Seed dormancy depth is partitioned more strongly between habitats than between species in tropical ephemerals

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Abstract

Seed biology in the annual herbaceous flora of ecologically stressful, seasonally wet habitats remains largely unexplored. Temporal and spatial species turnover between these habitats is often high, yet little is known about how fine-scale habitat variation drives intraspecific variability in seed dormancy depth and seed germination requirements. This study characterised seed dormancy and investigated the germination biology of six closely-related herbaceous annual species of *Byblis* from northern Australia. We assessed variation in the response of seeds of all species to temperature cues, as well as light and the naturally occurring germination stimulants KAR_1 and ethylene. We also examined intraspecific variation in germination response and seed dormancy depth for three widely-distributed species with overlapping distribution occurring in habitats with differing soil thermal and hydrological conditions. Seed germination in all six species was significantly increased by exposure to either KAR_1 or ethylene with this effect amplified in two species (*B. filifolia* and *B. rorida*) following a period of warm, dry afterripening. Seed dormancy depth and the germination response of seeds to both KAR_1 and ethylene was partitioned more strongly between habitats than between species. Populations on shallow (<20 cm soil depth) sandy soils produced less dormant seeds than populations of the same species on deeper sandy soils (40+ cm) or on heavy cracking clays. The upper soil profile of shallow soil habitats was exposed to higher average temperatures, greater diurnal temperature fluctuation and greatly reduced moisture persistence compared to deeper soils. Fine-scale differences in the thermal and hydrological conditions of seasonally wet habitats appear to be strong drivers of dormancy depth in seeds of tropical *Byblis*. Widely-distributed species exhibit high levels of plasticity in seed dormancy depth and germination response between different habitats, with similar responses observed for sympatric species. In order to fully understand species turnover in tropical ephemerals, future studies should examine phenotypic plasticity and the rate of local adaptation of seed traits in greater detail.

41

Introduction

43

The seasonality of precipitation in tropical regions is a major ecological driver of plant traits, with increasing duration
and intensity of the drought period strongly selecting for annual species reliant upon the formation of persistent seed
banks (Clary 2008; Cross *et al.* 2015a,b). Seasonality appears to have driven the assembly of a diverse suite of annual
species in the flora of northern Australia; annual herbs, forbs and grasses represent at least half of the ca. 8000 plant
species in the region (AVH 2016; Bostock and Holland 2016; Northern Territory Herbarium 2016; Western Australian
Herbarium 2016). The richness of annual species is particularly high in ephemeral, seasonally wet habitats; these
ecosystems are mostly rain-fed and may be waterlogged or flooded for weeks or months at a time during the wet
season but dry rapidly and completely after the cessation of seasonal rainfall (McKenzie *et al.* 2009). Ephemeral
habitats may experience drought periods even during the summer wet season, with high evaporation and unpredictable
rainfall often resulting in extended dry periods between inundation events (Cross *et al.* 2015a,b). Species turnover in
these habitats is often high (e.g., Krieger *et al.* 2003; Cross *et al.* 2015b), and they harbour numerous ecological
specialists including some highly localised rare species (<20 m known range) such as *Schoenus kimberleyensis* and
Trachymene pavimentum (Barrett and Barrett 2015). However, the reproductive ecology of tropical annuals in
northern Australia remains predominantly unexplored. Little is known about how habitat ephemerality acts as a
selection pressure on recruitment and as a driver of species turnover, and how this pressure varies spatially (e.g., at
scales from metres to kilometres and across different substrates) and temporally (e.g., within and between seasons).

60

Variation in the depth of seed dormancy within and between populations can be affected by factors in the parental
environment during seed maturation, as well as by genetic effects (Donohue and Schmitt 1998; Cochrane et al. 2015).
With respect to environmental factors, perhaps the most substantial are temperature and water availability (Long *et al.*
2014), with higher temperatures and greater water stress during the seed development period generally resulting in the
production of less dormant seeds (Steadman *et al.* 2004; Hoyle *et al.* 2008; Baskin and Baskin 2014). In species from
marginal and ephemeral aquatic habitats in seasonal regions, seedling emergence from the seed bank is strongly
influenced by hydrological regimes at fine scales (e.g., Aponte *et al.* 2010; Carta *et al.* 2013; Cross *et al.* 2014, 2015a).
Seed populations in these habitats often exhibit significant variation in germination requirements and timing, viewed
as bet hedging strategies (Cross *et al.* 2015a), probably conferring a degree of resilience against reproductive failure in
a capricious environment. Inconsistent seasonal conditions may engender a requirement for intraspecific variation in
dormancy depth for species reliant upon a persistent soil seed bank, which may be linked in part to the maternal
environment (Long *et al.* 2014).

73

A charismatic element of the annual herbaceous flora of seasonally wet habitats in northern Australia is the remarkable
abundance and diversity of carnivorous plants (ca. 85% of which are annual herbs; Lowrie 2014). The region harbours
around 40 of the ca. 200 species of *Drosera* (Droseraceae)*,* three of the ca. 160 species of *Nepenthes* (Nepenthaceae),
at least 60 of the ca. 230 known species of *Utricularia* (Lentibulariaceae) and, notably, six of the eight species of
Byblis (Byblidaceae). All six tropical *Byblis* species are barochorous annuals reliant upon extensive soil seed banks for
seasonal recruitment (Lowrie 2014; A. Cross unpubl.), and all occur in seasonally wet areas such as riparian lowlands,
marginal aquatic environments or temporary flush and seepage zones (Lowrie and Conran 1998; Lowrie 2014). Four
species are widely distributed, with *B. rorida* occurring throughout the northwest Kimberley, *B. filifolia* common

throughout the Kimberley as well as the Top End of the Northern Territory, *B. aquatica* known from disjunctive areas in the northwest Northern Territory and far northeast Queensland, and *B. liniflora* widespread throughout northern Australia as well as extending into southern Papua New Guinea (Lowrie 2014). In contrast *B. guehoi* is known from only a small area on the Dampier Peninsula in the western Kimberley (Lowrie and Conran 2007), and *B. pilbarana* is restricted to seepage habitats in the semi-arid northwest Pilbara in Western Australia (Lowrie 2014).

Seed dormancy and germination biology of annual plants in northern Australia remains predominantly unexplored, and the germination requirements of tropical *Byblis* species in particular remain completely unresolved. However, seeds of diverse taxa from northern Australia are known to exhibit a range of germination responses to factors such as temperature, light, wetting and drying cycles, soil disturbance, burning cycles and microsite variation (e.g., Setterfield 2002; Turner and Dixon 2009; Cross *et al.* 2014, 2015a). Previous research suggests that *Byblis* produce physiologically dormant seeds (Cross *et al.* 2013). Seed germination in species with physiological dormancy from ephemeral habitats in northern Australia is often increased after periods of warm, dry afterripening simulating seasonal drought and warm dry soil storage (Cross *et al.* 2015a). Additionally, ethylene is an important germination cue for seeds of species inhabiting wetlands in many parts of the world (Baskin and Baskin 2014). In fire-prone habitats, such as the kwongan in south west Western Australia, germination ecology frequently manifests as an interplay between dormancy break and fire-related cues such as the smoke-derived KAR_1 (Flematti *et al.* 2004; Merritt *et al.* 2007). Ethylene has been found to elicit strong germination in several species of wetland annuals from northern Australia (Cross *et al.* 2014), and fire is an intrinsic component of the highly seasonal ecology of northern Australia with savanna habitats considered to be among the most fire-prone ecosystems on the planet (Russell-Smith and Yates 2007; McKenzie *et al.* 2009; Bowman *et al.* 2010; Andersen *et al.* 2012). Extensive post-fire recruitment has been observed for several tropical *Byblis* species (Cross *et al.* 2013; Lowrie 2014), and fire has been implicated as a crucial mechanism in the ecology of both species of *Byblis* from south west Western Australia (Conran *et al.* 2002; Cross *et al.* 2013; Lowrie 2014). Smoke-related cues are responsible for promoting germination from a long-lived soil seed bank in *B. gigantea,* a species occurring in seasonally waterlogged swamp heath, while vigorous resprouting and abundant flowering following fire is also documented for *B. lamellata,* which occurs on sandplains in fire-prone kwongan heathland (Cross *et al.* 2013; Conran *et al.* 2002; Lowrie 2014).

This study examined the germination biology of all six northern Australian *Byblis* species (*B. aquatica, B. filifolia, B. guehoi, B, liniflora, B. pilbarana,* and *B. rorida*). We explored the hypotheses that i) seasonal temperature and moisture conditions in combination with the naturally occurring germination stimulants KAR_1 and ethylene are key ecological factors in the regulation of seed germination, and ii) dormancy and germination traits vary amongst seed populations from different habitats. To address these hypotheses we aimed to: 1) classify seed dormancy; 2) determine the dormancy break and germination responses to different light and temperature cues, particularly cold and warm stratification as well as dry afterripening; 3) test the effectiveness of KAR_1 and ethylene as germination stimuli when combined with dormancy breaking-treatment; 4) examine whether seed dormancy and germination traits varied between seed populations from different habitats; and 5) determine whether these habitats experienced different environmental conditions (temperature and moisture in the upper soil profile) during desiccation of the substrate at the end of the wet season. The rapidity of desiccation directly affects the length of the growing season and the rate of onset of aridity, which are two important variables in ephemeral habitats (Cross *et al.* 2015b).

123   **Materials and Methods**

124

125   *Seed collection*

126

127   Mature seeds (black and dehiscing) were collected from *B. aquatica* Lowrie & Conran, *B. filifolia* Planch., *B. guehoi*

128   Lowrie & Conran, *Byblis liniflora* Salisb., *B. pilbarana* Lowrie & Conran, and *Byblis rorida* Lowrie & Conran during

129   the late wet season (March-May) in 2012, 2015, or 2016 (Table 1). Multiple populations were sampled for the three

130   most widespread species (*B. filifolia* [7 populations]*, B. liniflora* [3 populations] and *B. rorida* [6 populations]) in

131   order to assess variation in germination response and seed dormancy between different habitats. Sampled habitats

132   included skeletal sandy soil lenses over sandstone pavement or granite supporting low herbaceous assemblages (SS),

133   deeper soils on the aprons of sandstone pavements and massive sandstone supporting herbfields of mixed annual

134   species (DS), and heavy cracking clays supporting mixed herbaceous species in open *Eucalyptus* woodland (CC).

135

136   # Table 1

137

138   *Habitat characteristics*

139

140   Soil depth was measured at all seed collection sites by driving a thin metal rod (1 cm diameter) into the soil either until

141   bedrock was contacted, or to a maximum depth of 150 cm. Nine depth measurements were taken at each site, in a $3 \times$

142   3 grid with 5 m spacing

143

144   A detailed assessment of the habitat characteristics of three species was carried out at sites on Theda Station (Table 1.)

145   To determine the chemical composition and physical texture of soils, three replicate 500 g samples from four *B.*

146   *filifolia* sites, two *B. liniflora* sites, and two *B. rorida* sites were collected and sent to ChemCentre (Bentley, Western

147   Australia) for analytical determination of soil properties and chemical factors (Table 2). Soil moisture and temperature

148   during the seed maturation period (17 March to 3 May 2016) were measured prior to seed collection at two sites each

149   for SS, DS, and CC. Three S-SMC-M005 soil moisture and one S-TMB-M006 temperature smart sensors attached to a

150   Micro Station data logger (Hobo H21-002, Onset, Bourne, USA) were inserted into undisturbed soil in open, unshaded

151   areas. *Byblis* have shallow and poorly developed root systems (Lowrie 2014).

152

153   Following examination of the roots of excavated individuals sensors were at installed 2 cm below the soil surface to

154   capture soil moisture and temperature in the upper soil profile. Soil temperature and moisture probes operated for 48

155   days, including 31 days without precipitation following the second of two significant rainfall events on the 19th March

156   (39 mm) and 31st March–1st April (41 mm). The increase in soil volumetric moisture content (%v/v) following each

157   rainfall event was measured from the first data point of increasing moisture content to the maximum value reached

158   (generally occurring within 12–24 h). However, damage from fauna to one logger resulted in only a single dataset for

159   SS. Rainfall data was drawn from the Theda Station weather station (Australian Bureau of Meteorology,

160   http://www.bom.gov.au/climate/data/) and all logger sites were located within 1 km of the weather station to minimise

161   site-specific variation in rainfall.

162

163 Seed collections of each species were pooled for each population, and were cleaned manually by gently rubbing fruits

164 over 250 µm to 2 mm gauge steel sieves with a handheld rubber stopper. Seeds were then separated from chaff and

165 debris using a Zig Zag vacuum aspirator (Selecta Machinefabriek BV, Enkhuizen, The Netherlands) and stored in a

166 controlled environment room at 15ºC and 15% relative humidity prior to use in experiments. Seed size (measured

167 digitally) and quality was determined for three replicates of 100 seeds from each population via X-ray analysis (MX-

168 20 digital X-ray cabinet, Faxitron, Tucson, USA). Seeds were scored as filled if the endosperm appeared as fully

169 developed, not shrunken or retracted from the testa, and showed no signs of internal damage. Germination experiments

170 were conducted on freshly collected seeds of *B. filifolia, B. guehoi*, *B. liniflora* and *B. rorida*, while seeds of *B.*

171 *aquatica* and *B. pilbarana* were stored for 1–3 years prior to germination testing.

172

173 *Germination biology*

174

175 To assess the seed germination response to temperature, light, and germination stimulants, seeds of each population of

176 each species were sterilised in a 2% calcium hypochlorite solution under vacuum for 30 min, before being washed in

177 sterile deionised water and plated in 90 mm Petri dishes onto 0.7 % (w/v) water agar only (control) or on water agar

178 containing 2.89 mM GA$_3$ (Sigma Aldrich Chemicals, Australia), 1 µM KAR$_1$ (Flematti *et al*. 2004), or on water agar

179 after exposure to 50 nmol ethylene gas (C$_2$H$_4$) for 24 h. Methods of ethylene exposure followed Cross *et al*. (2014).

180 Four replicates of 25 seeds for each treatment were placed in incubators at constant 10, 15, 20, 25, 30, or 35ºC on a 12

181 h photoperiod, or in constant darkness (plated in darkness and wrapped in aluminium foil to exclude light).

182 Germination (radicle emergence to >1 mm) was scored daily for one week then weekly for another seven weeks in

183 light treatments, but once only after eight weeks in dark treatments.

184

185 To investigate the impact of cold and warm stratification on the alleviation of seed dormancy, additional replicates of

186 25 seeds were prepared as described previously for control, GA$_3$, KAR$_1$, and ethylene treatments. For stratification,

187 four replicates for each treatment were incubated in Petri dishes on water agar at 10ºC (cold stratification) or at 35ºC

188 (warm stratification) for 8 weeks, before transfer to 25ºC for germination for a further 8 weeks. Seeds were cold or

189 warm stratified under a 12 h photoperiod and then incubated at 25ºC under either a 12 h photoperiod, or in constant

190 darkness. Four replicates of each treatment incubated at constant 10, 25, or 35ºC for 16 weeks served as control seeds.

191 Germination was scored weekly in light/dark treatments, and at the conclusion of the full 16-week period in dark

192 treatments.

193

194 To determine the effect of dry afterripening on dormancy alleviation, seeds of each species were enclosed in a

195 polycarbonate electrical enclosure box (28 × 28 × 14 cm; NHP Fibox, Richmond, Australia) above a non-saturated

196 solution of LiCl (364 gL^{-1}) creating a relative humidity of 50 % (Hay *et al.* 2008), and placed at constant 30ºC

197 (Tuckett *et al.* 2010). After 1 and 3 months, four replicates of 25 seeds were extracted and incubated at 25ºC under a

198 12 h photoperiod on water agar, or exposed to either GA$_3$, KAR$_1$, and ethylene treatments as previously described.

199 Germination was scored weekly for 8 weeks of incubation.

200

201 Upon completion of each experiment, all non-germinated seeds were cut-tested to determine viability with seeds

202 possessing a firm, white endosperm and embryo judged to be viable. Germination percentages are therefore based on

203 the number of viable seeds.

204

Embryo growth

205

206

207 To determine whether any embryo growth occurs inside *Byblis* seeds prior to radicle emergence, and thus if the seeds

208 have morphological/morphophysiological dormancy (Baskin and Baskin 2014), 100 seeds of each population of each

209 species were incubated on water agar after exposure to 2.89 mM GA_3 and incubated at 25ºC on a 12-h photoperiod.

210 Prior to incubation and after each week for 8 weeks, ten seeds were randomly selected and dissected, with the seed and

211 embryo length for each measured under a dissecting microscope equipped with an ocular micrometer to determine the

212 embryo length to seed length (E:S) ratio.

213

214 *Statistical analyses*

215

216 One-way ANOVA with Tukey post-hoc tests were used to assess variation in soil depth, chemistry factors, soil

217 temperature and moisture content, and germination percentages for each population between habitat types. Linear

218 regression was used to test the effect of soil depth on soil surface temperature (daily maximum, minimum, and mean

219 temperature, and maximum, minimum, and mean diurnal temperature variation) and surface hydrology (volumetric

220 moisture increase following rainfall, mean daily volumetric moisture loss, maximum daily volumetric moisture loss,

221 and minimum volumetric moisture content).

222

223 Binary logistic regression was used to assess the main and interaction effects of light, temperature, GA_3, KAR_1,

224 ethylene, stratification, and after-ripening on seed germination. One-way ANOVA with Tukey post-hoc tests were

225 used to test the effect of incubation duration on embryo length. Preliminary analyses of all data were conducted to test

226 the assumptions of normality (Kolmogorov–Smirnov test), linearity and homoscedasticity (Levene's test). Where

227 necessary, data were $\log_{10}$ transformed to help meet assumptions of normality and equal variance. All statistical tests

228 were conducted using the 95 % confidence interval (CI), with significance determined by $P < 0.05$. Data are presented

229 as mean $\pm$ 1 s.e. of the raw data unless stated otherwise.

230

231 **Results**

232

233 *Habitat characteristics*

234

235 All sampled soils were low in nutrients, varying significantly only in carbon and nitrogen content (Table 2). Soils

236 contained low concentrations of nitrogen (<0.2 mg/kg), phosphorus (<8.0 mg/kg), and potassium (ca. 17 mg/kg). Soil

237 at CC sites was deep (>150 cm) fine-textured sandy clay. Soil at SS and DS sites consisted of fine to coarse-textured

238 sandy loam. Average soil depth was approximately three times greater ($P = 0.008$) at DS sites (40–100 cm) than SS

239 sites (<20 cm).

240

241 **Table 2**

242

243 The three sampled habitats exhibited markedly different hydrological and thermal conditions in the upper soil profile

244 during desiccation of the substrate at the end of the wet season (Table 3). Soil moisture content remained relatively

245 constant in the two CC sites over the monitoring period, but declined rapidly in shallow-soil SS and DS habitats (Fig.

246 1). The persistence of soil moisture in SS and DS sites was strongly related to soil depth, with mean and maximum

247 daily volumetric moisture loss strongly positively associated with increasing soil depth ($P <0.001$ in both cases). Mean

248 daily moisture loss was approximately 20% greater in SS sites (nearly 0.7% per day) compared with DS (Fig. 1).

249

250 Highest temperatures and greatest diurnal temperature variation were recorded from shallow-soil habitats (Table 3).

251 Linear regression analyses provided strong negative correlations in all cases ($P <0.001$) between increasing soil depth

252 and both daily temperature (mean, maximum and minimum) and diurnal temperature variation (maximum, minimum,

253 and mean). The surface soil of SS and DS sites frequently exceeded 40ºC, and daily minimum temperature was

254 consistently 1–2ºC greater than at CC sites (Fig. 1). Temperature patterns were similar for SS and DS sites, although

255 soil moisture in SS was completely recharged by a rainfall event on 31st March–1st April while nearby DS sites showed

256 only a slight increase in surface soil moisture (ca. 2%). As a result, surface soils at both DS sites dried almost

257 completely over the monitoring period (to ca. 1% moisture content) while soil moisture remained at 12% after 31 days

258 without rain at the SS site (Fig 1).

259

260 **Table 3**

261

262 **Figure 1**

263

264 *Germination biology*

265

266 Seed viability was high (>80%) in all species (Table 4). Germination of fresh untreated seeds was negligible (0–12%)

267 across all temperatures for all populations of *B. filifolia*, *B. liniflora*, and *B. rorida*, and occurred predominantly at

268 20ºC and 25ºC (Fig. 2). Untreated seeds (water agar controls) germinated to relatively high percentages in light/dark

269 treatments for *B. aquatica* (60 ± 4% at 20ºC), *B. guehoi* (90 ± 10% at 20ºC) and *B. pilbarana* (67 ± 14% at 30ºC).

270

271 GA$_3$ exposure significantly improved seed germination percentage for all populations of *B. filifolia, B. liniflora* and *B.*

272 *rorida* ($P <0.001$ in all cases; Fig. 2). GA$_3$ exposure widened the temperature at which significant germination

273 occurred to include 30ºC in *B. filifolia*, and 30ºC and 35ºC in *B. guehoi, B. liniflora* and *B. rorida.* Germination

274 response to GA$_3$ exposure was greater in populations of *B. filifolia*, *B. liniflora* and *B. rorida* from SS (Fig. 2), being

275 on average ca. 50% higher in SS than DS for *B. filifolia* ($P = 0.032$, F = 8.7), ca. 65% higher in SS than DS for *B.*

276 *rorida* ($P <0.001$, F = 219.7), and ca. 40% higher in SS than CC for *B. liniflora* (Fig. 2). The main effect of GA$_3$

277 exposure on germination percentage was not significant for *B. aquatica* ($P = 0.078$) or *B. pilbarana* ($P = 0.660$).

278

279 **FIGURE 2**

280

281 The germination of freshly collected seeds was markedly higher in seeds exposed to KAR$_1$ or ethylene than in water

282 agar control seeds, in at least one incubation temperature (Fig. 2), for all six species (Table 5). KAR$_1$ exposure

283 increased seed germination for six of the seven populations of *B. filifolia* (6–47% increase), both CC populations of *B.*
284 *liniflora* (47–53% increase), and three of the four SS populations of *B. rorida* (2–28% increase). KAR$_1$ exposure also
285 increased germination for *B. guehoi* (up to 21% increase) and *B. pilbarana* (up to 32% increase), but suppressed
286 germination of *B. aquatica* (Fig. 2). Ethylene exposure increased germination in all three SS populations of *B. filifolia*
287 (6–31% increase) and two of the four SS populations of *B. rorida* (4–62% increase), but suppressed germination of *B.*
288 *pilbarana* and *B. guehoi* by up to 55% and 34%, respectively (Fig. 2).

289

290 ## TABLE 4

291

292 Most germination across all species was observed in treatments incubated under 12/12 hr photoperiod. No germination
293 was observed for untreated seeds incubated under constant darkness. Exposure to GA$_3$ promoted germination for *B.*
294 *filifolia*, *B. liniflora*, and *B. rorida* ($P >0.05$ in all cases; data not shown) in constant darkness to levels comparable
295 with GA$_3$ exposed seeds in light/dark treatments. No germination in constant darkness was observed for seeds exposed
296 to KAR$_1$ or ethylene.

297

298 No species exhibited a significantly enhanced germination response to cold stratification for 8 weeks at 10ºC or warm
299 stratification for 8 weeks at 35ºC compared with non-stratified seeds in any treatment (data not shown).

300

301 Although afterripening for 1 or 3 months did not increase the germination of seeds incubated in water ($P = 0.052$,
302 0.611, 0.221, and 0.994 for F6, F7, R5, and R6, respectively)*,* the main effect of afterripening on the germination of
303 seeds exposed to both KAR$_1$ and ethylene was highly significant in all four tested populations of *B. filifolia* and *B.*
304 *rorida* ($P < 0.001$ in all cases). Following afterripening for 3 months, germination increased by 24–32% (*B. filifolia*)
305 and 27–63% (*B. rorida*) for seeds incubated in KAR$_1$, and by 25–40% (*B. filifolia*) and 29–50% (*B. rorida*) for seeds
306 exposed to ethylene (Fig. 3). The germination response of seeds to GA$_3$ exposure after 3 months of afterripening also
307 increased by up to 30% in *B. filifolia* and by up to 23% in *B. rorida* ($P = <0.001$ in both cases).

308

309 ## Table 5

310

311 ## Figure 3

312

313 *Embryo characteristics*

314

315 The seeds of all species possessed an axile, linear embryo occupying roughly one-quarter of the seed volume (Table
316 4). No significant embryo growth occurred in any species prior to the emergence of the radicle.

317

318 **Discussion**

319

320 This study provides evidence of fine-scale local variation in the depth of physiological seed dormancy and germination
321 cues between populations of tropical *Byblis*. Seasonal temperature and moisture conditions, in combination with

322 naturally occurring germination stimuli such as KAR_1 and ethylene, appear to be major environmental factors

323 regulating seed dormancy and germination. Data show that a degree of phenotypic plasticity in seed dormancy exists

324 within the tested species. This is coincident with different seed accessions arising from plant populations that vary in

325 microhabitat factors such as soil temperature and the persistence of soil moisture. Each of the three seasonally wet

326 habitats studied clearly represents a distinct environmental niche, and similar patterns of intraspecific plasticity were

327 observed in the seed dormancy depth and germination response of sympatric species between these habitats. Studied

328 species exhibited similar seed germination responses across the sampled range of substrates, suggesting that variation

329 in seed germination traits may reflect localised adaptation.

330

331 Seeds of all six tropical *Byblis* species exhibit non-deep physiological dormancy (PD), as determined by low

332 germination (or temperature-conditional germination) of freshly collected or stored untreated seeds, the presence of a

333 fully developed linear embryo, and a strong response to GA_3 (Baskin and Baskin 2014). Although we acknowledge

334 that the storage of *B. aquatica* and *B. pilbarana* seeds prior to experimental use may have influenced dormancy depth,

335 both species exhibited similar germination patterns in response to light, temperature and germination stimuli to those

336 of freshly collected seeds from other tested species. Non-deep PD has previously been demonstrated for the south

337 western Australian endemic *Byblis gigantea* (Cross *et al.* 2013), as well as for many species from numerous other

338 families in the Lamiales (Baskin and Baskin 2014). Data from this study suggest that dormancy loss in tropical *Byblis*

339 (at least in *B. filifolia* and *B. rorida*) occurs following a period of warm dry afterripening. This is probably reflective of

340 conditions experienced by seeds in the soil seed bank during the April–November dry season. Seedling emergence in

341 most tropical *Byblis* occurs after early wet season rainfall in November–December (A Cross and M Barrett, pers. obs.).

342 The alleviation of dormancy during the dry season would result in seeds being non-dormant and rapidly able to exploit

343 soil moisture at the onset of the summer growing season. Afterripening is a common method facilitating the

344 maintenance of seeds through warm dry periods in unpredictable, highly seasonal environments such as northern

345 Australia (McIvor and Howden 2000; Tuckett *et al.* 2010; Carta *et al.* 2013), and has been shown to alleviate seed

346 dormancy in a number of other species from seasonally wet habitats in the Kimberley (Cross *et al.* 2015a).

347

348 Untreated seeds of all six species required exposure to light to germinate and germinated predominantly at 20–25ºC,

349 with the exception of the more arid-climate *B. pilbarana* which germinated optimally at 30ºC. Light exposure appears

350 to be a relatively common requirement for germination in the seeds of species with non-deep PD and may be a depth-

351 sensing mechanism in aquatic habitats subject to periodic inundation (Pons 2000; Baskin and Baskin 2014). Indeed,

352 the seeds of many species from ephemeral wetland habitats, including annual aquatic herbs from shallow freshwater

353 rock pools on sandstone in the northern Kimberley, exhibit an absolute light requirement (e.g. Tuckett *et al.* 2010a,b;

354 Carta *et al.* 2013; Cross *et al.* 2014, 2015a). Additionally, as the seeds of all studied *Byblis* species are small they may

355 lack the resources to emerge if seeds were buried in darkness.

356

357 Smoke-derived KAR_1, and to a lesser extent ethylene, plays a significant role in promoting seed germination in

358 tropical *Byblis*. Dormancy status significantly influences the amplitude of this germination response and mechanisms

359 such as afterripening may work synergistically with naturally occurring stimulants such as KAR_1 and ethylene for

360 species with non-deep PD (Merritt *et al.* 2007; Turner *et al.* 2009). Exposure to smoke stimulates the germination of

361 numerous species with different life histories from the seed bank of fire-prone savanna habitats in northern Australia

362 (Williams *et al.* 2003; Clarke and French 2005), including ephemeral wetland habitats (Cross *et al.* 2015a). Indeed,

363   smoke-derived chemicals are a common germination cue in many fire-prone ecosystems worldwide (e.g., Brown

364   1993; Dixon *et al.* 1995; Pierce *et al.* 1995; Roche *et al.* 1998; Morris 2000). Although soil lenses on large areas of

365   sandstone pavement probably burn less frequently than the surrounding savanna matrix as sandstone outcrops and

366   pavements are considered to be areas of fire refugia (Bowman *et al.* 2010), these areas almost certainly experience

367   significant ash deposition during fires and the washing of this material into soil lenses and apron habitats by rainfall

368   could result in a strong KAR_1 signal. Ethylene is recognised as a notable germination cue in a variety of habitats

369   worldwide (Baskin and Baskin 2014). Biogenic ethylene, which originates predominantly from the decomposition of

370   organic matter by soil microbes (Arshad and Frankenberger 1990; Jackel *et al.* 2004), has recently been implicated as

371   a major germination stimulant for the inhabitant flora of seasonally wet habitats in the North Kimberley (Cross *et al.*

372   2014, 2015a). Emergence from the seed bank in ephemeral wetland habitats is likely to be regulated by the response of

373   the sediment microbial community to the depth and duration of flooding (Cross *et al.* 2014). This potentially explains

374   why the greatest germination response to ethylene was observed in seeds of *B. aquatica* and populations of *B. filifolia*

375   and *B. rorida* from shallower soils.

376

377   The longevity and predictability of seasonal water availability, as well as localised climatic factors in the parental

378   environment, are drivers of plasticity in germination traits (e.g., Gutterman 2000; Baskin and Baskin 2014; Long *et al.*

379   2014). Individuals from populations in warmer, drier environments appear to produce less dormant seeds than

380   populations of the same species in cooler, wetter areas (Probert 2000; Steadman *et al.* 2004; Hoyle *et al.* 2008; Baskin

381   and Baskin 2014). Freshly collected seeds of *B. liniflora* and *B. rorida* from populations in the King Leopold Ranges

382   in the south western part of the North Kimberley (L2 and R4) germinated to higher percentages than seeds from

383   populations on the Gardner Plateau in the central North Kimberley (L1 and L3, and R1, R2, R3, R5, and R6),

384   corresponding with significantly lower annual rainfall and higher average seasonal temperatures in the former region

385   (McKenzie *et al.* 2009). Depth of seed dormancy and the degree of sensitivity to germination stimulants also varied

386   markedly between sampled habitats at local scale. Seeds of both *B. filifolia* and *B. rorida* from SS habitats germinated

387   to significantly higher percentages (50–65% greater) than those from DS habitats after exposure to GA_3, indicating

388   weaker PD in seeds from SS habitats. Similarly, seed germination after exposure to GA_3 was ca. 40% greater for seeds

389   of *B. liniflora* from shallow sandy soils compared those from deeper cracking clays.

390

391   Hydroperiod (persistence of soil moisture) during the seed maturation period in shallow sandy soils was strongly

392   positively associated with soil depth, with rates of daily moisture loss nearly 20% greater in soil lenses (<20 cm deep)

393   compared with apron areas (30–70 cm deep). The hydrological stability of CC sites compared with sandy soils is

394   likely to reflect the higher water retention capacity of heavy cracking clays rather than soil depth (Table 1). Soil lenses

395   over bedrock depressions are reservoirs fed by the surrounding rock catchment in a similar fashion to freshwater rock

396   pools (FRP) on exposed rock (though at larger scale and without persistent free-standing water). The soil moisture data

397   obtained in this study indicate that the hydrology and hydroperiod of soil lenses over sandstone are similar to those of

398   FRP in the Kimberley (Cross *et al.* 2015b). Shallower habitats experience higher temperatures and greater diurnal

399   temperature fluctuation, and despite desiccating with much greater rapidity than deeper depressions, they can be fully

400   recharged by even small rainfall events. The study site has between 36–130 rainfall days each year during the

401   November to April wet season, interspersed with between 2–15 drought periods of mean duration 10.4 days on

402   average (Cross *et al.* 2015b). This suggests that even though the duration and timing of moisture availability in SS

habitats might be unpredictable, in most years rainfall probably occurs with sufficient regularity to recharge most shallow-soil systems for a period long enough to ensure reproductive success.

Results from this study further highlight the length of the growing season as a driver of ecology in the monsoon tropics, and provide additional evidence of the importance of ethylene and the smoke-derived chemical KAR_1 as seed germination stimuli in seasonally wet habitats. The plasticity in seed dormancy and seed germination traits observed for tropical *Byblis* may reflect the need for resilience within seed populations to the seasonal climatic extremes and environmental stochasticity of northern Australia. Many species inhabiting seasonally wet habitats in northern Australia exhibit wide geographical distribution and high occupancy of large-scale wetland habitats (e.g., Wheeler 1992; Cowie *et al.* 2000), while range-restricted species are more frequently associated with small-scale and highly ephemeral habitats (Cross 2014; Cross *et al.* 2015b). If ephemerality in the tropics has such a strong impact on seed ecology as has been hypothesised (Clary 2008; Cross *et al.* 2015a), then range-restricted ecological specialists in northern Australia are likely to possess among the most resilient and finely tuned seed dormancy and germination strategies of any vegetation communities in Australia. Future studies should examine a wider suite of marginal and ephemeral aquatic taxa in the monsoon tropics, to elucidate in greater detail habitat-specific variation in seed dormancy and germination response both within and between species over longer periods. Multi-generational and reciprocal transplant studies would also be desirable to differentiate between maternal effects and fixed adapted traits.

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Figure legends

Figure 1. Daily minimum and maximum temperature (top) and volumetric moisture curves in response to rainfall (bottom) for soil at 2 cm depth in tropical *Byblis* habitats in the central North Kimberley during the late wet season seed maturation period. A- heavy cracking clays supporting open *Eucalyptus* woodland (CC); B- shallow soil lenses on sandstone aprons supporting sparse herbaceous assemblages (SS); C- deeper soil lenses between exposed sandstone pavements supporting low herbfields (DS). Each curve represents the data from a single probe for temperature, and the averaged data from three probes for volumetric moisture. Loggers were established at two sites for each habitat type (solid and dotted lines, respectively), but damage to one logger resulted in only a single dataset for B.

Figure 2. Germination (mean probability with exact binomial 95% confidence limits) of the seeds of six tropical *Byblis* species following eight weeks of incubation at five different incubation temperatures under alternating light/dark conditions (12 h/12 h) from either shallow soil lenses on sandstone aprons supporting sparse herbaceous assemblages (SS, closed symbols), deeper soil lenses between exposed sandstone pavements supporting low herbfields (DS, open symbols), or heavy cracking clays supporting open *Eucalyptus* woodland (CC, crosses). For each treatment combination, four replicates of 25 seeds were assessed.

Figure 3. Germination (mean probability with exact binomial 95% confidence limits) of freshly collected or afterripened (1 or 3 months) seeds of *Byblis filifolia* and *Byblis rorida* following eight weeks of incubation at 25ºC under alternating light/dark conditions (12 h/12 h). Both *B. filifolia* populations were from shallow soil lenses on sandstone aprons supporting sparse herbaceous assemblages (SS), while both *B. rorida* populations were from deeper soil lenses between exposed sandstone pavements supporting low herbfields (DS). For each treatment combination, four replicates of 25 seeds were assessed.
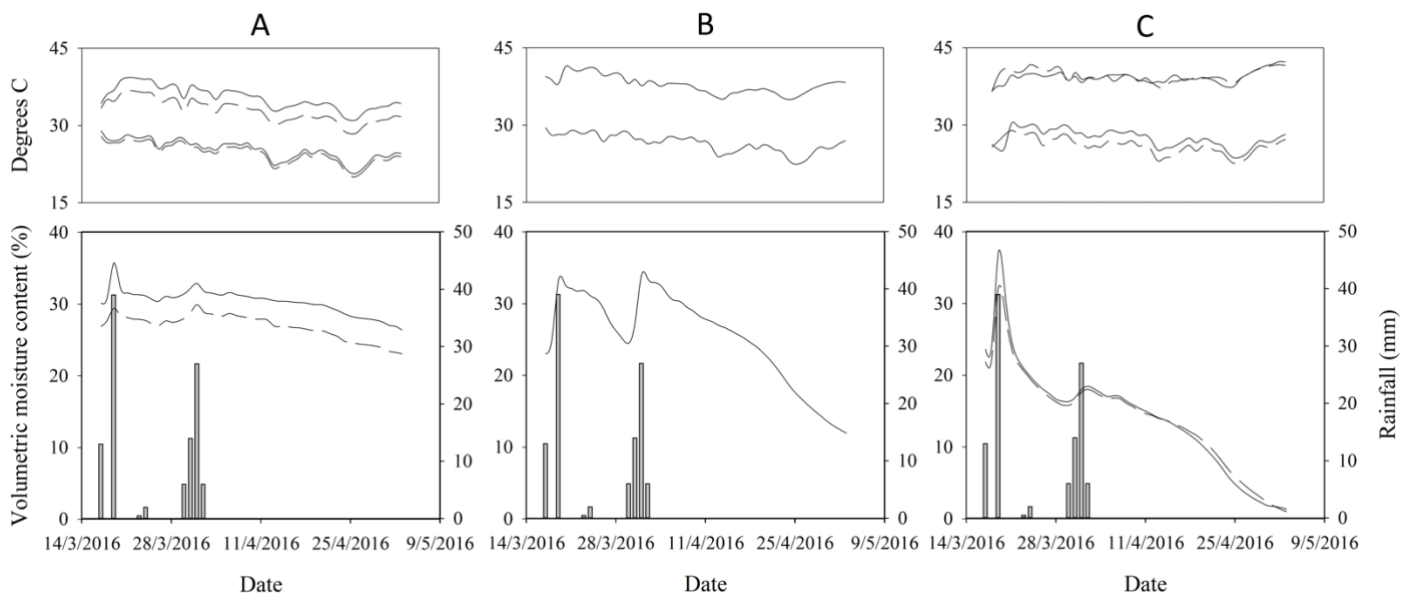
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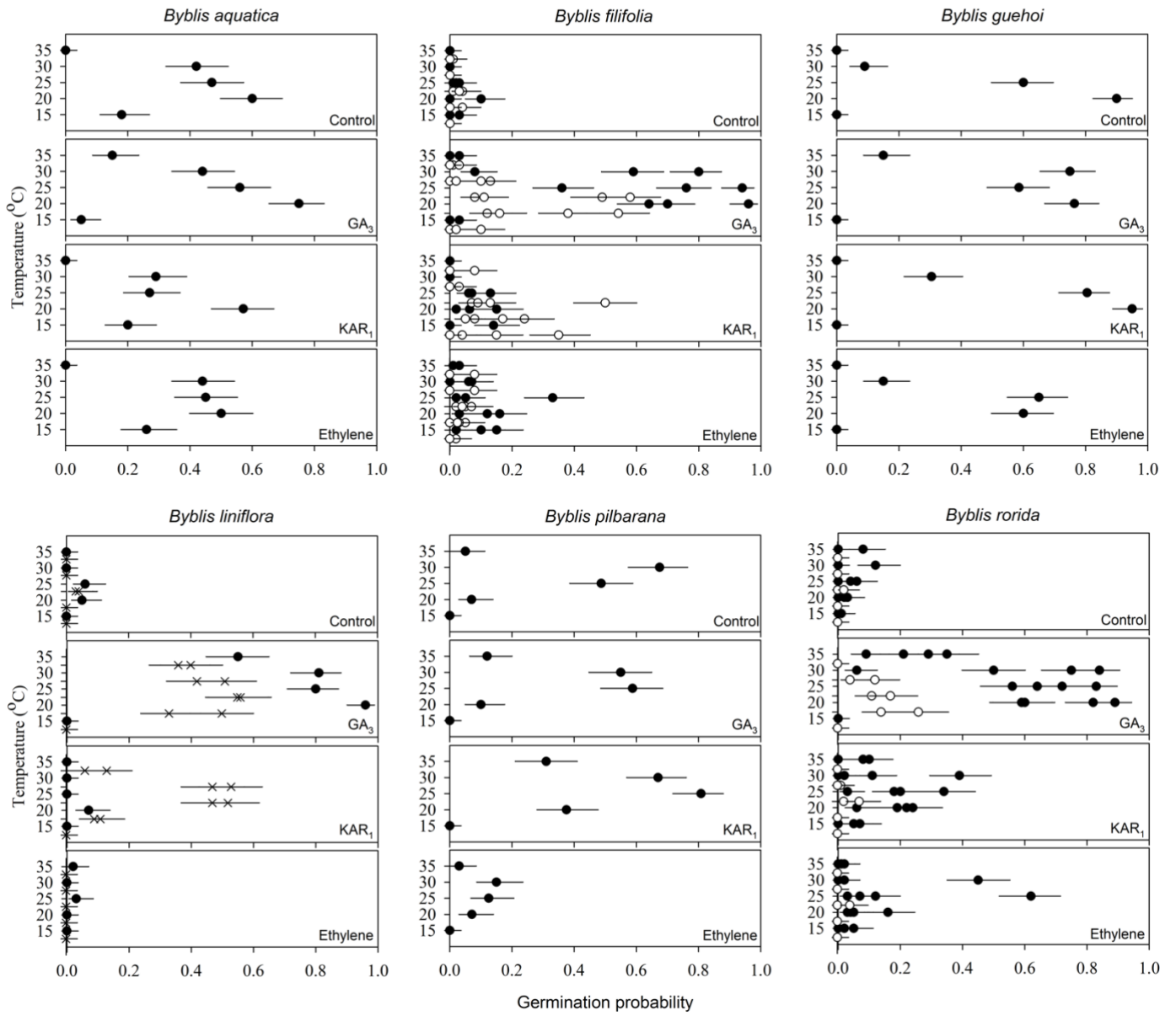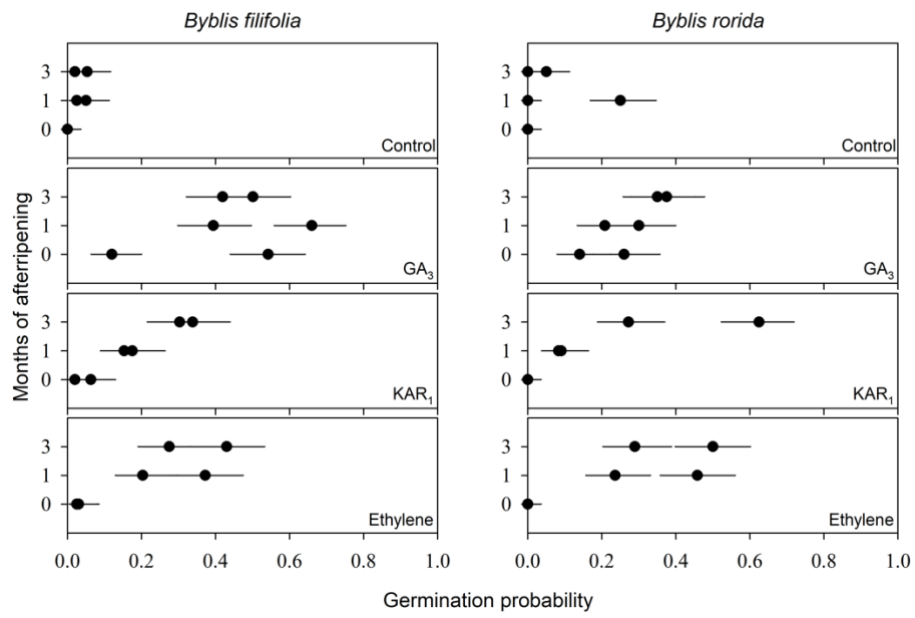
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737   Figure 3.