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

3
4 Running title: Seed biology of coastal rainforest species in the NT.

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12
13 **Abstract.** Seed germination traits of seasonal rainforest species differ from permanently moist
14 evergreen rainforest species due to the prolonged seasonal drought. We investigated whether
15 seed germination traits used to categorize evergreen rainforest species into pioneer and climax
16 guilds were applicable to seasonal rainforest species. Seed dormancy, light requirements for
17 germination and seed storage types of five climax and thirteen pioneer species of a coastal vine
18 thicket were studied. Results were compared to published studies of evergreen rainforest species.
19 Evergreen rainforest pioneer species are typically dormant, require light to germinate and
20 tolerate desiccation, whereas climax species are typically non-dormant, tolerate shade during
21 germination and are sensitive to desiccation. In seasonal rainforest we found that a high
22 proportion of pioneer species had seeds that were non-dormant (62%), and a high proportion of
23 pioneer species germinated equally well in light and dark conditions. In seasonal rainforest, we
24 found that the majority of climax species had desiccation tolerant seeds, whereas in evergreen
25 rainforest the proportion of climax species producing desiccation sensitive seeds is equal to or
26 greater than the proportion of species with desiccation tolerant seeds. In seasonal rainforest
27 species physical, physiological and epicotyl dormancy types were found. Generally, for seasonal
28 rainforest species, the prevalent form of dormancy in pioneer species was physical dormancy
29 whereas physiological dormancy was most common in evergreen rainforest pioneer species with
30 dormancy. Our results suggest that the contrasting seed biology traits that typically apply to
31 pioneer and climax species of evergreen rainforest species don't typically apply to seasonal
32 rainforest species.

33 **Additional keywords:** Pioneer, climax, seed dormancy, seed storage, seasonal rainforest,
34 evergreen rainforest

36

37 **Introduction**

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

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

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

63

64 Seeds of most species tolerate desiccation in seasonal rainforest, whereas a higher proportion of
65 species tend to be desiccation sensitive in evergreen rainforest (Daws *et al.* 2005; Tweddle *et al.*

66 2003). Desiccation sensitive seeds, which are dispersed with greater than >15% moisture, are
67 killed when moisture drops to 10-15% of the seed total fresh mass (Hong and Ellis 1996). Thus,
68 they are susceptible to mortality due to water stress. In contrast, desiccation tolerant seeds
69 tolerate seed moisture content falling to 10-15% and can be viable even when the moisture drops
70 to 5% or below (Hong and Ellis 1996). Woody taxa which tolerate desiccation are frequent in the
71 seasonal rainforest habitats (Khurana and Singh 2001; Tweddle *et al.* 2003; Galindo-Rodriguez
72 and Roa-Fuentes 2017). Woody species which produce desiccation sensitive seeds are common
73 in moist, evergreen rainforest, but are infrequent in seasonal rainforest. In their study of 225
74 species from a seasonal rainforest in Panama, Daws *et al.* (2005) found that 189 species are
75 desiccation tolerant and only 36 species have desiccation sensitive seeds. In a comparative
76 analysis of 886 trees and shrubs, Tweddle *et al.* (2003) reported that > 45% of species from
77 evergreen rainforest are desiccation sensitive, whereas in seasonal rainforest < 25% of species
78 are desiccation sensitive. However, Wyse and Dickie (2017) indicated that the proportion of
79 desiccation sensitive species in evergreen rainforest drops to 18.5% when herbaceous species are
80 included.

81
82 Seed dormancy occurs in about half of evergreen rainforest species (53% of 2563 species
83 (Baskin and Baskin 2014)), whereas a greater proportion of species in seasonal rainforest
84 produce dormant seeds. According to Baskin and Baskin (2014), a species is dormant if $\geq 50\%$
85 of viable seeds take more than one month to germinate. From their compiled data set on seed
86 dormancy of seasonal rainforest species, Baskin and Baskin (2014) report that 66% of the 221
87 seasonal rainforest species have dormant seeds. Dormancy is primarily found in species which
88 disperse seeds in the dry season. This is to prevent germination during the infrequent early dry
89 season rains which are unfavourable for seedling establishment and survival (Khurana and Singh
90 2001).

91
92 Light is an important abiotic factor affecting seed germination and establishment of rainforest
93 species. Seeds of some rainforest species require light to germinate and their germination and
94 establishment are associated with forest gaps (Swaine and Whitmore 1988). Gap creation causes
95 an increase in irradiance and in the R:FR ratio (Lee 1987; Vazquez-Yanes *et al.* 1990; Orozco-
96 Segovia *et al.* 1993). Often gap dependent species have seed dormancy that is broken by gap

97 conditions. An increase in irradiance causes an increase in temperature and in the magnitude of
98 temperature fluctuations at the soil surface (Vazquez-Yanes and Orozco-Segovia, 1982). These
99 changes can break seed dormancy of gap-demanding species, allowing them to germinate
100 (Vazquez-Yanes and Orozco-Segovia, 1982; Pons 2000; Pearson *et al.* 2003).

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

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

121 In the Northern Territory of Australia, little is known about the seed biology of species that
122 dominate seasonally dry rainforest. Bach (1998) studied the phenology, germination rate and the
123 effect of pulp removal on the emergence of seedlings of eight dry seasonal rainforest species in
124 the Northern Territory. She categorized the species as dormant if they did not germinate within
125 six months. Baskin and Baskin (2014) class rainforest species as dormant if $\geq 50\%$ of viable
126 seeds take more than 30 days to germinate, so some species Bach (1998) categorised as non-

127 dormant may be dormant according to this classification. Russell-Smith (1991) scored the NT
128 rainforest taxa as dormant if seeds retained viability in dry storage for at least six months,
129 approximately the duration of the regional annual dry season. However, many non-dormant
130 species that tolerate desiccation can remain viable and quiescent for six months. Thus, there is a
131 clear need to understand the presence of dormancy in seeds of seasonally dry rainforest species
132 based on the globally accepted dormancy classification system by Baskin and Baskin (2004;
133 2014). There are also knowledge gaps for seed storage behaviour, light requirements and suitable
134 dormancy breaking treatments for seasonally dry rainforest species.

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

141

142 **Materials and methods**

143 *Seed material*

144 Mature seeds/fruits of 18 native species were collected from at least ten adult plants per species
145 from coastal vine forest in East Point Reserve, Darwin, Northern Territory (12°24'39" S,
146 130°49'26" E). Seeds of nine species were collected between June and October during the dry
147 season and another nine species were collected between November-March during the wet season
148 (Table 1).

149 Fruits were checked fortnightly and were collected when they started to disperse. Seed/fruit
150 morphology was assessed based on the presence or absence of: a fleshy or dry pericarp, grooves
151 for dehiscence, stony mesocarp and hesperidium. The fruit type of each species was determined
152 (Harris and Harris 2001). The number of seeds per fruit in at least 30 fruits were counted. Seeds
153 were dissected to classify the embryo type based on Baskin and Baskin (2007). Studied species
154 were classified as climax or pioneer by Jeremy Russell-Smith (pers.comm.) on the basis of
155 unpublished field observations as to whether seedlings of the species established under a closed

156 canopy. Germination, imbibition, dormancy breaking treatments and assessment of seed storage
157 behaviour were started within one week of seed collection. Seed fresh weight was assessed
158 within three days of collection.

159

160 *Seed viability*

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

170

171 *Seed germination and dormancy*

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

184
$$MTG = \sum(nd)/N$$

185

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

189

190 *Effect of light on seed germination*

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

198

199 *Seed imbibition and physical dormancy*

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

$$I\% = \frac{(\text{Final weight of the seeds after imbibition} - \text{Initial weight of the seeds}) \times 100}{\text{Initial weight of the seeds}}$$

211

212 If a significant increase in percent imbibition of treated seeds compared to untreated seeds
213 occurred PY was present (Baskin *et al.* 2006).

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

222

223 *Physiological dormancy (PD)*

224 *Morinda citrifolia* and *Drypetes deplanchei*, which did not have all viable seeds germinate
225 following scarification, were tested for PD. Five Petri dishes, each with twenty five seeds, were
226 subjected to each of the following treatments: incubation of intact seeds on 5 ml of 500 ppm GA₃
227 (Sigma-Aldrich, Sydney, Australia) soaked filter paper; similarly on 1000 ppm GA₃ soaked
228 filter paper; incubation of manually scarified seeds on 5 ml of 500 ppm GA₃ filter paper;
229 manually scarified seeds on 1000 ppm GA₃ soaked filter paper; and manual scarification of the
230 seed coat without GA₃.

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

234

235 *Morphological dormancy (MD)*

236 Species that were not PY, and had endosperm, had seeds assessed for an underdeveloped or
237 undifferentiated embryo, as indicated by the embryo not being differentiated into an embryonic

238 plumular-radicular axis and cotyledons (Baskin and Baskin 2014). Under-developed embryos
239 were assessed by measuring the embryo-length (E):seed-length (S) ratio.

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

249

250 *Epicotyl dormancy (eD)*

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

256

257 *Seed moisture content*

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

265 $MC (\%) = ([\text{Initial weight} - \text{Final weight}] / \text{Initial weight}) \times 100$ (ISTA 2008).

266 For *Ficus racemosa* testing of individual seeds was not feasible because the seeds weighed <
267 0.0001 g. Therefore, three samples each with 1 g of seeds were tested for seed moisture at 120°C
268 for 3 hours with an electronic moisture balance (MOC-120H, SHIMADZU).

269

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

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

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

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

286

287 *Seed storage of desiccation tolerant species*

288 Eleven species with seed moisture < 15% had fresh, cleaned and dried seeds stored in paper bags
289 at ambient room temperature ($27.5 \pm 1.3^\circ\text{C}$) in an airconditioned room from the day of
290 collection. In March 2017, stored seeds were subjected to a germination test. The minimum
291 storage period until March 2017 from initial seed collection day was 6 months for *Diospyros*
292 *calycantha* and the maximum storage period was 19 months for *Dodonaea platyptera*. Species
293 that required a dormancy treatment had a suitable dormancy breaking treatment applied prior to

294 the germination test. Incubation was in 12 hour light/12 hour dark at 30°C temperature and
295 germination was checked at 3-d intervals for 30 days.

296

297 *Statistical analysis*

298 One-way ANOVA was used to assess the significant differences in the final mass increment in
299 the non-treated and scarified/drilled seeds for the imbibition tests. Paired Student's *t*-tests were
300 used to determine the significant difference in the E:S ratio before and after seed coat split.
301 Generalized Linear Model (GLM) with binomial error structure and logit link function was used
302 to determine the effect of dormancy breaking treatments and the effect of seed storage on seed
303 germination. Quasi-binomial error structure with logit link function was used to account for the
304 small over-dispersion in the data (Zuur and Ieno 2016) when assessing the effect of light and
305 dark on germination. When the final germination proportions were significantly different,
306 Tukey's *post hoc* test was used for multiple comparisons among treatments (Hothorn *et al.*
307 2008). All analyses were done using the R statistical platform (R Core Team 2017).

308

309 **Results**

310 *Study species and their fruit and seed morphology*

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

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

318 Endosperm was present in seeds of all five climax species but only in two of the thirteen pioneer
319 species, *Strychnos lucida* and *Sterculia quadrifida*. The embryo length to seed length ratio was
320 ≥ 0.5 for all the species, except *Strychnos lucida* was 0.48 ± 0.01 . During incubation, the E:S
321 ratio of *Strychnos lucida* seeds increased and when the seed coat was about to split, the E:S ratio

322 was 0.52 ± 0.02 . However the E:S ratio of incubated and unincubated *Strychnos lucida* seeds
323 didn't differ significantly ($P = 0.112$), therefore, all the species had a developed embryo and no
324 species had morphological dormancy. Climax species had linear or spatulate embryo types while
325 the pioneer species contained a range of embryo types.

326

327 *Viability and germination*

328 All the species had greater than 77% viability except the climax species *Diospyros cordifolia*,
329 which had $52.0 \pm 0.1\%$ viability (Table 2).

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

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

338

339 *Requirement for light for seed germination*

340 In the climax group, $92.0 \pm 2.3\%$ of *Glycosmis trifoliata* seeds germinated in the light condition
341 whereas only $2.4 \pm 1.6\%$ of seeds germinated in complete darkness, a significant difference ($P <$
342 0.05). Germination of *D. compacta*, *D. cordifolia* and *D. calycantha* seeds in light and dark
343 conditions did not differ significantly (Table 2). Dormant seeds of *Drypetes deplanchei* had
344 minimal germination occur in light and no germination in dark.

345 In the pioneer group, *Sterculia quadrifida*, *Erythrina variegata*, *Bombax ceiba* and *Micromelum*
346 *minutum* germinated significantly higher in light compared to dark ($P < 0.05$). More than 70% of
347 *Breynia cernua* and *Opilia amentacea* seeds germinated in the light condition. However, none of
348 their seeds germinated when incubated in darkness. Germination of *Ficus racemosa*, *Strychnos*
349 *lucida* and *Wrightia pubescens* seeds in light and dark conditions did not differ significantly.

350 No dormant seeds of *Abrus precatorius* germinated in light or dark. There was minimal
351 germination of dormant seeds of the other dormant species in light and no germination of
352 dormant seeds in dark.

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

355

356 *Imbibition test on dormant seeds*

357 Among the five-dormant species assessed for PY, the non-treated seeds of *Abrus precatorius*,
358 *Alphitonia excelsa* and *Dodonaea platyptera* increased in weight when imbibed by $0.12 \pm 0.03\%$,
359 $8.5 \pm 4.6\%$ and $0.12 \pm 0.03\%$ respectively. Scarification significantly increased their weights
360 following imbibition to $89.7 \pm 1.7\%$, $86.0 \pm 5.6\%$ and $67.9 \pm 5.3\%$ respectively ($P < 0.001$)
361 therefore *Abrus precatorius*, *Alphitonia excelsa* and *Dodonaea platyptera* have PY.

362 Non-treated seeds of *Morinda citrifolia* increased in weight by $40.3 \pm 1.7\%$, whereas manually
363 scarified seeds increased by $44.1 \pm 6.6\%$, following imbibition. For *Drypetes deplanchei* non-
364 treated seeds increased by $36.7 \pm 7.5\%$ whereas manually scarified seeds increased by $50.8 \pm$
365 7.5% . Mass increase following imbibition of the non-treated and manually scarified seeds did not
366 differ significantly for either *Morinda citrifolia* or *Drypetes deplanchei*, therefore neither species
367 had PY.

368

369 *Effects of dormancy breaking treatments on germination.*

370 No intact *Abrus precatorius* seeds germinated. Drilled seeds of *Abrus precatorius* germinated to
371 $100.0 \pm 0.0\%$ and hot water treatment at 100°C for 2 min improved the germination to $73.6 \pm$
372 7.1% . The germination percentage of hot water treated and drilled seeds did not differ
373 significantly ($P=0.073$) (Fig. 2A). Intact seeds of *Alphitonia excelsa* germinated to $10.4 \pm 2.0\%$,
374 while, the hot water treatment at 92°C for 3 min and manual scarification significantly improved
375 ($P<0.001$) the germination to $93.7 \pm 3.9\%$ and $83.2 \pm 5.8\%$ respectively. Again, the germination
376 percentage of manually scarified and hot water treated seeds did not differ significantly
377 ($P=0.226$) (Fig. 2B). Non-treated seeds of *Dodonaea platyptera* germinated to $2.4 \pm 1.6\%$. Hot

378 water treatment at 88°C for 30 seconds and drilling significantly ($P < 0.001$) improved the
379 germination to $83.2 \pm 5.8\%$ and $93.7 \pm 3.92\%$ respectively. Germination of hot water treated
380 seeds and drilled seeds did not differ significantly ($P = 0.344$) (Fig. 2C).

381 The 500 ppm GA₃ and 1000 ppm GA₃ treatments applied to intact *Drypetes deplanchei* seeds
382 germinated to $3.2 \pm 0.8\%$ and $4.8 \pm 0.8\%$ respectively, which were not significantly different to
383 the control. Manual scarification significantly improved the germination to $64.0 \pm 7.0\%$ (P
384 < 0.001). Manually scarified seeds treated with either GA₃ 500 ppm or GA₃ 1000 ppm
385 germinated to $75.2 \pm 5.0\%$ and $79.2 \pm 4.6\%$ respectively and were significantly higher than the
386 control ($P < 0.001$). However, the germination percentages of manually scarified seeds, or
387 manually scarified seeds treated with either 500 ppm or 1000 ppm GA₃ did not differ
388 significantly.

389 For *Morinda citrifolia* the non-treated, manually scarified and intact seeds incubated in 500 ppm
390 GA₃ and 1000 ppm GA₃ treatments all had one seed germinate ($0.8 \pm 0.8\%$). When manually
391 scarified seeds were incubated in 500 ppm GA₃ or in 1000 ppm GA₃ germination increased
392 significantly ($P < 0.001$) to $28.0 \pm 4.4\%$ and to $56.8 \pm 4.3\%$ respectively. The 1000 ppm GA₃
393 significantly improved the germination of manually scarified seeds compared to 500 ppm GA₃ (P
394 < 0.001) (Fig 2E). Therefore, *Morinda citrifolia* and *Drypetes deplanchei* have PD.

395

396 *Seed storage behaviour*

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

403 When seed germination of the desiccation tolerant species was tested again in March 2017, only
404 two species had a lower proportion of seeds germinate (Table 3). Seeds of the pioneer species
405 *Erythrina variegata* stored for seven months had significantly lower germination compared to
406 non-stored seeds ($P < 0.05$). In the climax group, *Diospyros calycantha* seeds stored for six

407 months had significantly lower germination compared to non-stored seeds ($P < 0.001$).
408 Germination of the rest of the desiccation tolerant species didn't differ significantly between
409 stored and non-stored seeds (Table 3).

410

411 **Discussion**

412 In this seasonal rainforest a high proportion of pioneer species had seeds that were non-dormant
413 (62%), unlike in evergreen rainforest where most pioneer species have dormant seeds (Baskin
414 and Baskin 2014). Swaine and Whitmore (1988) found that pioneer species generally produce
415 dormant seeds and their dormancy break and germination is associated with gap conditions. In
416 evergreen rainforest the canopy remains closed throughout the year and gap conditions stimulate
417 dormancy break and provide light for the survival and growth of the pioneer seedlings (Vazquez-
418 Yanes and Orozco-Segovia, 1982; Pons 2000; Pearson *et al.* 2003). However, in seasonal
419 rainforest a high proportion of pioneer species produce non-dormant seeds because dormancy is
420 not needed to delay germination until high light conditions. The start of early wet season rains
421 are reliably associated with relatively high light levels (pers. obs). Non-dormant seeds are
422 quiescent during the dry season and then germinate with the first wet season rains when the
423 canopy is relatively open. They then have a long growth season over the moist summer to
424 develop a deep root to acquire moisture from the deep soil during the dry season. Most species
425 are non-dormant and time their dispersal close to the early wet season rain (Garwood 1983). In
426 contrast, in evergreen rainforest, moisture is available throughout the year and gaps with high
427 light levels are infrequent. If pioneer seeds were non-dormant and germinated upon dispersal the
428 emerging seedlings would get shaded by the closed canopy (Pickett 1983).

429 In this seasonal rainforest only 46% of pioneer species had germination increased by light,
430 whereas in evergreen rainforest a high proportion of pioneer species require light or have
431 germination increased by light. For 28 evergreen rainforest pioneer species, Baskin and Baskin
432 (2014) report 68% require light for germination, 11% have significantly higher germination in
433 light, and thus 79% of pioneer species require light or have germination increased by light. Only
434 21% of species had equal germination in light and dark. In contrast, in seasonal rainforest, of the
435 thirteen-pioneer species in this study, only 46% of species required light or had germination
436 increased by light and 54% (seven of the thirteen species) germinated equally in light and dark.

437 The germination window of seasonal rainforest species is narrowed to a short wet season when
438 water and nutrients are not limited, but irradiance is reduced by the closed canopy. Therefore, a
439 proportion of dry seasonal rainforest species germinate in the wet season irrespective of the light
440 as a strategy to avoid the drought in the following dry season (Khurana and Singh 2001). Similar
441 to this study, for 19 pioneer species of seasonal dry rainforest, Baskin and Baskin (2014)
442 reported 68% of the species germinate equally in light and dark, whereas only 26% of species
443 have significantly higher germination in light. McLaren and McDonald (2003) studied two
444 dominant pioneer tree species at a dry rainforest in Jamaica and found they also germinated
445 equally in light and shaded conditions.

446 Desiccation tolerance was common for dry seasonal rainforest climax species. Three of the five
447 climax species studied were desiccation tolerant, and an additional three climax species at the
448 study site were investigated by Russell-Smith (1994) and found to be desiccation tolerant.
449 Russell-Smith (1994) assessed the soil seed bank of three climax species present at the current
450 study site (*Aidia racemosa*, *Antidesma parvifolium* and *Maranthes corymbosa*) and found they
451 had a persistent soil seed bank. *Diospyros maritima*, another climax species from the study site,
452 had 82% germination after desiccation and freezing (Ben Wirf, George Brown Darwin Botanic
453 Gardens, pers. comm.) indicating it is desiccation tolerant. Thus, seven of the nine climax
454 species at the study site that have been assessed have desiccation tolerant seeds. In evergreen
455 rainforest, published studies indicate 50% or more climax species have desiccation sensitive
456 seeds. Tweddle *et al.* (2003) reports that 52.2% of 157 evergreen rainforest non-pioneer species
457 are desiccation sensitive, 2.6% are intermediate, and the remaining 45.2% of species are
458 desiccation tolerant. Similarly, a study of eastern Australian evergreen rainforest (Hamilton *et al.*
459 2013) reports that of the 41 climax species, 60% were sensitive to desiccation and 40% tolerate
460 desiccation. In evergreen rainforest moisture is available throughout the year. Seeds are less
461 prone to desiccation and seeds can germinate throughout the year. **Therefore, a substantial**
462 **proportion of woody climax species in evergreen rainforest have not adapted to tolerate**
463 **desiccation.** In seasonal rainforest, there is a prolonged dry season, which is variable in duration,
464 seeds of are more likely to be exposed to drying conditions on shedding. For example, in the
465 study site, temperatures remain relatively uniform throughout the year but humidity declines in
466 the dry season, increasing desiccation (Bureau of Meteorology 2018). Thus, seasonal rainforest

467 species frequently have desiccation tolerant seeds as an adaptation to tolerate drought (Khurana
468 and Singh 2001).

469

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

489 An unusual dormancy type, epicotyl dormancy, occurred in *Strychnos lucida* and this is the first
490 report of this type of dormancy in this genus. In other species of *Strychnos* PD is common but
491 epicotyl dormancy has not been reported (Nchanji and Plumptre 2003). *Strychnos lucida* is
492 found in forest margins where conditions are usually drier than in the interior (Bach 1998). Of
493 the 13 pioneer species studied, it produces the second largest initial leaves after the epicotyls
494 emerge (VT pers. obs). Therefore, leaves will be more prone to desiccation. Having a well-
495 developed root system before leaf growth and transpiration occur could help this species to
496 establish in drier habitats.

497 Once dormancy is identified, knowledge of the location of dormancy and suitable dormancy
498 breaking treatments is important to enable propagation of species for forest rehabilitation.
499 Without treatment no viable seeds of *Abrus precatorius* and few viable seeds of *Dodonaea*
500 *platyptera* and *Alphitonia excelsa* germinated, due to physical dormancy. Therefore, manual
501 scarification or hot-water treatments are useful to break PY in these three species. *Morinda*
502 *citrifolia* and *Drypetes deplanchei* had embryos with lower growth potential, insufficient to
503 overcome the mechanical restraint of the seed coat or endosperm, and have PD. GA₃ application
504 facilitates cell elongation in the embryo and manual scarification may reduce the mechanical
505 restraint on the embryo from the endosperm/seed coat. Some species lack the potential to grow
506 due to inadequate oxygen permeability to the embryo. Scarification of the seed coat can facilitate
507 oxygen flow into physiologically dormant seeds (Baskin and Baskin 2014). Species with
508 dormant seeds are often excluded from rehabilitation plantings due to the lack of information on
509 their propagation techniques. Knowledge on dormancy breaking treatments will help to
510 propagate such species and to ensure they aren't under-represented when rehabilitating lands.

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

524 Based on their seed traits, we predict that seasonal dry rainforests species are resilient to future
525 intra- and inter-annual changes in rainfall compared to evergreen rainforest species. Seasonally
526 dry rainforests are adapted to predictable, seasonal drought whereas evergreen rainforests are

527 adapted to regular moisture throughout the year. Possible effects of climate change on
528 seasonally dry forests include: reduced rainfall during the wet season, multi-year droughts with
529 reduced rainfall, a shorter wet season with rainfall condensed in a shorter duration, and earlier or
530 later starts to the wet season (Allen *et al.* 2017). Current climate modelling for the wet/dry
531 tropics of the Northern Territory is uncertain about future rainfall patterns, although temperatures
532 are expected to rise (Chevuturi *et al.* 2018). Already, rainfall during the wet season is highly
533 variable in amount and timing (Drosdowsky 1996), so seasonal rainforest species already
534 experience variation in annual wet season rainfall, multi-year droughts and variation in the start
535 and end of the wet season. Seasonal rainforest species are generally better able to tolerate periods
536 of desiccation compared to evergreen rainforest species because a higher proportion of seasonal
537 dry rainforests species have desiccation tolerant seeds. Germination and seedling establishment
538 of evergreen rainforest species that are desiccation sensitive will be affected if climate change
539 causes drought periods. Non-dormant, desiccation sensitive seeds germinate rapidly when
540 rainfall occurs, and their seedlings would be killed by periods of drought. Dormancy is frequent
541 in seasonal rainforest species and would prevent seedlings germinating if there is an increase in
542 dry season rains that are potentially unfavourable for seedling establishment (Khurana and Singh
543 2001). Desiccation sensitive seeds of seasonally dry rainforest species, which are dispersed well
544 into the wet season would not be affected unless the wet season shifts markedly, which seems
545 unlikely. Thus, the potential of seasonal rainforest species to adapt to intra and inter annual
546 changes in rainfall and drought stress is high compared to evergreen rainforest species.

547 Generalizations made about the seed biology of pioneer species by Swaine and Whitmore
548 (1988), which apply to evergreen tropical rainforest species, don't necessarily apply to seasonal
549 rainforest species. General seed traits of pioneer species of evergreen rainforest are that they
550 produce dormant seeds that are desiccation tolerant and most species have germination increased
551 by light (Baskin and Baskin 2014). However, in seasonal rainforest a high proportion of pioneer
552 species were non-dormant and half of the species germinated equally well in light and dark
553 conditions. Thus many pioneer species in seasonal rainforest have similar seed biology traits to
554 those of evergreen rainforest climax species, which tend to be non-dormant, desiccation sensitive
555 and germinate equally well in light and dark conditions. In evergreen rainforest the most limiting
556 resource is light and early successional pioneer species have adapted to high light conditions,
557 whereas late successional climax species have adapted to germinate in moist low light

558 conditions. However, in seasonal rainforest, moisture and light are both major limiting factors
559 (Khurana and Singh 2001). The effects of light on germination are less defined, as high light
560 conditions occur at the start of the wet season before the deciduous canopy closes. For all
561 species, seed germination early in the rainy season may be advantageous as nutrients are released
562 (Garwood 1979) and it allows a long first growing season prior to seasonal drought. Thus, many
563 early successional and late successional species have seeds dispersed in the dry season that
564 germinate during the early wet season irrespective of the light conditions. Therefore, we consider
565 the pioneer and climax classification described by Swaine and Whitmore (1988) based on the
566 effects of light on germination is not appropriate for seasonal rainforest species.

567

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573

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

Species	Lifeform	Fruit type	Seed collection month	No of seeds per fruit	Embryo length: Seed length ratio (E:S) (mean \pm SEM)	Embryo type
Climax species						
<i>Diospyros calycantha</i> O.Schwarz	Tree	Berry	Sep 2016	5-7	0.65 \pm 0.01	Spatulate
<i>Diospyros compacta</i> (R.Br.) Kosterm.	Tree	Berry	Feb 2016	4-6	0.75 \pm 0.01	Spatulate
<i>Diopsiros cordifolia</i> Roxb.	Tree/Shrub	Berry	Jun 2016	4-6	0.61 \pm 0.12	Spatulate
<i>Drypetes deplanchei</i> (Brongn. & Gris) Merr.	Tree	Berry	Feb 2016	1	0.62 \pm 0.37	Linear
<i>Glycosmis trifoliata</i> (Blume) Spreng.	Shrub	Berry	Nov 2016	1-3	0.56 \pm 0.01	Linear
Pioneer species						
<i>Abrus precatorius</i> L.	Vine	Follicle	Aug 2015	10-14	na	Investing
<i>Alphitonia excelsa</i> (A.Cunn.ex Fenzl) Benth.	Tree	Drupe	Aug 2015	4-5	na	Investing
<i>Bombax ceiba</i> L.	Tree	Capsule	Oct 2015	>100	na	Folded
<i>Breynia cernua</i> (Poir.) Mull.Arg.	Shrub	Berry	Nov 2015	5-6	na	Investing
<i>Dodonaea platyptera</i> F.Muell.	Shrub	Capsule	Aug 2015	1	na	Folded
<i>Erythrina variegata</i> L.	Shrub	Legume	Aug 2016	1-2	na	Investing
<i>Ficus racemosa</i> L.	Tree	Syconium	Feb 2016	>100	na	Investing
<i>Micromelum minutum</i> (G.Forst.) Wight & Arn.	Shrub	Berry	Dec 2015	1	na	Folded
<i>Morinda citrifolia</i> L.	Tree	Berry	Feb 2016	>40	na	Investing
<i>Opilia amentacea</i> Roxb.	Vine	Berry	Dec 2015 - Jan 2016	1	0.95 \pm 0.01	Linear
<i>Sterculia quadrifida</i> R.Br.	Tree	Follicle	Oct - Nov 2015	5-6	0.99 \pm 0.01	Linear
<i>Strychnos lucida</i> R.Br.	Tree	Berry	Aug 2015	2-4	0.48 \pm 0.01	Spatulate
<i>Wrightia pubescens</i> R.Br.	Shrub	Follicle	Aug 2015	>100	na	Folded

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750 **Table 2. Viability, germination and dormancy status of the climax and pioneer species** (mean \pm SEM). Different lower case
 751 letters above data indicate significant differences between light and dark treatments for a species (GLM $P < 0.05$). Final germination
 752 was the mean length of days to complete germination in 12hr light/12 hr dark treatment. Values in square brackets are germination of
 753 species with dormancy in light and dark after application of the best dormancy breaking treatment.

Species name	Viability (%)	Germination (%) (12hr light/dark)	Germination (%) (Darkness)	Final germination (days)	Dormant
<i>Diospyros calycantha</i>	94.7 \pm 5.3	96.8 \pm 3.2 ^a	96.0 \pm 2.5 ^a	14 \pm 1	No
<i>Diospyros compacta</i>	98.0 \pm 1.3	96.0 \pm 3.1 ^a	92.0 \pm 1.3 ^a	9 \pm 1	No
<i>Diopsyros cordifolia</i>	52.0 \pm 0.1	55.2 \pm 6.4 ^a	55.2 \pm 6.4 ^a	12 \pm 1	No
<i>Drypetes deplanchei</i>	88.0 \pm 6.1	0.8 \pm 0.8 [79.2 \pm 4.6 ^a]	0.0 \pm 0.0 [74 \pm 4.5 ^a]	-	Yes
<i>Glycosmis trifoliata</i>	94.7 \pm 5.0	92.0 \pm 2.3 ^a	2.4 \pm 1.6 ^b	5 \pm 0	No
<i>Abrus precatorius</i>	84.0 \pm 3.5	0.0 \pm 0.0 [100.0 \pm 0.0 ^a]	0.0 \pm 0.0 [95.2 \pm 2.3 ^a]	-	Yes
<i>Alphitonia excelsa</i>	94.7 \pm 2.7	10.4 \pm 2.0 [94.0 \pm 4.1 ^a]	0.0 \pm 0.0 [90.4 \pm 4.1 ^a]	26 \pm 1	Yes
<i>Bombax ceiba</i>	88.0 \pm 2.3	92.0 \pm 4.0 ^a	78.4 \pm 1.0 ^b	12 \pm 2	No
<i>Breynia cernua</i>	93.3 \pm 6.1	85.6 \pm 5.2 ^a	0.0 \pm 0.0 ^b	15 \pm 0	No
<i>Dodonaea platyptera</i>	94.7 \pm 3.7	2.4 \pm 1.6 ^a [93.7 \pm 3.9 ^a]	0.0 \pm 0.0 ^a [89.1 \pm 2.3 ^a]	9 \pm 6	Yes
<i>Erythrina variegata</i>	93.3 \pm 1.3	94.4 \pm 2.7 ^a	68.8 \pm 2.9 ^b	13 \pm 1	No
<i>Ficus racemosa</i>	77.3 \pm 8.3	81.6 \pm 5.3 ^a	78.4 \pm 2.7 ^a	19 \pm 1	No
<i>Micromelum minutum</i>	96.0 \pm 2.3	100.0 \pm 0.0 ^a	57.6 \pm 10.1 ^b	6 \pm 0	No
<i>Morinda citrifolia</i>	85.3 \pm 3.5	0.8 \pm 0.8 ^a [56.8 \pm 4.3 ^a]	0.0 \pm 0.0 ^a [54.4 \pm 5.3 ^a]	26 \pm 1	Yes
<i>Opilia amentacea</i>	77.3 \pm 7.4	70.4 \pm 3.7 ^a	0.0 \pm 0.0 ^b	9 \pm 1	No
<i>Sterculia quadrifida</i>	99.3 \pm 1.3	96.0 \pm 1.3 ^a	54.4 \pm 5.2 ^b	7 \pm 0	No
<i>Strychnos lucida</i>	96.0 \pm 2.3	99.2 \pm 0.2 ^a	90.2 \pm 0.5 ^a	17 \pm 0	Yes
<i>Wrightia pubescens</i>	93.3 \pm 3.5	94.4 \pm 2.0 ^a	93.6 \pm 0.7 ^a	8 \pm 1	No

754 **Table 3.** Seed moisture content, germination (after treatment of dormancy if required) and seed longevity of species with moisture
 755 content < 15% (mean \pm SEM). Different lower case above the germination data indicate significant differences in germination
 756 between stored and non-stored seeds.

Species	Moisture content (%)	Germination (%) of fresh seeds	Germination (%) March (2017) after storage
<i>Abrus precatorius</i>	8.3 \pm 0.2	73.6 \pm 7.1 ^a	69.6 \pm 7.1 ^a
<i>Alphitonia excelsa</i>	7.6 \pm 0.3	93.7 \pm 3.9 ^a	95.2 \pm 3.8 ^a
<i>Diopsiros cordifolia</i>	11.3 \pm 0.5	55.2 \pm 6.4 ^a	53.6 \pm 4.1 ^a
<i>Diospyros calycantha</i>	10.2 \pm 0.7	96.8 \pm 3.2 ^a	74.4 \pm 4.2 ^b
<i>Dodonaea platyptera</i>	6.8 \pm 0.2	68.8 \pm 6.8 ^a	72.8 \pm 7.3 ^a
<i>Drypetes deplanchei</i>	12.1 \pm 2.1	64.0 \pm 7.0 ^a	64.8 \pm 10.6 ^a
<i>Erythrina variegata</i>	5.6 \pm 0.3	94.4 \pm 2.7 ^a	62.4 \pm 2.8 ^b
<i>Ficus racemosa</i>	12.6 \pm 0.3	81.6 \pm 5.3 ^a	87.6 \pm 1.6 ^a
<i>Morinda citrifolia</i>	7.1 \pm 0.3	56.8 \pm 4.3 ^a	56.8 \pm 4.3 ^a
<i>Strychnos lucida</i>	7.1 \pm 0.5	98.4 \pm 1.0 ^a	84.0 \pm 1.8 ^a
<i>Wrightia pubescens</i>	8.2 \pm 3.2	94.4 \pm 2.0 ^a	88.8 \pm 2.3 ^a

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760 **Table 4.** Seed moisture content, germination (after treatment of dormancy if required) and germination of species with a moisture
761 content of greater than 15% (mean \pm SEM).

Species	Moisture content (%)	Germination of treated fresh seeds (%)	Germination after storage at 10°C for 2 months (%)	Germination after desiccation to 10% moisture (%)
<i>Diospyros compacta</i>	19.1 \pm 0.3	96.0 \pm 3.1	0.0 \pm 0.0	0.0 \pm 0.0
<i>Glycosmis trifoliata</i>	53.2 \pm 1.0	92.0 \pm 2.3	0.0 \pm 0.0	0.0 \pm 0.0
<i>Micromelum minutum</i>	40.7 \pm 0.7	100.0 \pm 0.0	0.0 \pm 0.0	0.0 \pm 0.0
<i>Opilia amentacea</i>	54.3 \pm 0.2	70.4 \pm 3.7	0.0 \pm 0.0	0.0 \pm 0.0
<i>Sterculia quadrifida</i>	28.4 \pm 1.1	96.0 \pm 1.3	0.0 \pm 0.0	0.0 \pm 0.0

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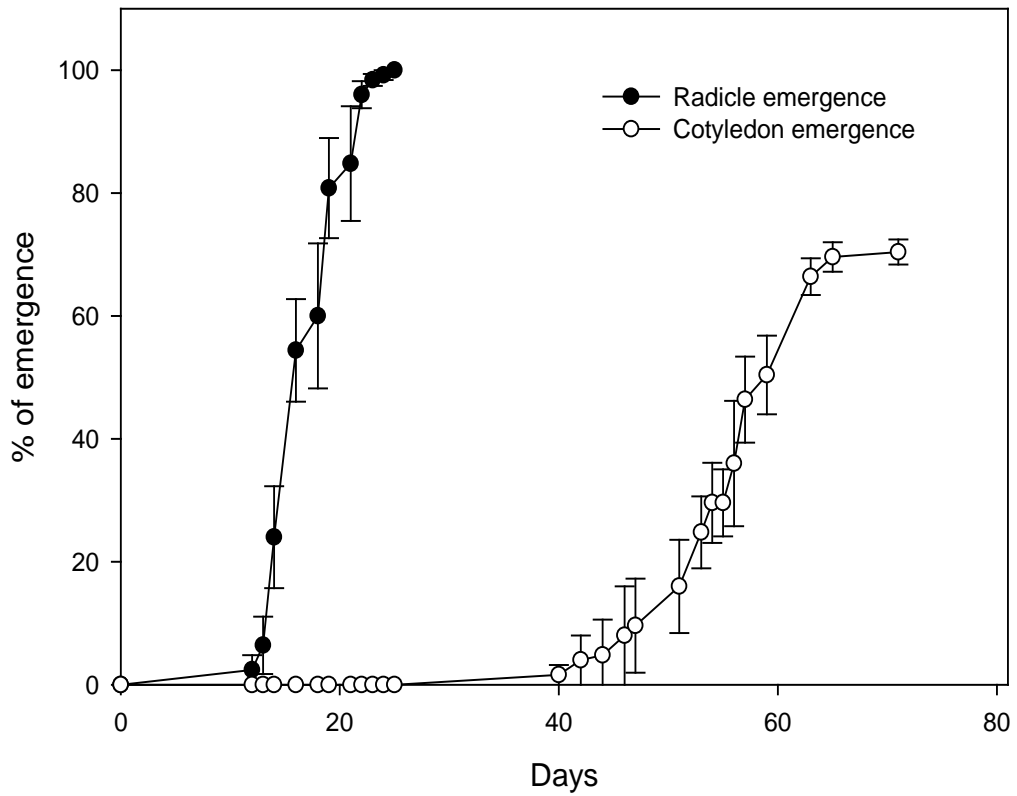
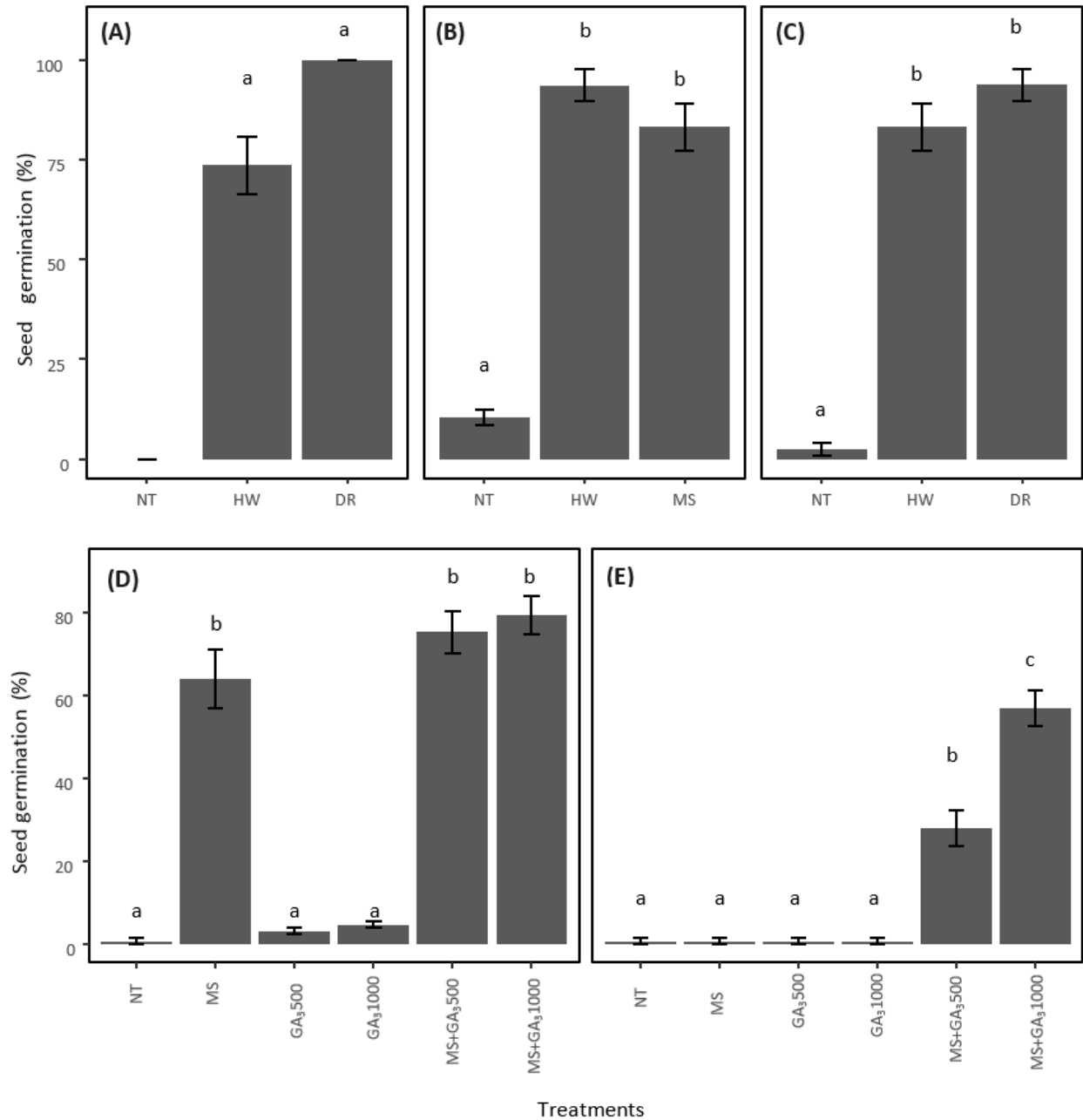


Fig. 1. Number of days until *Strychnos lucida* radicle and cotyledon emergence (mean \pm SEM).



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784 **Fig. 2.** Effects of dormancy breaking treatments on germination (mean \pm SEM). (A); *Abrus*
 785 *precatorius*, (B) *Alphitonia excelsa*, (C); *Dodonaea platyptera*, (D); *Drypetes deplanchei*, (E);
 786 *Morinda citrifolia*. Different lowercase letters above columns indicate significant differences
 787 between treatments (Tuckey post hoc, $p < 0.05$). NT - no treatment; MS - manual scarification;
 788 DR - scarified by drilling; HW (hot water treatments) HW in (A) - 98 °C for 2 min, HW in (B) -
 789 92 °C for 3 min, HW in (C) - 88°C for 30 sec; GA₃500 - Gibberellic acid 500 ppm; GA₃1000 -
 790 Gibberellic acid 1000 ppm.

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