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Proximate causes and possible adaptive functions of mast seeding and barren flower shows in arid spinifex grasses (Triodia spp.)

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1   **Proximate causes and possible adaptive functions of**

2   **mast seeding and barren flower shows in arid spinifex**

3   **grasses (*Triodia* spp.)**

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13   Running Head: Proximate and adaptive causes of masting in spinifex grasses

14   **Summary text:** Arid *Triodia* grasses are masting plants that occur in regions

15   where episodic wildfires occur after fuel accumulations following high rainfall

16   periods. We conducted a herbarium-based study and found that *Triodia*

17   reproduction is driven by precipitation over 12 months, and that high-yield

18   years corresponded to years of high fire likelihood. We hypothesise that

19   masting in *Triodia* is a fire-related environmentally predictive masting

20   syndrome, which facilitates post-fire stand replacement via the satiation of

21   seed predators during flammable periods.

22 **Abstract.** Arid *Triodia* grasses are fire-sensitive masting plants that occur in

23 regions where episodic wildfires are driven by fuel accumulations after high

24 rainfall years. Despite their reliance on seed banks for post-fire regeneration,

25 seed set in *Triodia* is extremely rare, and levels of flower abortion are high.

26 This study investigated the proximal and evolutionary drivers behind seed

27 production in spinifex by relating the seed set percentages of 79 specimens

28 collected between 1947 and 2012 to the following environmental covariates:

29 antecedent rainfall over 6, 12 and 36 months, relative humidity, and the

30 number of days above 40° C and below 0° C during anthesis. We also

31 investigated whether intermittent seed production by *Triodia* could represent a

32 fire-related form of masting by testing whether high-yield years corresponded

33 to years of increased fire likelihood. Examination of the dataset showed that

34 43% of specimens were completely barren (0% seed fill), while seed set

35 ranged from 2–69% in the remaining specimens. High levels of insect activity

36 were also found, with 42% of specimens showing evidence of insect

37 occupation. Our statistical analyses showed that the main environmental

38 driver of seed set was precipitation over 12 months, and that high yield years

39 were strongly related to years of high fire likelihood. The number of days over

40 40° C was a mildly significant driver of yield, while the remaining covariates

41 were not significant. It is suggested that intermittent reproduction by *Triodia* is

42 an evolved, environmentally predictive masting syndrome that maximises

43 chances of post-fire regeneration by satiating seed predators during periods

44 of high fire likelihood (i.e. after heavy rain years). Furthermore, we propose

45 that non-viable flower crops after initial low rainfalls may have an adaptive

46   function, by diluting pre-dispersal seed predator densities with 'decoy' ovules

47   that do not mature and will lead to the starvation of developing larvae.

48   **Additional keywords:** environmentally predictive masting, arid zone, seed

49   predation, seed bank, fire regime, obligate seeder, spinifex.

50

51   **Introduction**

52   Grasses of the genus *Triodia* form fire-prone grasslands across vast regions

53   of arid and semi-arid Australia (Jacobs 1973). Fires within the grasslands

54   occur primarily in spring or summer seasons after exceptionally high rainfall

55   years, as heavy rains promote fuel accumulation (Griffin *et al.* 1983; McArthur

56   1972; Wright 2007), and the combination of high temperatures and low

57   humidity in warmer seasons provides ideal conditions for flame spread (Allan

58   and Southgate 2001; Allan *et al.* 2003). Burning generally kills arid *Triodia*

59   plants (Burbidge 1943; Suijdendorp 1981), and regeneration after fire is from

60   long-lived, soil-borne seeds that are released from dormancy by smoke during

61   fire (Jacobs 1973; Wells *et al.* 1999; Wright and Clarke 2009).

62   Despite the reliance of spinifex populations on soil seed banks for post-

63   fire seedling recruitment, anecdotal evidence suggests that substantial

64   population-wide seed crops may occur as rarely as once in ten years or more,

65   with little or no seed being produced by flower shows during inter-crop periods

66   (Cunningham *et al.* 1981; Jacobs 1984; Kassell, G., 2013, pers. comm.;

67   Wright, B.R., pers. obs.). Previous ecological works that illustrate *Triodia's*

68   high level of reproductive intermittency include Jacobs' (1973) central

69   Australian PhD research that found little viable seed during a four-year search

70   over a study area comprising many thousands of square kilometers; and the

71 Millennium Seed Bank Project (Kew Gardens) (2006-2009) which consistently

72 came across barren *Triodia* flower shows and failed to return any viable seeds

73 for numerous common arid species (Randall, D., 2013, pers. comm.). High

74 degrees of reproductive intermittency in arid *Triodia* may also be inferred from

75 the paucity of mention in the anthropological literature of *Triodia* seed being

76 used as a food source by Australian Aboriginal peoples (Long 1971; Cane

77 1987). This is in spite of the widespread occurrence of spinifex grasslands

78 within Aboriginal tribal lands, and the fact that the seeds of *Triodia* are non-

79 toxic and much larger in size (and presumably contain higher calorific content)

80 than those of other commonly harvested grasses such as *Panicum* spp. or

81 *Eragrostis* spp. (Cleland and Tindale 1959; Latz 1995).

82   High levels of reproductive intermittency among arid *Triodia*

83 populations indicate that these grasses are masting plants (plants with

84 synchronised but highly variable inter-year seed crop production). Masting

85 plants use environmental cues to synchronise reproduction among

86 populations, and in some cases these cues may be associated with increased

87 resource abundance (Fenner 1998; Davies *et al.* 2013) and in others not

88 (Ashton *et al.* 1988; Wright *et al.* 1999). When inter-year variation in plant

89 reproductive effort mirrors climatic variability, masting syndromes are

90 generally assumed to be non-adaptive and simply tracking favourable weather

91 conditions (i.e. the resource-matching hypothesis (Büsgen and Münch 1929;

92 Norton and Kelly 1988)). However, when annual variation in seed production

93 greatly exceeds climatic variability, evolutionary causes that could have

94 favoured the evolution of 'stricter' masting phenologies are normally looked

95 for. The most popular adaptive explanation for highly variable inter-year

96   reproduction is the predator satiation hypothesis (Salisbury 1942; Janzen

97   1971; Janzen 1976). This hypothesis predicts that mast seeding enhances

98   seed survival because i) synchronous production of bumper crops

99   overwhelms predators and enables some seeds to escape and establish

100   during mast years, and ii) that predators may experience starvation during

101   inter-mast years when there is little available seed.

102   A specialised from of masting that may be relevant to flammable

103   spinifex systems is environmentally predictive masting (EPM). EPM plants

104   use environmental cues to predict years that will be favourable for seedling

105   establishment, and only produce mast crops in such years (Janzen 1971;

106   Silvertown 1980; Burns 2012). While EPM syndromes have been recognised

107   in tropical and temperate ecosystems (Williamson and Ickes 2002; Burns

108   2012), they are best documented in fire-prone habitats (Payton and Mark

109   1979; Gill 1981; Keeley and Bond 1999). In flammable vegetation types,

110   plants may use fire itself as a cue to synchronise flowering and seed

111   production, and this enables capitalization of post-fire environments that are

112   favourable for seedling growth (i.e. have increased soil nutrient status and

113   reduced competition). Examples of post-fire flowerers include monocots in the

114   Australian Xanthorrhoeaceae (Gill 1981), and New Zealand alpine grasses of

115   the genus *Chionochloa* (Payton and Mark 1979).

116   An alternative fire-related EPM syndrome occurs in northern

117   hemisphere boreal forests (Selås *et al.* 2002). Here, spruce trees (*Picea* spp.)

118   initiate 'fire-predictive' mast crops in response to hot and dry summer weather

119   conditions that portend years of increased fire likelihood (Larsen and

120   MacDonald 1995). Producing large seed crops during such times is

121 hypothesised to confer selective advantage on these conifers due to reduced

122 competition for seedlings from higher forest strata after fire. Other fire-related

123 forms of EPM include serotiny (O'Dowd and Gill 1981), and bamboos that

124 produce mast seed crops and then die, thereby promoting high fuel conditions

125 that are conducive to wildfire and will kill off competition to resprouting

126 bamboo seedlings (Keeley and Bond 1999).

127   If both proximate and ultimate factors could be associated with high

128 levels of reproductive intermittency in spinifex, there may also be selective

129 factors involved behind *Triodia*'s frequently observed aborted flower shows. In

130 systems where flower abortion by plants is frequent, excess flowers may i)

131 permit selective abortion of 'poor quality' fruits (the 'selective abortion'

132 hypothesis) (Koslowsky and Stearns 1989); ii) improve a plant's ability to

133 exploit unexpectedly favourable resources (i.e. a bet-hedging strategy)

134 (Guitian 1993; Brown and McNeil 2006); or iii) reduce specialist seed predator

135 populations by luring in ovipositing parents that cannot detect the difference

136 between ovules that will mature, and those which will abort and starve

137 developing larvae (Ramos-Ordonez *et al.* 2008; Ghazoul and Satake 2009).

138 Nevertheless, despite the array of adaptive factors that may explain high

139 levels of flower abortion, there has been no scientific investigation to date into

140 whether any such factors may be relevant to the issue of barren flower shows

141 in *Triodia*.

142   This paper investigated the proximate causes and possible adaptive

143 functions of flower abortion and masting in *Triodia* by examining a dataset that

144 comprised seed yield information from seven species of fire-sensitive central

145 Australian *Triodia* collected between 1947 and 2012. Approximately 5,000

146   florets from 79 plant specimens were examined, and the percentage seed set

147   from these samples was related to the antecedent rainfall, temperature and

148   relative humidity (RH) conditions associated with the period of anthesis for

149   each specimen. We tested the hypotheses that high levels of antecedent

150   rainfall drive seed set in *Triodia*, and that extremes of temperature and RH

151   have negative impacts on overall seed yield. In 59 specimens that had

152   accompanying fire history data, we also tested the hypothesis that a fire-

153   related EPM syndrome could exist in *Triodia*, by relating the yield of

154   specimens with the area burnt across the study area during the 24 months

155   after the collection date of each specimen.

156   **Materials and methods**

157   *Study species*

158   The genus *Triodia* comprises 64 species, all of which are endemic to Australia

159   and most of which occur in arid and semi-arid regions across the northern and

160   central parts of the continent (Lazarides 1997). Plants are long lived (> 30 yr

161   (Latz, P.K., 2013, pers. comm.) and adults have a characteristic hummock

162   growth form, with some species forming rings up to 6 m in diameter as

163   photosynthetically inactive leaves age and decay in the centre. Plants flower

164   after rainfall, and while certain species such as *T. basedowii* may flower at

165   any time of the year (Cunningham *et al.* 1981), most appear to flower

166   following rainfalls during warmer months, from late spring through to the

167   following autumn (Jacobs 1984). Inflorescences generally consist of open or

168   contracted panicles composed of numerous spikelets, with each spikelet

169   being subtended by a pair of glabrous glumes and each comprising 5−21

170 florets (Jessop 1981). For most species, the period from initiating rains to full

171 anthesis takes approximately 4−6 weeks, and seed fall is normally complete

172 within 5−7 days after grain maturation (Wells *et al.* 1999).

173   The breeding systems of *Triodia* are not well understood, though

174 Burbidge (1945) found that plants were self-infertile. However, more recent

175 examinations of the reproductive biology of Australian grasses have failed to

176 identify any cases of obligatory cross-pollination (Whalley *et al.* 2013). It is

177 therefore possible that *Triodia* may possess both self- and cross-fertilising

178 systems.

179   *Triodia* seeds are subject to high levels of seed predation. Common

180 pre-dispersal predators of *Triodia* include the seed-consuming larvae of

181 coleopteran beetles and wasps (Burbidge 1960; Jacobs 1973), and flower

182 feeding katydids (stick insects) (Rentz 2010) and thrips (L. Mound, 2013,

183 pers. comm.). Post-dispersal seed predators of *Triodia* include granivorous

184 ants (Fig. 1*a,b*), various rodents belonging to the genera *Mus, Notomys* and

185 *Pseudomys* (Predavec 1994), an abundant avian fauna, and numerous small–

186 medium sized native marsupials such as the western hare wallaby and the

187 bilby (Bolton and Latz 1978; Westoby *et al.* 1988). Certain ant fauna such as

188 *Iridomyrmex roseatus* also act as dispersers of seed following mast years, but

189 may consume little or none of the seed collected (Anderson, A., 2012, pers.

190 comm.). The ecological significance of the large seed middens of these ant

191 species, some of which may contain > 200,000 collected seeds (Wright, B.R.

192 unpub. data; Fig. 1*b*), therefore remains unclear.

193

194 *Pilot study*

195 Field observations and previous laboratory studies (Wells *et al.* 1999) suggest

196 that the following premises may apply concerning the inflorescence

197 development and seed fill potential of spinifex grasses during a typical seed

198 production event: i) almost all plants in a population produce inflorescences;

199 ii) all inflorescences on a plant produce similar proportions of fertile florets;

200 and iii) there is no statistically significant relationship between seed set

201 potential and spikelet position within an inflorescence (basal, middle or distal).

202 If these three premises are correct, then the examination of seed set

203 percentages of even a small number of spikelets from collected specimens

204 should provide useful information on the seed set percentages of the wider

205 populations from which the specimens have been drawn.

206   These assumptions justified the use of herbarium and seed company

207 collections in the current study to make inferences about the masting

208 dynamics of *Triodia* populations. Therefore, in order to test the validity of

209 these assumptions, a pilot study was conducted on two flowering *Triodia*

210 populations to test for between-hummock and between-inflorescence

211 variations in seed set, and for any effects of within-inflorescence spikelet

212 position on seed fill. The examined *T. pungens* populations were collected

213 from Deep Well station (one collected in May 2012, one in April 2013). From

214 each population, four hummocks spaced >20 m apart were randomly

215 selected, and from each of these hummocks four randomly selected

216 inflorescences were removed. Within each inflorescence, three spikelets were

217 selected from each of the basal, middle and distal portions, resulting in nine

218 spikelets in total from each inflorescence. Each floret within each of these

219 spikelets was then examined under a stereomicroscope for the presence or

220 absence of a healthy mature caryopsis (excluding the top floret which was

221 always sterile).

222 *Herbarium study*

223 The herbarium-based seed yield study examined seed set percentages in the

224 following seven species of fire-sensitive *Triodia*: *T. basedowii* (lobed spinifex)

225 E. Pritz, *T. brizoides* N.T. Burb, *T. irritans* R.Br., *T. longiceps* (giant or hard

226 spinifex) J.M. Black, *T. pungens* (soft spinifex) R.Br., *T. schinzii* (feathertop

227 spinifex) (Henr.) Lazarides, and *T. spicata* (spike flowered spinifex) N.T. Burb.

228 Specimens used for the investigation came from a range of sources, including

229 the Alice Springs Herbarium (in these cases florets from specimen seed

230 pouches were examined), the Alice Springs Desert Park, the Olive Pink

231 Botanic Gardens, various seed companies, and from specimens collected

232 across a span of years by the first author and by staff of the Northern Territory

233 Herbarium (Alice Springs) and the Northern Territory Parks and Wildlife

234 Commission. The specimens were primarily collected from the southern

235 Northern Territory (below the 23rd parallel) and from far north South Australia

236 (above the 27th parallel) (see Appendix for collection localities). A small

237 number of specimens were also collected from regions in the Northern

238 Territory (NT) between the 23rd parallel and 19th parallel.

239 It is acknowledged that the current study had no way of controlling for

240 the possibility that occasional collections may have been made from plants

241 growing in well-watered areas such as roadside verges, thus potentially

242 subjecting these plants to environmental conditions that were not

243   representative of the conditions experienced by wider populations (and hence

244   may have possessed seed fill percentages that were not representative of the

245   seed fill of wider populations). However, it would not be expected that the

246   distribution of such collections would differ among years, and it would

247   therefore not be expected that they would impose any overall statistical effect

248   on our data analysis.

249   The study deliberately avoided using specimens of strongly

250   stoloniferous resprouting forms/species of *Triodia*, as the seeding responses

251   of this functional group may be expected to be different from those of fire-

252   sensitive forms/species of *Triodia*. Consequently, specimens of *T. pungens*

253   above the 23rd parallel were not included, as certain northern forms of this

254   species are strongly stoloniferous and capable of resprouting after fire. It is

255   acknowledged that most *Triodia* are capable of resprouting after fire under

256   some circumstances. However, the conditions that facilitate vegetative

257   recovery are relatively uncommon under natural field situations - that is, very

258   low intensity fire and/or high soil moisture at the time of fire.

259   During the investigation, only collections that had been made during

260   seed fall provided meaningful information regarding percentage seed set.

261   Inspection of collections made too early could not reveal whether fertilisation

262   of ovules had occurred. Consequently, collections that had been made prior to

263   fertilisation were discarded (as evidenced by greenish, unopened florets).

264   Only specimens that had just begun to drop spikelets at the time collections

265   had been made were examined (as evidenced by a straw-coloured tinge that

266   indicated spikelet maturity, and the presence of occasional empty glumes

267   from which spikelets had already fallen).

268   For each specimen, a stereomicroscope was used to examine ovule

269   development and seed fill of approximately 50 florets. As in the pilot study, the

270   terminal floret of each spikelet was always discarded, as these florets were

271   obligatorily sterile. From each specimen, the following data were recorded: the

272   number of florets that had produced viable seed (with viability being assessed

273   by the appearance of a healthy, well-formed caryopsis) (Fig. 2 *a*); the number

274   of florets that possessed fertilised ovules that had swollen and then aborted

275   (late aborted seeds) (Fig. 2 *b*); the number of florets in which ovules did not

276   show any signs of swelling (Fig. 2 *c*); and the proportion of unopened florets

277   (as evidenced by the presence of intact glumes that enclosed both male and

278   female reproductive structures).

279   The proportion of florets that had been subject to pre-dispersal insect

280   predation was also recorded. Evidence of insect activity in florets was

281   documented as being present or absent (such evidence included the

282   presence of frass, eggs, pupal shells, exit holes or actual pupae). A smut,

283   *Ustilago altilis,* and an unidentified Ascomycota fungus were also observed in

284   a number of specimens (Fig. 1*a*). However, these specimens were not

285   included in the study as high densities of spores of these plant diseases

286   generally completely inhibit any possibility of seed fill of grass inflorescences

287   (McTaggart, A., 2012, pers. comm.).

288   *Data analysis*

289   For the pilot study, a multilevel logistic regression was used to examine the

290   effect of hummock, inflorescence and spikelet position on seed fill. Hummock

291   and inflorescence were entered as random intercepts, and the nested

292   structure of the analysis was specified as inflorescence nested in hummock (4

293   inflorescences from each of 4 hummocks). Spikelet position on the

294   inflorescences (basal, middle, distal) was entered as a fixed effect. A $\bar{\chi}^2$

295   statistic was then used to assess whether variation in seed fill existed across

296   hummocks, inflorescences or spikelet position by comparing the model fit of

297   the multilevel logistic regression with a standard logistic regression.

298   In the main herbarium analysis, seed yield data from all the *Triodia*

299   species were pooled and analysed together. This was done because, from the

300   evidence available, the seed production phenologies of all the examined

301   spinifex species are believed to respond in similar positive ways to high

302   rainfall periods (Jacobs 1973; Cunningham *et al.* 1981; Wells *et al.* 1999).

303   Data exploration of the herbarium dataset followed a protocol described by

304   Zuur *et al*. (2010). The presence of outliers was investigated with Cleveland

305   dotplots, while colinearity of covariates was assessed using scatterplots,

306   Pearson correlation coefficients and variance inflation factors (VIF). Initial

307   covariates included in the analysis were: the 6-, 12-, 24- and 36-month

308   antecedent rainfall prior to a specimen's collection date; the number of days

309   with maximum temperatures above 35° and 40° C during the expected

310   anthesis period of a specimen; the number of days with minimum

311   temperatures below 2° and 0° C during anthesis; and the mean relative

312   humidity at 3 pm during anthesis. Covariate data were obtained from the

313   nearest possible Bureau of Meteorology (BOM) weather station, and in most

314   cases these stations existed < 50 km from the collection site. The timing of

315   anthesis for each specimen was estimated to have occurred sometime during

316   the three months prior to the recorded collection date of the specimen

317   (because floret maturation and seed fall generally takes place 6−8 weeks

318   from the time of flower initiation, and all the examined specimens were

319   collected at the time of seed fall).

320   For the analysis of the herbarium study, a generalised linear model

321   (GLM) with a binomial distribution was used to model the number of florets

322   with seeds out of the total number of florets. Initial results indicated

323   overdispersion caused by the excessive number of zeros (43%), and

324   therefore a zero inflated binomial GLM (ZIB) was applied. A ZIB GLM is the

325   binomial equivalent of a zero inflated Poisson GLM (Zuur *et al.* 2012). The

326   model was of the form:

327
$$FloretsSeeds_i \sim ZIB(\pi_i, N_i, \tau_i)$$
$$\text{logit}(\pi_i) = function(\text{Covariates})$$
$$\text{logit}(\tau_i) = constant$$

328   Floret seed fill was modelled with a binomial GLM in which N_i was the total

329   number of florets, and π_i was the probability that observation *i* had florets that

330   contained filled seeds. A logistic link function was used to model the

331   probability of encountering a seed-filled floret as a function of the selected

332   covariates. The zero inflated component of the ZIB GLM model accounted for

333   any excessive zeros that could not be explained by the binomial part of the

334   model. Due to the low sample size (79 observations) no covariates were used

335   for the zero inflated part of the analysis. Parameters of the ZIB GLM model

336   were estimated using Markov Chain Monte Carlo techniques (MCMC) in

337   JAGS (Plummer 2003) via the software package R (Yu-Sung and Masanao

338   2012). In these processes, a burn-in of 40,000 iterations, a thinning rate of 10,

339   and 50,000 iterations for three chains were used. This resulted in 3,000

340   iterations for each posterior distribution.

341   A second ZIB GLM was conducted on a dataset that contained fire

342   history data relating to the area burnt across the study area in the year during,

343   and the year after, the collection date of each specimen. This analysis was

344   intended to test the hypothesis that a fire-related form of environmentally

345   predictive masting could exist in *Triodia*. The fire data had been obtained from

346   a broader dataset provided to the authors by the Northern Territory Bush Fires

347   Council. This dataset had used Landsat satellite imagery to analyse fire

348   occurrence within the study region between 1980 and 2012. The restricted

349   sampling period for the BFC dataset meant that only 59 of the 79*Triodia*

350   specimens could be included in this analysis. Additionally, for six specimens

351   collected in 2012, only the current year's area burnt could be included as no

352   fire history data were available for 2013. The statistical protocols and

353   procedure of the fire ZIB GLM were identical to those of the climate GLM, with

354   the fire analysis modelling the relationship between the seed fill of the

355   specimens and the area burnt during the two-year period after the collection

356   date of each specimen.

357   **Results**

358   *Pilot study*

359   In the pilot studies, no seeds were found in the April 2013 *T. pungens*

360   flowering event. Consequently, no analyses were conducted on these data,

361   and it was accepted that for this event seed set was zero for all hummocks,

362   inflorescences and inflorescence positions.

363   Seeds were recorded in the May 2012 collections of *T. pungens* and

364 the results of the logistic regression of the seed fill data showed that the fit of

365 the multilevel model was not significantly better than the standard model, $\bar{\chi}^2$

366 (2) = 0.00, *p* = 1.00 (Fig. 3). This demonstrated that there was no significant

367 variation in seed fill across the examined factors (hummock, inflorescence,

368 and spikelet position). The results of both the May 2012 and the April 2013

369 pilot analyses therefore indicated that spikelets and inflorescences collected

370 from single hummocks could be used to reliably estimate the percentage seed

371 fill for sample populations.

372 *Herbarium study*

373 Data exploration of the main dataset revealed that 43% of specimens were

374 completely barren (0% seed fill), and that seed fill in the remaining 'viable'

375 specimens (>0% seed fill) ranged from 2–69% (see Appendix). Twelve

376 percent of florets from 'viable' specimens contained late-aborted seeds, while

377 7% of florets of 'barren' specimens contained late-aborted seeds (Fig. 4).

378 'Viable' specimens also contained a mean of 46% undeveloped ovules and

379 15% unopened seedless florets, while 'barren' specimens contained a mean

380 of 45% of undeveloped ovules and 39% unopened seedless florets.

381   A large proportion of specimens also contained evidence of insect

382 activity (42%), and rates of infestation ranged from 0–48% of florets (see

383 Appendix). Nineteen percent of insect-infested specimens were from

384 completely aborted (barren) specimens (Fig. 5). Insect activity came largely

385 from an unidentified cecidomyiid fly, believed to belong to the genus

386 *Stenodiplosis* (Kolesik, P., 2013, pers. comm.) (Fig. 1*b*). The oviposited larvae

387   of *Stenodiplosis* feed on the seeds of host plants (generally grasses), and are

388   known to be major pests of crop grasses in certain regions of the world

389   (Damte *et al.* 2009). In some cases, these larvae were found inside the

390   florets. However, it was impossible to determine whether freezing or

391   chemicals had killed them during fumigation in herbaria, or whether the larvae

392   had died of natural causes in the field. A number of species of parasitoid wasp

393   (Hymenoptera) were also encountered occasionally. These wasp complexes,

394   whose larvae may be seed-eaters or consumers of the eggs, larvae or pupae

395   of flies, are recognised as important control agents of invasive cecidomyiid

396   flies globally (Lambkin *et al.* 2008).

397   Data exploration of the main herbarium specimen dataset indicated

398   that there were no outliers present. However, colinearity among many of the

399   explanatory variables was severe, with Pearson correlations between some

400   covariates as high as 0.9 (e.g. the 24- and 36- month antecedent rainfall).

401   Therefore, following an assessment of colinearity (using a VIF threshold of 3)

402   the following covariates were selected for inclusion in the analysis: the 6-, 12-

403   and 36-month antecedent rainfall, the number of days above > 40^0 C, the

404   number of days < 0^0 C, and relative humidity. Figure 6 shows a multi-panel

405   scatterplot visualising the relationship between the proportions of florets with

406   seeds versus each selected covariate.

407   From the 95% posterior intervals of the MCMC analysis, it was

408   observed that the mean of the posterior distribution of 12-month antecedent

409   rainfall was well away from zero, indicating that this variable had a significant

410   effect on seed fill (Table 1). Conversely, rainfall over 6 and 36 months were

411   not significant drivers of seed fill. The number of days with maximum

412 temperatures > 40^0 C during anthesis was interpreted as having a mildly

413 significant positive effect on yield, while mean daily humidity (RH at 3 pm) and

414 the number of days with minimum temperatures < 0^0 C during anthesis were

415 not significant. From the fire analysis, the posterior distribution was well away

416 from zero (Table 1), indicating that *Triodia* seed production is strongly

417 positively related to the likelihood of increased area burnt during the 2 years

418 after seed fall (Fig. 7).

419 **Discussion**

420 *Proximate drivers of seed set*

421 This investigation demonstrated that antecedent rainfall over protracted

422 periods (12 months) is the primary driver of seed set in arid *Triodia*. The

423 finding that precipitation influenced reproduction in *Triodia* was not at all

424 unanticipated, as seed set in crop and pasture grasses invariably has a

425 positive response to rainfall (Robertson and Holland 2004; Bannayan *et al.*

426 2011). However, the discovery that spinifex yield was more correlated with

427 antecedent rain over 12 rather than 6 months was unexpected, as the seed

428 production of grasses should be tied to soil moisture conditions immediately

429 prior to and/or during the grain-filling season (Bannayan *et al.* 2011).

430   The finding that protracted high soil moisture conditions are conducive

431 to seed set in *Triodia* indicates the presence of an internal response

432 mechanism that switches from vegetative growth to reproductive output once

433 a threshold long-term rainfall volume is reached. From our results, it appears

434 that this threshold lies somewhere around 500−600 mm over 12 months.

435 Interestingly, similar large quantities of protracted antecedent rainfall are

436   required to allow spinifex fuels to accumulate to levels that will permit

437   widespread wildfires to occur (Allan and Southgate 2001; Allan *et al.* 2003,

438   Allan, G., pers. comm.). Consequently, the peak periods of *Triodia* seed filling

439   coincided with the three main periods of widespread fires – the mid-1970s, the

440   early 2000s and most recently between 2010 and 2012 (see Appendix). It

441   would be of interest to determine whether further protracted rains after initial

442   *Triodia* mast years would elicit subsequent high seed production, or whether

443   mast crops substantially deplete resources and delay the production of

444   successive large crops (as has been recently established by Davies and

445   Kenny (2013) in arid woody masting species in Western Australia). However,

446   further research would be required to test this hypothesis.

447   The finding that the number of days above 40° C had a significant

448   positive effect on seed set in *Triodia* was unexpected. Previous studies have

449   shown that exceptionally high temperatures during reproductive phases can

450   reduce seed set in grasses by imposing negative physiological stresses on

451   male and female gametophyte development, disrupting pollen release, and

452   having negative overall effects on fertilisation and embryo development

453   (Bykova *et al.* 2012). The finding that *Triodia* specimens still exhibited good

454   seed set despite high numbers of days > 40° C suggests a high level of innate

455   resilience to elevated temperatures during reproductive phases (which may

456   not necessarily be unexpected given the benefits that *Triodia's* C4 metabolism

457   should confer in hot and dry climates). However, it is also probable that this

458   finding could reflect the preference for these species to flower primarily during

459   warmer months, when the influence of the north Australian summer monsoon

460   is strongly in arid Australia.

461   *Adaptive functions of mast seed production*

462   While the current study identified antecedent rainfall over preceding seasons

463   as the environmental cue that initiates seed set in arid *Triodia*, it is possible

464   that the high degree of reproductive intermittency in these species could be

465   more than simply a response to fluctuations in soil moisture resources. If

466   *Triodia* seed production is non-adaptive and simply tracks seasonal weather

467   conditions, we would expect between-year fluctuations in seed production that

468   largely mirrored weather variability (i.e. with reduced seed set in low rainfall

469   years and increased crop viability in high rain years). However, as the current

470   and previous studies have shown, this is not the case in *Triodia* (Jacobs 1973,

471   1984).

472   *Triodia* grasses exhibit a strongly bimodal reproductive cycle, with no

473   seed output in most years, but with massive crops produced occasionally.

474   This contrasts with the weather conditions in arid Australia, which are highly

475   variable between years, but certainly not bimodal. The seeding response of

476   arid spinifex therefore differs markedly from other annually seeding grass and

477   shrub species that occur in *Triodia* grasslands (e.g. certain woody *Acacia*,

478   *Eremophila, Hakea* and *Santalum* species (Davies 1976, Friedel *et al*. 1994;

479   Davies and Kenny 2013), and perennial grasses such as *Eragrostis eriopoda*

480   and *Astrebla* spp. (Orr and Evenson 1991)), and appears more in line with

481   classical 'strict' masting plants, in which the adaptive benefits of masting are

482   well established (e.g. New Zealand's alpine grass genus *Chionochloa* (Kelly

483   *et al.* 2001), members of the Dipterocarpaceae from southeast Asia (Wells

484   and Bagchi 2005; Visser *et al.* 2011) and bamboos (Janzen 1976; Keeley and

485   Bond 1999)).

486   If seed production in arid *Triodia* is more variable than would be

487   expected under a 'resource-matching' scenario, what adaptive advantage

488   could explain the production of bumper seed crops after well-above-average

489   rain periods? One possibility is that rain-driven masting in *Triodia* is an

490   environmentally predictive masting (EPM) syndrome, with plants using

491   protracted rainfall as an environmental signal to mast because protracted

492   rains reliably predict future periods of high fire likelihood. Such a syndrome

493   would limit wastage of reproductive effort during periods of low flammability

494   (when seedling regeneration is constrained by competition from parent *Triodia*

495   plants), and improve the likelihood of satiating pre- and post-dispersal seed

496   predators during periods of high flammability. Predator satiation at this time

497   would increase the numbers of seeds available to be released from dormancy

498   by smoke during fire, and effectively maximise the chances that freshly

499   recruited seedlings would replace fire-killed adult stands after fire. Limiting

500   mast seed production to occasional periods of high flammability might also

501   have the added benefit of eliciting a 'numerical response' on seed predators,

502   by starving populations during low output inter-mast periods (Janzen 1971;

503   Kelly 1994).

504   The finding of the current study that *Triodia* seed production is

505   statistically associated with periods of high fire likelihood supports the

506   possibility that a fire-related form of EPM exists in *Triodia*. However, for such

507   a syndrome to be present, protracted rainfall and fire must have been

508   correlated with each other in Australian deserts for long periods of

509   evolutionary time (Satake, A., 2013, pers. comm.). This seems highly likely,

510   as increased flammability following high rainfall is an intrinsic feature of dry,

fuel-limited ecosystems the world over (Meyn *et al.* 2007), and is likely to have

existed in inland Australia since the mid–late Miocene, some 10−6 million

years ago (Kemp 1981; Truswell 1993; Enright and Thomas 2008). In

sedimentological records that relate to this period, grass pollen becomes

progressively more apparent, and aridity increases as the Australian continent

moved northward into higher latitudinal zones. Charcoal signals from fires

also intensify during this time, with lightning believed to have been the main

vector of ignition (Kemp 1981).

It would be of interest to determine whether a similar 'fire-predictive'

masting syndrome exists in *Triodia* from more mesic regions of Australia.

However, such a seeding phenology may be unlikely as the link between

antecedent rainfall and fire disappears in moist environments, and fuel

dryness rather than fuel load becomes the critical factor in allowing large fires

to occur (McArthur 1972). Furthermore, spinifex species that occur in more

mesic regions are either resprouters (and hence would not be subject to the

same strong selective pressure for a seed source in post-fire environments as

obligate seeding arid species), or are fire-killed but seed regularly on an

annual basis (Armstrong and Legge 2011).

Adaptive functions of barren flower shows

If some portion of the high levels of seeding intermittency in *Triodia* is linked

to adaptive factors, there could also be adaptive function/s that explain the

high degree of flower abortion commonly exhibited by arid *Triodia*. The

'selective abortion' hypothesis seems unlikely, as the frequent occurrence of

completely aborted flower shows does not suggest any form of selection for

535   genetically superior ovules is taking place. Likewise, the possibility of some

536   kind of 'resource prediction' trait seems doubtful (where plants would use an

537   initial rain event to begin a flower crop, and then 'wait' for follow-up rainfall to

538   mature fruits), as the short lead time between *Triodia* flower initiation and full

539   seed maturity (~6−8 weeks) does not seem conducive to this type of

540   reproductive phenology. Furthermore, from the current study, examination of

541   the rainfall data showed no evidence that seed fill was constrained when

542   flowerings were driven by only a single rainfall event, and Rice *et al.* (1994)

543   found no effect of resource addition (in the form of fertiliser) on seed set in *T.*

544   *basedowii, T. pungens* or *T. schinzii*.

545   A possible adaptive explanation for high proportions of late-aborted

546   seeds in *Triodia* is that plants are using excess flowers to dilute pre-dispersal

547   seed predator populations with 'decoy' ovules that lack endosperm and will

548   ultimately starve developing larvae (*sensu* the 'sacrificial sibling hypothesis'

549   (SSH) of Ghazoul and Satake (2009)). In resource-limited environments,

550   plants would be expected to have developed mechanisms to abort seed as

551   early as possible to avoid wasting resources. However, under the SSH, plants

552   should retain such seed until after oviposition of seed predators. The findings

553   of the current study support this possibility, as there was often evidence of

554   insect activity on completely barren flower crops (indicating that ovipositing

555   adults had not discriminated against flowers with ovules that would eventually

556   abort). There was also evidence of dead (starved?) seed-feeding larvae on

557   some specimens that contained high numbers of florets with late-aborted

558   ovules. However, at this stage it is impossible to say whether these larvae had

559   died in the field as the result of starvation due to incomplete caryopsis

560   maturation, or as the result of herbarium fumigation or freezing.

561   If 'decoy' masts dilute predator numbers, they may confer considerable

562   benefit to fire-killed *Triodia* populations that are subjected to subsequent

563   heavy rainfall events after initial 'decoy' flowerings. In these situations, the

564   likelihood of burning increases greatly and the requirement for large volumes

565   of fresh seed becomes paramount. If such subsequent rains are accompanied

566   by fecund flowering efforts (as the current study indicates happens during

567   protracted, high rainfall periods) then these 'follow-up' flowering efforts should

568   be subject to reduced pre-dispersal seed predator densities as the result of

569   predator declines following the initial 'decoy' masts. Consequently, the overall

570   percentage seed set of the follow-up masts should be higher, and the

571   likelihood of predator satiation and successful post-fire regeneration should

572   increase. If no such subsequent rains (or fires) occur after initial 'decoy'

573   masts, these initial masts may have resulted in little energetic loss to the

574   plants, as grass inflorescences are largely comprised of photosynthetic tissue

575   and hence may cover the costs of their own production.

583 Deep Well station. Jaboury Ghazoul, Ken Hodgkinson, Peter Latz, Richard

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586

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Table 1. Results of the MCMC analysis. The column labelled 'Mean' gives the mean value
of the posterior distribution for each covariate. The columns labeled 2.5% and 97.5% define
the 95% credible interval for each covariate (the Bayesian equivalent of a 95% confidence
interval). If 0 is within the credible interval, the corresponding covariate is considered
unimportant in the analysis.

|	Mean	SE	2.5%	97.5%
Climatic variable analysis				
(Intercept)	-0.74	0.13	-0.99	-0.48
Rainfall 6 Month	-0.16	0.08	-0.33	-0.01
Rainfall 12 Month	**0.67**	**0.09**	**0.49**	**0.85**
Rainfall 36 Month	-0.08	0.07	-0.22	0.05
Days Max >40°C	**0.40**	**0.08**	**0.25**	**0.55**
Days Min <0°C	-0.13	0.05	-0.22	-0.04
RH at 3pm	0.04	0.07	-0.09	0.18
Fire analysis				
Area Burnt	**0.66**	**0.10**	**0.47**	**0.86**
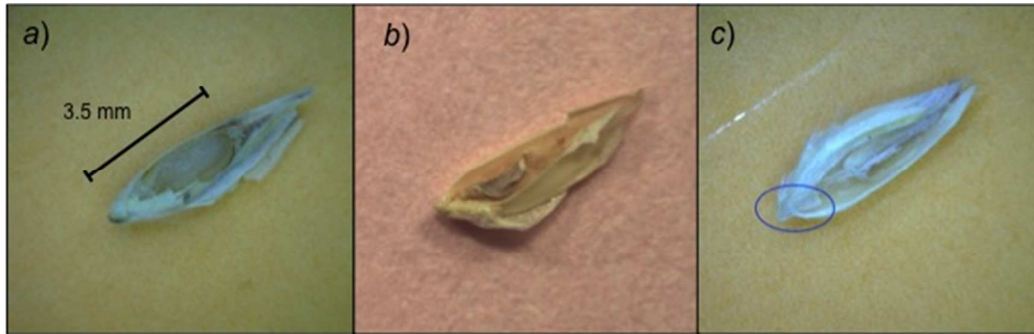
Fig. 2. Fully formed *T. pungens* caryopsis (*a*), late-aborted *T. pungens* seed (*b*), and *T. pungens* floret with intact anther and no sign of ovule development (*c*).
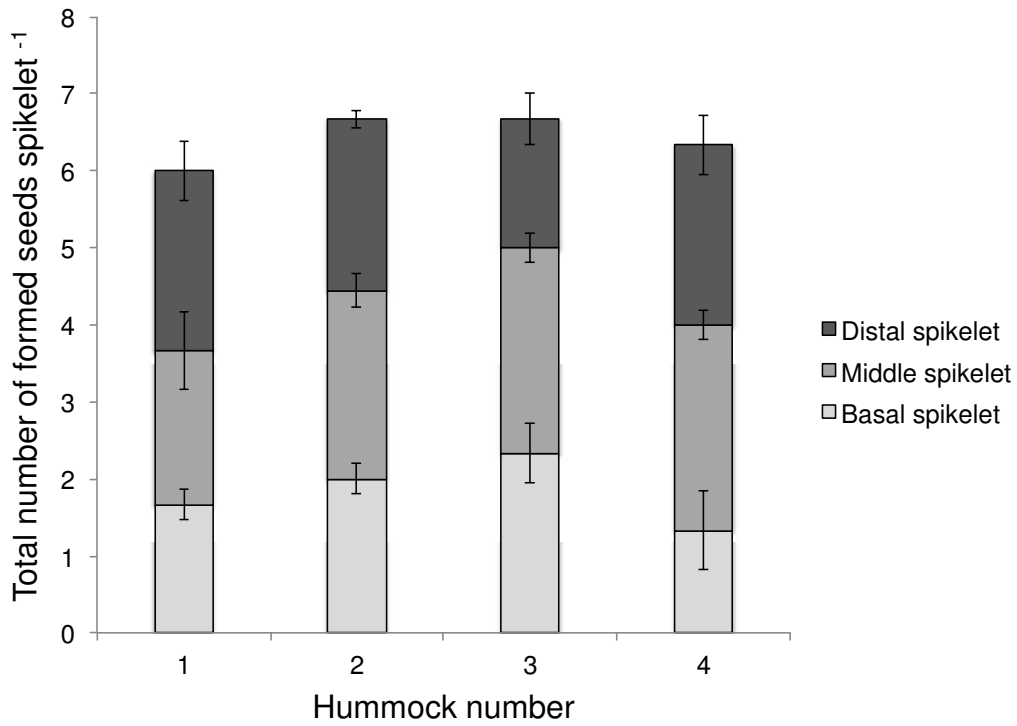
Fig. 3. Mean seed fill of spikelets obtained from three positions (basal, middle and distal) of four inflorescences from each of four *T. pungens* hummocks collected from Deep Well station in May 2012.
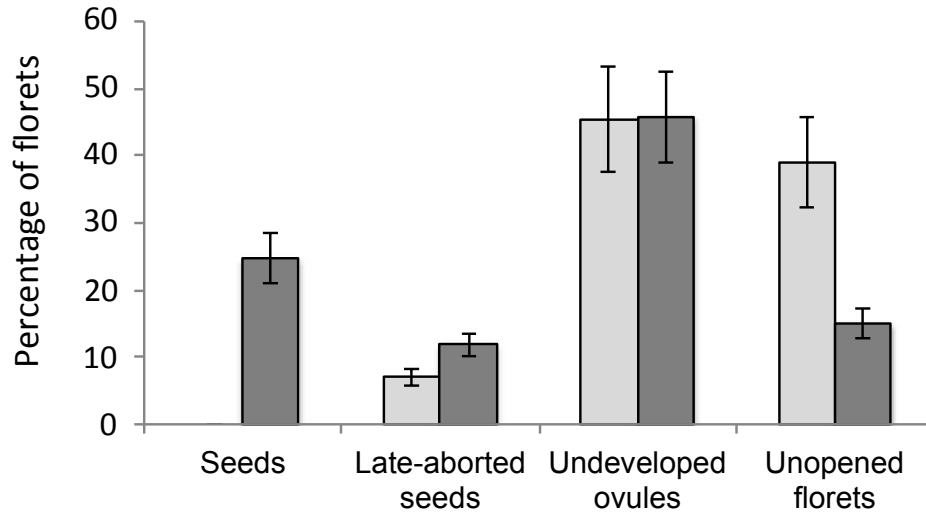
Fig. 4. Mean proportion of florets across all specimens that contained seeds, late-aborted seeds, undeveloped ovules or unopened florets. The four developmental groups are further categorised according to whether specimens were 'barren' (light shading), or had set seed ('viable') (dark shading).
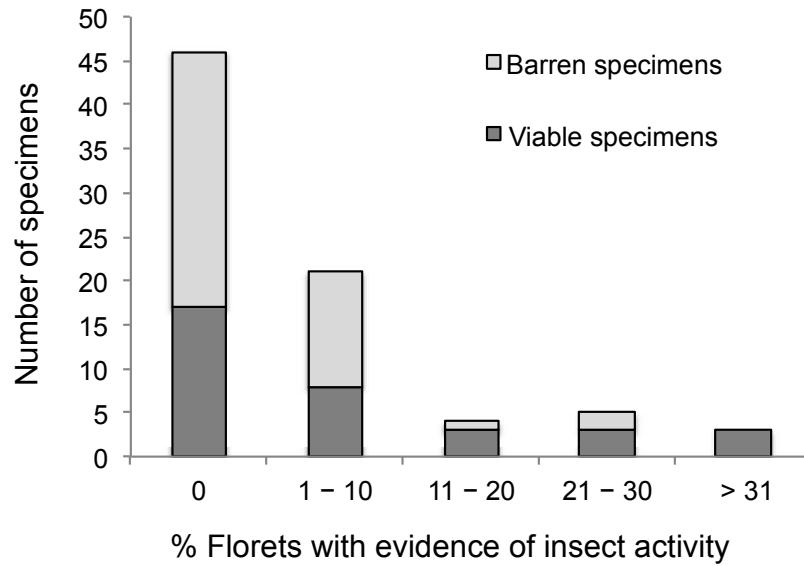
Fig. 5. The number of examined specimens that contained evidence of insect activity, grouped according to the percentage of examined florets within a specimen that contained evidence of insect activity. Groups are further partitioned into the number of specimens that came from inflorescences that were 'barren' or 'viable'.
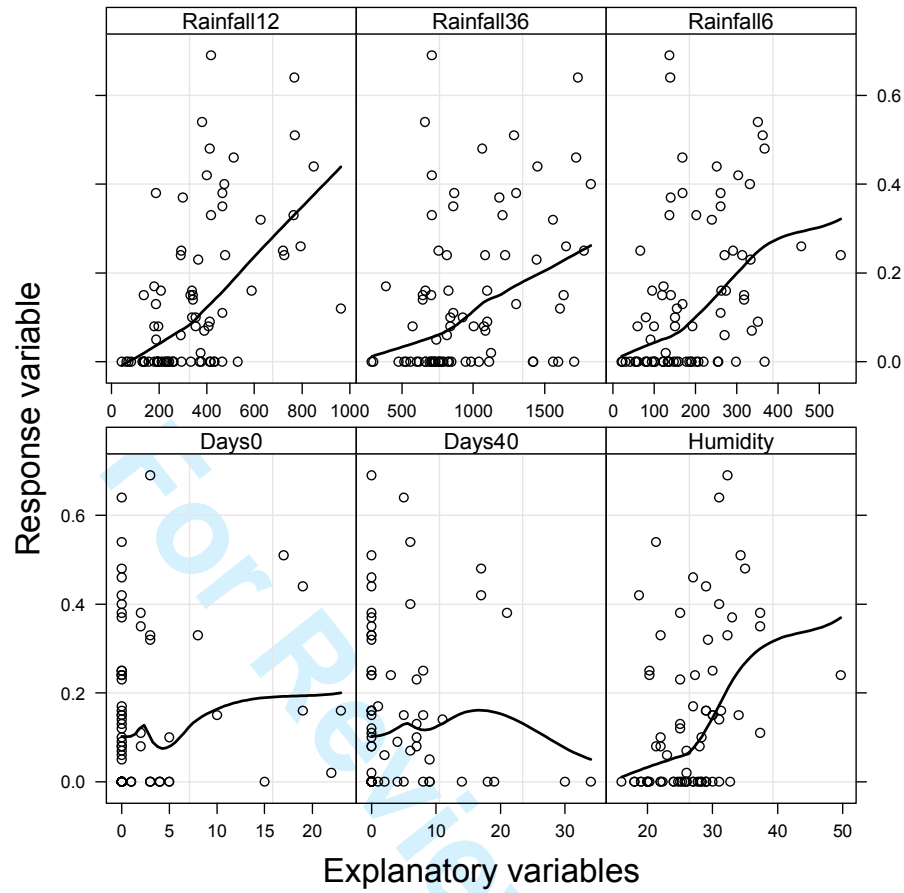
Fig. 6. Percentage *Triodia* seed fill (response variable) versus six explanatory environmental variables: 6-, 12- and 36-month antecedent rainfall, number of days above 40^0 C and below 0^0 C during anthesis, and the mean relative humidity at 3 pm during anthesis.
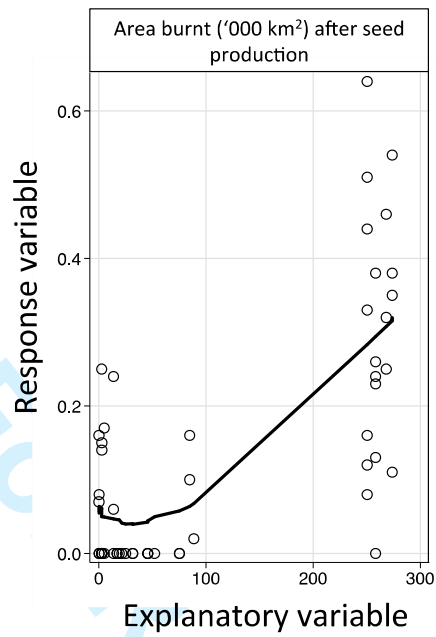
Fig. 7. Proportion *Triodia* seed fill (response variable) versus the area burnt ('000 km^2) across the study area during the 2 years after the collection date of the corresponding specimen (explanatory variable).