient seeds. For each species, 20 - 25 seeds were weighed individually using a digital balance to the nearest 0.00001 g. Then, seeds were oven dried at 120°C for 3 hours and reweighed individually (ISTA 2008). Moisture content was measured using the following equation:

\[
MC (\%) = \left(\frac{\text{Initial weight} - \text{Final weight}}{\text{Initial weight}}\right) \times 100 \quad \text{(ISTA 2008)}
\]
For *Ficus racemosa* testing of individual seeds was not feasible because the seeds weighed < 0.0001 g. Therefore, three samples each with 1 g of seeds were tested for seed moisture at 120°C for 3 hours with an electronic moisture balance (MOC-120H, SHIMADZU).

Effect of drying and low temperature storage on seeds with >15% moisture content

Seeds of species with >15% seed moisture were subjected to a drying and a storage experiment. The seed moisture content determined above was used to calculate the weight of the dry seeds plus 10% moisture. Three samples, each consisting of 20 or 25 seeds, were weighed and air dried in open Petri dishes at ambient laboratory conditions (Jayasuriya *et al.* 2013). Samples were reweighed at 1-week intervals until seeds had reached the calculated target weight of the dry seed plus 10% moisture.

When seeds reached the target weight, seeds were subjected to a standard germination test to check whether the seeds germinated (at 2-d intervals for 30 d), after which non-germinated seeds were dissected and the embryos checked for viability with TTC.

For the storage treatment, five replicates each with 25 untreated fresh seeds were stored at 10°C for 2 months in sealed ziplock plastic bags. After the storage period, seeds were placed on filter papers moistened with distilled water and placed in 9 cm diameter Petri dishes and incubated in a germination cabinet in 12 hour light/12 hour dark at 30°C temperature. They were checked for germination at 3-d intervals for 30 d, after which non-germinated seeds had viability determined (as above).

Seed storage of desiccation tolerant species

Eleven species with seed moisture < 15% had fresh, cleaned and dried seeds stored in paper bags at ambient room temperature (27.5 ± 1.3°C) in an airconditioned room from the day of collection. In March 2017, stored seeds were subjected to a germination test. The minimum storage period until March 2017 from initial seed collection day was 6 months for *Diospyros calycantha* and the maximum storage period was 19 months for *Dodonaea platyptera*. Species that required a dormancy treatment had a suitable dormancy breaking treatment applied prior to
the germination test. Incubation was in 12 hour light/12 hour dark at 30°C temperature and germination was checked at 3-d intervals for 30 days.

Statistical analysis

One-way ANOVA was used to assess the significant differences in the final mass increment in the non-treated and scarified/drilled seeds for the imbibition tests. Paired Student’s *t*-tests were used to determine the significant difference in the E:S ratio before and after seed coat split. Generalized Linear Model (GLM) with binomial error structure and logit link function was used to determine the effect of dormancy breaking treatments and the effect of seed storage on seed germination. Quasi-binomial error structure with logit link function was used to account for the small over-dispersion in the data (Zuur and Ieno 2016) when assessing the effect of light and dark on germination. When the final germination proportions were significantly different, Tukey’s *post hoc* test was used for multiple comparisons among treatments (Hothorn *et al.* 2008). All analyses were done using the R statistical platform (R Core Team 2017).

 Results

Study species and their fruit and seed morphology

The fruits of all five climax species were berries, whereas the thirteen pioneer species had a variety of fruit types including berry, capsule, drupe, follicle and syconium (Table 1). The berry type was the most common fruit type, with five pioneer species also having berries.

The climax species had less than seven seeds per fruit. Eight of the pioneer species had less than seven seeds per fruit. *Abrus precatorius* had 10 – 14 seeds per fruit and *Bombax ceiba, Ficus racemosa, Morinda citrifolia* and *Wrightia pubescens* all had more than 100 seeds per fruit (Table 1).

Endosperm was present in seeds of all five climax species but only in two of the thirteen pioneer species, *Strychnos lucida* and *Sterculia quadrifida*. The embryo length to seed length ratio was ≥0.5 for all the species, except *Strychnos lucida* was 0.48 ± 0.01. During incubation, the E:S ratio of *Strychnos lucida* seeds increased and when the seed coat was about to split, the E:S ratio
was 0.52 ± 0.02. However the E:S ratio of incubated and unincubated *Strychnos lucida* seeds didn’t differ significantly (*P* = 0.112), therefore, all the species had a developed embryo and no species had morphological dormancy. Climax species had linear or spatulate embryo types while the pioneer species contained a range of embryo types.

**Viability and germination**

All the species had greater than 77% viability except the climax species *Diospyros cordifolia*, which had 52.0 ± 0.1% viability (Table 2).

Thirteen of the eighteen species achieved greater than 80% germination within 19 days, including four climax species and eight pioneer species. For *Strychnos lucida* radicle emergence occurred quickly but cotyledon emergence occurred three weeks after radicle emergence (Fig. 1). For the rest of the species cotyledon emergence was observed 2-6 days after germination (pers. obs). Thus, only *Strychnos lucida* had epicotyl dormancy.

Four pioneer species, *Abrus precatorius*, *Alphitonia excelsa*, *Dodonaea platyptera* and *Morinda citrifolia*, and one climax species, *Drypetes deplanchei*, achieved less than 50% germination of viable seeds within 30 days (Table 2) and thus were dormant.

**Requirement for light for seed germination**

In the climax group, 92.0 ± 2.3% of *Glycosmis trifoliata* seeds germinated in the light condition whereas only 2.4 ± 1.6% of seeds germinated in complete darkness, a significant difference (*P* < 0.05). Germination of *D. compacta*, *D. cordifolia* and *D. calycantha* seeds in light and dark conditions did not differ significantly (Table 2). Dormant seeds of *Drypetes deplanchei* had minimal germination occur in light and no germination in dark.

In the pioneer group, *Sterculia quadrifida*, *Erythrina variegata*, *Bombax ceiba* and *Micromelum minutum* germinated significantly higher in light compared to dark (*P* < 0.05). More than 70% of *Breynia cernua* and *Opilia amentacea* seeds germinated in the light condition. However, none of their seeds germinated when incubated in darkness. Germination of *Ficus racemosa*, *Strychnos lucida* and *Wrightia pubescens* seeds in light and dark conditions did not differ significantly.
No dormant seeds of *Abrus precatorius* germinated in light or dark. There was minimal germination of dormant seeds of the other dormant species in light and no germination of dormant seeds in dark.

All the dormant species germinated equally in light and dark conditions after applying the optimum dormancy breaking treatments.

**Imbibition test on dormant seeds**

Among the five-dormant species assessed for PY, the non-treated seeds of *Abrus precatorius, Alphitonia excelsa* and *Dodonaea platyptera* increased in weight when imbibed by 0.12 ± 0.03%, 8.5 ± 4.6% and 0.12 ± 0.03 % respectively. Scarification significantly increased their weights following imbibition to 89.7 ± 1.7 %, 86.0 ± 5.6% and 67.9 ± 5.3% respectively (*P* < 0.001) therefore *Abrus precatorius, Alphitonia excelsa* and *Dodonaea platyptera* have PY.

Non-treated seeds of *Morinda citrifolia* increased in weight by 40.3 ± 1.7%, whereas manually scarified seeds increased by 44.1 ± 6.6 %, following imbibition. For *Drypetes deplanchei* non-treated seeds increased by 36.7 ± 7.5% whereas manually scarified seeds increased by 50.8 ± 7.5%. Mass increase following imbibition of the non-treated and manually scarified seeds did not differ significantly for either *Morinda citrifolia* or *Drypetes deplanchei*, therefore neither species had PY.

**Effects of dormancy breaking treatments on germination.**

No intact *Abrus precatorius* seeds germinated. Drilled seeds of *Abrus precatorius* germinated to 100.0 ± 0.0% and hot water treatment at 100°C for 2 min improved the germination to 73.6 ± 7.1%. The germination percentage of hot water treated and drilled seeds did not differ significantly (*P*=0.073) (Fig. 2A). Intact seeds of *Alphitonia excelsa* germinated to 10.4 ± 2.0%, while, the hot water treatment at 92°C for 3 min and manual scarification significantly improved (*P*<0.001) the germination to 93.7 ± 3.9% and 83.2 ± 5.8% respectively. Again, the germination percentage of manually scarified and hot water treated seeds did not differ significantly (*P*=0.226) (Fig. 2B). Non-treated seeds of *Dodonaea platyptera* germinated to 2.4 ±1.6 %. Hot
water treatment at 88°C for 30 seconds and drilling significantly ($P < 0.001$) improved the germination to 83.2 ± 5.8% and 93.7 ± 3.92% respectively. Germination of hot water treated seeds and drilled seeds did not differ significantly ($P = 0.344$) (Fig. 2C).

The 500 ppm GA$_3$ and 1000 ppm GA$_3$ treatments applied to intact *Drypetes deplanchei* seeds germinated to 3.2 ± 0.8% and 4.8 ± 0.8% respectively, which were not significantly different to the control. Manual scarification significantly improved the germination to 64.0 ± 7.0% ($P < 0.001$). Manually scarified seeds treated with either GA$_3$ 500 ppm or GA$_3$ 1000 ppm germinated to 75.2 ± 5.0% and 79.2 ± 4.6% respectively and were significantly higher than the control ($P < 0.001$). However, the germination percentages of manually scarified seeds, or manually scarified seeds treated with either 500 ppm or 1000 ppm GA$_3$ did not differ significantly.

For *Morinda citrifolia* the non-treated, manually scarified and intact seeds incubated in 500 ppm GA$_3$ and 1000 ppm GA$_3$ treatments all had one seed germinate (0.8 ± 0.8%). When manually scarified seeds were incubated in 500 ppm GA$_3$ or in 1000 ppm GA$_3$ germination increased significantly ($P < 0.001$) to 28.0 ± 4.4% and to 56.8 ± 4.3% respectively. The 1000 ppm GA$_3$ significantly improved the germination of manually scarified seeds compared to 500 ppm GA$_3$ ($P < 0.001$) (Fig 2E). Therefore, *Morinda citrifolia* and *Drypetes deplanchei* have PD.

**Seed storage behaviour**

Of the 16-species studied, 11 species had seeds with <15% moisture when collected (Table 3) and therefore tolerate desiccation, including eight pioneer species and three climax species. The other five species which had fresh seed lots with >15% moisture (two climax and three pioneer) lost their viability when stored at 10°C for two months or if dried to 10% moisture (Table 4). Therefore, all of the species which had fresh seed lots with >15% moisture were desiccation sensitive.

When seed germination of the desiccation tolerant species was tested again in March 2017, only two species had a lower proportion of seeds germinate (Table 3). Seeds of the pioneer species *Erythrina variegata* stored for seven months had significantly lower germination compared to non-stored seeds ($P < 0.05$). In the climax group, *Diospyros calycantha* seeds stored for six
months had significantly lower germination compared to non-stored seeds ($P < 0.001$). Germination of the rest of the desiccation tolerant species didn’t differ significantly between stored and non-stored seeds (Table 3).

Discussion

In this seasonal rainforest a high proportion of pioneer species had seeds that were non-dormant (62%), unlike in evergreen rainforest where most pioneer species have dormant seeds (Baskin and Baskin 2014). Swaine and Whitmore (1988) found that pioneer species generally produce dormant seeds and their dormancy break and germination is associated with gap conditions. In evergreen rainforest the canopy remains closed throughout the year and gap conditions stimulate dormancy break and provide light for the survival and growth of the pioneer seedlings (Vazquez-Yanes and Orozco-Segovia, 1982; Pons 2000; Pearson et al. 2003). However, in seasonal rainforest a high proportion of pioneer species produce non-dormant seeds because dormancy is not needed to delay germination until high light conditions. The start of early wet season rains are reliably associated with relatively high light levels (pers. obs). Non-dormant seeds are quiescent during the dry season and then germinate with the first wet season rains when the canopy is relatively open. They then have a long growth season over the moist summer to develop a deep root to acquire moisture from the deep soil during the dry season. Most species are non-dormant and time their dispersal close to the early wet season rain (Garwood 1983). In contrast, in evergreen rainforest, moisture is available throughout the year and gaps with high light levels are infrequent. If pioneer seeds were non-dormant and germinated upon dispersal the emerging seedlings would get shaded by the closed canopy (Picket 1983).

In this seasonal rainforest only 46% of pioneer species had germination increased by light, whereas in evergreen rainforest a high proportion of pioneer species require light or have germination increased by light. For 28 evergreen rainforest pioneer species, Baskin and Baskin (2014) report 68% require light for germination, 11% have significantly higher germination in light, and thus 79% of pioneer species require light or have germination increased by light. Only 21% of species had equal germination in light and dark. In contrast, in seasonal rainforest, of the thirteen-pioneer species in this study, only 46% of species required light or had germination increased by light and 54% (seven of the thirteen species) germinated equally in light and dark.
The germination window of seasonal rainforest species is narrowed to a short wet season when water and nutrients are not limited, but irradiance is reduced by the closed canopy. Therefore, a proportion of dry seasonal rainforest species germinate in the wet season irrespective of the light as a strategy to avoid the drought in the following dry season (Khurana and Singh 2001). Similar to this study, for 19 pioneer species of seasonal dry rainforest, Baskin and Baskin (2014) reported 68% of the species germinate equally in light and dark, whereas only 26% of species have significantly higher germination in light. McLaren and McDonald (2003) studied two dominant pioneer tree species at a dry rainforest in Jamaica and found they also germinated equally in light and shaded conditions.

Desiccation tolerance was common for dry seasonal rainforest climax species. Three of the five climax species studied were desiccation tolerant, and an additional three climax species at the study site were investigated by Russell-Smith (1994) and found to be desiccation tolerant. Russell-Smith (1994) assessed the soil seed bank of three climax species present at the current study site (Aidia racemosa, Antidesma parvifolium and Maranthes corymbosa) and found they had a persistent soil seed bank. Diospyros maritima, another climax species from the study site, had 82% germination after desiccation and freezing (Ben Wirf, George Brown Darwin Botanic Gardens, pers. comm.) indicating it is desiccation tolerant. Thus, seven of the nine climax species at the study site that have been assessed have desiccation tolerant seeds. In evergreen rainforest, published studies indicate 50% or more climax species have desiccation sensitive seeds. Tweddle et al. (2003) reports that 52.2% of 157 evergreen rainforest non-pioneer species are desiccation sensitive, 2.6% are intermediate, and the remaining 45.2% of species are desiccation tolerant. Similarly, a study of eastern Australian evergreen rainforest (Hamilton et al. 2013) reports that of the 41 climax species, 60% were sensitive to desiccation and 40% tolerate desiccation. In evergreen rainforest moisture is available throughout the year. Seeds are less prone to desiccation and seeds can germinate throughout the year. Therefore, a substantial proportion of woody climax species in evergreen rainforest have not adapted to tolerate desiccation. In seasonal rainforest, there is a prolonged dry season, which is variable in duration, seeds of are more likely to be exposed to drying conditions on shedding. For example, in the study site, temperatures remain relatively uniform throughout the year but humidity declines in the dry season, increasing desiccation (Bureau of Meteorology 2018). Thus, seasonal rainforest
species frequently have desiccation tolerant seeds as an adaptation to tolerate drought (Khurana and Singh 2001).

At least four of the five dormancy types identified by Baskin and Baskin (2004) occur in seasonal rainforest species. PY was common in pioneer species of seasonal rainforest whereas a relatively high proportion of evergreen pioneers have PD seeds. Out of five dormant pioneer species in the seasonal rainforest, three species had PY, one species had PD and one species had epicotyl dormancy. In this small sample size, physical dormancy was more common in seasonal rainforest. Similarly, Baskin and Baskin (2014) report that in seasonal deciduous forest elsewhere, 60% species had PY, 39% of species had PD and 1% species had MPD. The impermeable seed coat could prevent germination during isolated showers in the middle of a long dry season and if it is broken during the dry season it would then allow seeds to germinate in the start of the sustained rainy season. Out of 120 evergreen rainforest species in Baskin and Baskin (2014), 3% of species had MD, 8% had PY, 15% of species had MD+PD and 25% of species had PD. PD is common in evergreen rainforest species. A relatively high proportion of species with dormancy in evergreen rainforest occur in the pioneer species guild and their dormancy break is generally associated with gap conditions where high light levels occur. PD is an adaptive trait in evergreen rainforest pioneer species so that they germinate under gap conditions. A study of seasonal rainforest in Panama, which was seasonal but with generally higher rainfall, showed an intermediate trend with similar proportions of PY and PD species. In that study Sautu et al. (2006) report 45 of 94 tree species are dormant: 13 species with PY, 23 species with PD, seven with MD and two species with MPD.

An unusual dormancy type, epicotyl dormancy, occurred in Strychnos lucida and this is the first report of this type of dormancy in this genus. In other species of Strychnos PD is common but epicotyl dormancy has not been reported (Nchanji and Plumptre 2003). Strychnos lucida is found in forest margins where conditions are usually drier than in the interior (Bach 1998). Of the 13 pioneer species studied, it produces the second largest initial leaves after the epicotyls emerge (VT pers. obs). Therefore, leaves will be more prone to desiccation. Having a well-developed root system before leaf growth and transpiration occur could help this species to establish in drier habitats.
Once dormancy is identified, knowledge of the location of dormancy and suitable dormancy breaking treatments is important to enable propagation of species for forest rehabilitation. Without treatment no viable seeds of *Abrus precatorius* and few viable seeds of *Dodonaea platyptera* and *Alphitonia excelsa* germinated, due to physical dormancy. Therefore, manual scarification or hot-water treatments are useful to break PY in these three species. *Morinda citrifolia* and *Drypetes deplanchei* had embryos with lower growth potential, insufficient to overcome the mechanical restraint of the seed coat or endosperm, and have PD. GA₃ application facilitates cell elongation in the embryo and manual scarification may reduce the mechanical restraint on the embryo from the endosperm/seed coat. Some species lack the potential to grow due to inadequate oxygen permeability to the embryo. Scarification of the seed coat can facilitate oxygen flow into physiologically dormant seeds (Baskin and Baskin 2014). Species with dormant seeds are often excluded from rehabilitation plantings due to the lack of information on their propagation techniques. Knowledge on dormancy breaking treatments will help to propagate such species and to ensure they aren’t under-represented when rehabilitating lands.

As seasonally dry rainforest experiences a prolonged drought season, species establishing in this community generally have adaptive physiological traits at seed, seedling and adult stages to tolerate water stress (Khurana and Singh 2001; Vieira and Scariot 2006). At seed level, a high proportion of species produce desiccation tolerant seeds with dormancy or quiescence, but a few species have desiccation sensitive seeds (Khurana and Singh 2001). In our study 68% of species had desiccation tolerant seeds. Desiccation tolerant seeds are dispersed in the dry season. They form a soil seed bank and remain viable during the drought period and germinate in the early wet season rain. In contrast, seeds of species with desiccation sensitive seeds disperse at the beginning or peak of the rainy season and have rapid germination to establish before the upcoming seasonal drought (Garwood 1983; Vieira and Scariot 2006). In our study site, of the 16 species assessed for seed desiccation tolerance, all the dry season dispersers had desiccation tolerant seeds, whereas, all five desiccation sensitive seeds dispersed in the wet season and completed germination within 10 days.

Based on their seed traits, we predict that seasonal dry rainforests species are resilient to future intra- and inter-annual changes in rainfall compared to evergreen rainforest species. Seasonally dry rainforests are adapted to predictable, seasonal drought whereas evergreen rainforests are
adapted to regular moisture throughout the year. Possible effects of climate change on seasonally dry forests include: reduced rainfall during the wet season, multi-year droughts with reduced rainfall, a shorter wet season with rainfall condensed in a shorter duration, and earlier or later starts to the wet season (Allen et al. 2017). Current climate modelling for the wet/dry tropics of the Northern Territory is uncertain about future rainfall patterns, although temperatures are expected to rise (Chevuturi et al. 2018). Already, rainfall during the wet season is highly variable in amount and timing (Drosdowsky 1996), so seasonal rainforest species already experience variation in annual wet season rainfall, multi-year droughts and variation in the start and end of the wet season. Seasonal rainforest species are generally better able to tolerate periods of desiccation compared to evergreen rainforest species because a higher proportion of seasonal dry rainforests species have desiccation tolerant seeds. Germination and seedling establishment of evergreen rainforest species that are desiccation sensitive will be affected if climate change causes drought periods. Non-dormant, desiccation sensitive seeds germinate rapidly when rainfall occurs, and their seedlings would be killed by periods of drought. Dormancy is frequent in seasonal rainforest species and would prevent seedlings germinating if there is an increase in dry season rains that are potentially unfavourable for seedling establishment (Khurana and Singh 2001). Desiccation sensitive seeds of seasonally dry rainforest species, which are dispersed well into the wet season would not be affected unless the wet season shifts markedly, which seems unlikely. Thus, the potential of seasonal rainforest species to adapt to intra and inter annual changes in rainfall and drought stress is high compared to evergreen rainforest species.

Generalizations made about the seed biology of pioneer species by Swaine and Whitmore (1988), which apply to evergreen tropical rainforest species, don’t necessarily apply to seasonal rainforest species. General seed traits of pioneer species of evergreen rainforest are that they produce dormant seeds that are desiccation tolerant and most species have germination increased by light (Baskin and Baskin 2014). However, in seasonal rainforest a high proportion of pioneer species were non-dormant and half of the species germinated equally well in light and dark conditions. Thus many pioneer species in seasonal rainforest have similar seed biology traits to those of evergreen rainforest climax species, which tend to be non-dormant, desiccation sensitive and germinate equally well in light and dark conditions. In evergreen rainforest the most limiting resource is light and early successional pioneer species have adapted to high light conditions, whereas late successional climax species have adapted to germinate in moist low light
conditions. However, in seasonal rainforest, moisture and light are both major limiting factors (Khurana and Singh 2001). The effects of light on germination are less defined, as high light conditions occur at the start of the wet season before the deciduous canopy closes. For all species, seed germination early in the rainy season may be advantageous as nutrients are released (Garwood 1979) and it allows a long first growing season prior to seasonal drought. Thus, many early successional and late successional species have seeds dispersed in the dry season that germinate during the early wet season irrespective of the light conditions. Therefore, we consider the pioneer and climax classification described by Swaine and Whitmore (1988) based on the effects of light on germination is not appropriate for seasonal rainforest species.

**Acknowledgements**

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**Conflicts of Interest:** The authors declare no conflicts of interest.

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Tiansawat P, Beckman NG, Dalling JW (2017) Pre-dispersal seed predators and fungi differ in their effect on Luehea seemannii capsule development, seed germination, and dormancy across two Panamanian forests. *Biotropica* 49, 871-880.


Table 1. **Ecological and reproductive attributes of study species.** Successional stage details provided by Russell-Smith (pers. comm.). Embryo type (Baskin and Baskin 2007). na – not applicable

<table>
<thead>
<tr>
<th>Species</th>
<th>Lifeform</th>
<th>Fruit type</th>
<th>Seed collection month</th>
<th>No of seeds per fruit</th>
<th>Embryo type</th>
<th>Embryo length: Seed length ratio (E:S) (mean ± SEM)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Climax species</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diospyros calycantha O.Schwarz</td>
<td>Tree</td>
<td>Berry</td>
<td>Sep 2016</td>
<td>5-7</td>
<td>0.65 ± 0.01</td>
<td>Spatulate</td>
</tr>
<tr>
<td>Diospyros compacta (R.Br.) Kosterm.</td>
<td>Tree</td>
<td>Berry</td>
<td>Feb 2016</td>
<td>4-6</td>
<td>0.75 ± 0.01</td>
<td>Spatulate</td>
</tr>
<tr>
<td>Diospyros cordifolia Roxb.</td>
<td>Tree/Shrub</td>
<td>Berry</td>
<td>Jun 2016</td>
<td>4-6</td>
<td>0.61 ± 0.12</td>
<td>Spatulate</td>
</tr>
<tr>
<td>Drypetes deplanchei (Brongn. &amp; Gris) Merr.</td>
<td>Tree</td>
<td>Berry</td>
<td>Feb 2016</td>
<td>1</td>
<td>0.62 ± 0.37</td>
<td>Linear</td>
</tr>
<tr>
<td>Glycosmis trifoliata (Blume) Spreng.</td>
<td>Shrub</td>
<td>Berry</td>
<td>Nov 2016</td>
<td>1-3</td>
<td>0.56 ± 0.01</td>
<td>Linear</td>
</tr>
<tr>
<td><strong>Pioneer species</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Abrus precatorius L.</td>
<td>Vine</td>
<td>Follicle</td>
<td>Aug 2015</td>
<td>10-14</td>
<td>na</td>
<td>Investing</td>
</tr>
<tr>
<td>Alphitonia excelsa (A.Cunn.ex Fenzl) Benth.</td>
<td>Tree</td>
<td>Drupe</td>
<td>Aug 2015</td>
<td>4-5</td>
<td>na</td>
<td>Investing</td>
</tr>
<tr>
<td>Bombax ceiba L.</td>
<td>Tree</td>
<td>Capsule</td>
<td>Oct 2015</td>
<td>&gt;100</td>
<td>na</td>
<td>Folded</td>
</tr>
<tr>
<td>Breynia cernua (Poir.) Mull.Arg.</td>
<td>Shrub</td>
<td>Berry</td>
<td>Nov 2015</td>
<td>5-6</td>
<td>na</td>
<td>Investing</td>
</tr>
<tr>
<td>Dodonaea platyptera F.Muell.</td>
<td>Shrub</td>
<td>Capsule</td>
<td>Aug 2015</td>
<td>1</td>
<td>na</td>
<td>Folded</td>
</tr>
<tr>
<td>Erythrina variegata L.</td>
<td>Shrub</td>
<td>Legume</td>
<td>Aug 2016</td>
<td>1-2</td>
<td>na</td>
<td>Investing</td>
</tr>
<tr>
<td>Ficus racemosa L.</td>
<td>Tree</td>
<td>Syconium</td>
<td>Feb 2016</td>
<td>&gt;100</td>
<td>na</td>
<td>Investing</td>
</tr>
<tr>
<td>Micromelum minutum (G.Forst.) Wight &amp; Arn.</td>
<td>Shrub</td>
<td>Berry</td>
<td>Dec 2015</td>
<td>1</td>
<td>na</td>
<td>Folded</td>
</tr>
<tr>
<td>Morinda citrifolia L.</td>
<td>Tree</td>
<td>Berry</td>
<td>Feb 2016</td>
<td>&gt;40</td>
<td>na</td>
<td>Investing</td>
</tr>
<tr>
<td>Opilia amentacea Roxb.</td>
<td>Vine</td>
<td>Berry</td>
<td>Dec 2015 - Jan 2016</td>
<td>1</td>
<td>0.95 ± 0.01</td>
<td>Linear</td>
</tr>
<tr>
<td>Sterculia quadrifida R.Br.</td>
<td>Tree</td>
<td>Follicle</td>
<td>Oct - Nov 2015</td>
<td>5-6</td>
<td>0.99 ± 0.01</td>
<td>Linear</td>
</tr>
<tr>
<td>Strychnos lucida R.Br.</td>
<td>Tree</td>
<td>Berry</td>
<td>Aug 2015</td>
<td>2-4</td>
<td>0.48 ± 0.01</td>
<td>Spatulate</td>
</tr>
<tr>
<td>Wrightia pubescens R.Br.</td>
<td>Shrub</td>
<td>Follicle</td>
<td>Aug 2015</td>
<td>&gt;100</td>
<td>na</td>
<td>Folded</td>
</tr>
</tbody>
</table>
Table 2. Viability, germination and dormancy status of the climax and pioneer species (mean ± SEM). Different lower case letters above data indicate significant differences between light and dark treatments for a species (GLM P< 0.05). Final germination was the mean length of days to complete germination in 12hr light/12 hr dark treatment. Values in square brackets are germination of species with dormancy in light and dark after application of the best dormancy breaking treatment.

<table>
<thead>
<tr>
<th>Species name</th>
<th>Viability (%)</th>
<th>Germination (%)</th>
<th>Germination (%)</th>
<th>Final germination (days)</th>
<th>Dormant</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(12hr light/dark)</td>
<td>(Darkness)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diospyros calycantha</td>
<td>94.7 ± 5.3</td>
<td>96.8 ± 3.2 a</td>
<td>96.0 ± 2.5 a</td>
<td>14 ± 1</td>
<td>No</td>
</tr>
<tr>
<td>Diospyros compacta</td>
<td>98.0 ± 1.3</td>
<td>96.0 ± 3.1 a</td>
<td>92.0 ± 1.3 a</td>
<td>9 ± 1</td>
<td>No</td>
</tr>
<tr>
<td>Diospyros cordifolia</td>
<td>52.0 ± 0.1</td>
<td>55.2 ± 6.4 a</td>
<td>55.2 ± 6.4 a</td>
<td>12 ± 1</td>
<td>No</td>
</tr>
<tr>
<td>Drypetes deplanchei</td>
<td>88.0 ± 6.1</td>
<td>0.8 ± 0.8</td>
<td>0.0 ± 0.0</td>
<td>-</td>
<td>Yes</td>
</tr>
<tr>
<td>Glycosmis trifoliata</td>
<td>94.7 ± 5.0</td>
<td>92.0 ± 2.3 a</td>
<td>2.4 ± 1.6 b</td>
<td>5 ± 0</td>
<td>No</td>
</tr>
<tr>
<td>Abrus precatorius</td>
<td>84.0 ± 3.5</td>
<td>0.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
<td>-</td>
<td>Yes</td>
</tr>
<tr>
<td>Alphitonia excelsa</td>
<td>94.7 ± 2.7</td>
<td>10.4 ± 2.0</td>
<td>0.0 ± 0.0</td>
<td>26 ± 1</td>
<td>Yes</td>
</tr>
<tr>
<td>Bombax ceiba</td>
<td>88.0 ± 2.3</td>
<td>92.0 ± 4.0 a</td>
<td>78.4 ± 1.0 b</td>
<td>12 ± 2</td>
<td>No</td>
</tr>
<tr>
<td>Breynia cernua</td>
<td>93.3 ± 6.1</td>
<td>85.6 ± 5.2 a</td>
<td>0.0 ± 0.0 b</td>
<td>15 ± 0</td>
<td>No</td>
</tr>
<tr>
<td>Dodonaea platyptera</td>
<td>94.7 ± 3.7</td>
<td>2.4 ± 1.6 a</td>
<td>0.0 ± 0.0 a</td>
<td>9 ± 6</td>
<td>Yes</td>
</tr>
<tr>
<td>Erythrina variegata</td>
<td>93.3 ± 1.3</td>
<td>94.4 ± 2.7 a</td>
<td>68.8 ± 2.9 b</td>
<td>13 ± 1</td>
<td>No</td>
</tr>
<tr>
<td>Ficus racemosa</td>
<td>77.3 ± 8.3</td>
<td>81.6 ± 5.3 a</td>
<td>78.4 ± 2.7 a</td>
<td>19 ± 1</td>
<td>No</td>
</tr>
<tr>
<td>Micromelum minutum</td>
<td>96.0 ± 2.3</td>
<td>100.0 ± 0.0 a</td>
<td>57.6 ± 10.1 b</td>
<td>6 ± 0</td>
<td>No</td>
</tr>
<tr>
<td>Morinda citrifolia</td>
<td>85.3 ± 3.5</td>
<td>0.8 ± 0.8 a</td>
<td>0.0 ± 0.0 a</td>
<td>26 ± 1</td>
<td>Yes</td>
</tr>
<tr>
<td>Opilia amentacea</td>
<td>77.3 ± 7.4</td>
<td>70.4 ± 3.7 a</td>
<td>0.0 ± 0.0 b</td>
<td>9 ± 1</td>
<td>No</td>
</tr>
<tr>
<td>Strychnos lucida</td>
<td>96.0 ± 2.3</td>
<td>99.2 ± 0.2 a</td>
<td>90.2 ± 0.5 a</td>
<td>17 ± 0</td>
<td>Yes</td>
</tr>
<tr>
<td>Wrightia pubescens</td>
<td>93.3 ± 3.5</td>
<td>94.4 ± 2.0 a</td>
<td>93.6 ± 0.7 a</td>
<td>8 ± 1</td>
<td>No</td>
</tr>
</tbody>
</table>
Table 3. Seed moisture content, germination (after treatment of dormancy if required) and seed longevity of species with moisture content < 15% (mean ± SEM). Different lower case above the germination data indicate significant differences in germination between stored and non-stored seeds.

<table>
<thead>
<tr>
<th>Species</th>
<th>Moisture content (%)</th>
<th>Germination (%) of fresh seeds</th>
<th>Germination (%) March (2017) after storage</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abrus precatorius</td>
<td>8.3 ± 0.2</td>
<td>73.6 ± 7.1&lt;sup&gt;a&lt;/sup&gt;</td>
<td>69.6 ± 7.1&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Alphitonia excelsa</td>
<td>7.6 ± 0.3</td>
<td>93.7 ± 3.9&lt;sup&gt;a&lt;/sup&gt;</td>
<td>95.2 ± 3.8&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Diopsys cordifolia</td>
<td>11.3 ± 0.5</td>
<td>55.2 ± 6.4&lt;sup&gt;a&lt;/sup&gt;</td>
<td>53.6 ± 4.1&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Diospyros calycantha</td>
<td>10.2 ± 0.7</td>
<td>96.8 ± 3.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>74.4 ± 4.2&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Dodonaea platyptera</td>
<td>6.8 ± 0.2</td>
<td>68.8 ± 6.8&lt;sup&gt;a&lt;/sup&gt;</td>
<td>72.8 ± 7.3&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Drypetes deplanchei</td>
<td>12.1 ± 2.1</td>
<td>64.0 ± 7.0&lt;sup&gt;a&lt;/sup&gt;</td>
<td>64.8 ± 10.6&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Erythrina variegata</td>
<td>5.6 ± 0.3</td>
<td>94.4 ± 2.7&lt;sup&gt;a&lt;/sup&gt;</td>
<td>62.4 ± 2.8&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Ficus racemosa</td>
<td>12.6 ± 0.3</td>
<td>81.6 ± 5.3&lt;sup&gt;a&lt;/sup&gt;</td>
<td>87.6 ± 1.6&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Morinda citrifolia</td>
<td>7.1 ± 0.3</td>
<td>56.8 ± 4.3&lt;sup&gt;a&lt;/sup&gt;</td>
<td>56.8 ± 4.3&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Strychnos lucida</td>
<td>7.1 ± 0.5</td>
<td>98.4 ± 1.0&lt;sup&gt;a&lt;/sup&gt;</td>
<td>84.0 ± 1.8&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Wrightia pubescens</td>
<td>8.2 ± 3.2</td>
<td>94.4 ± 2.0&lt;sup&gt;a&lt;/sup&gt;</td>
<td>88.8 ± 2.3&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
</tbody>
</table>
Table 4. Seed moisture content, germination (after treatment of dormancy if required) and germination of species with a moisture content of greater than 15% (mean ± SEM).

<table>
<thead>
<tr>
<th>Species</th>
<th>Moisture content (%)</th>
<th>Germination of treated fresh seeds (%)</th>
<th>Germination after storage at 10°C for 2 months (%)</th>
<th>Germination after desiccation to 10% moisture (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diospyros compacta</td>
<td>19.1 ± 0.3</td>
<td>96.0 ± 3.1</td>
<td>0.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
</tr>
<tr>
<td>Glycosmis trifoliata</td>
<td>53.2 ± 1.0</td>
<td>92.0 ± 2.3</td>
<td>0.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
</tr>
<tr>
<td>Micromelum minutum</td>
<td>40.7 ± 0.7</td>
<td>100.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
</tr>
<tr>
<td>Opilia amentacea</td>
<td>54.3 ± 0.2</td>
<td>70.4 ± 3.7</td>
<td>0.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
</tr>
<tr>
<td>Sterculia quadrifida</td>
<td>28.4 ± 1.1</td>
<td>96.0 ± 1.3</td>
<td>0.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
</tr>
</tbody>
</table>
Fig. 1. Number of days until *Strychnos lucida* radicle and cotyledon emergence (mean ± SEM).
Fig. 2. Effects of dormancy breaking treatments on germination (mean ± SEM). (A); Abrus precatorius, (B) Alphitonia excelsa, (C); Dodonaea platyptera, (D); Drypetes deplanchei, (E); Morinda citrifolia. Different lowercase letters above columns indicate significant differences between treatments (Tuckey post hoc, p< 0.05). NT - no treatment; MS - manual scarification; DR - scarified by drilling; HW (hot water treatments) HW in (A) - 98 °C for 2 min, HW in (B) - 92 °C for 3 min, HW in (C) - 88 °C for 30 sec; GA₃500 - Gibberellic acid 500 ppm; GA₃1000 - Gibberellic acid 1000 ppm.