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**Fire after a mast year triggers mass recruitment of slender mulga (*Acacia aptaneura*), a desert shrub with heat-stimulated germination**

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1 **Fire after a mast year triggers mass recruitment of slender mulga**  
2 **(*Acacia aptaneura*), a desert shrub with heat-stimulated**  
3 **germination**

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16 Running Head: 'Burning after masting triggers mass recruitment in slender mulga (*Acacia*  
17 *aptaneura*)'

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20 **PREMISE OF THE STUDY:** Fire typically triggers extensive regeneration of plants with  
21 heat-stimulated germination by causing short periods of intense soil heating. If plants with  
22 heat-stimulated germination are also subject to seed predation and display mast-seeding  
23 cycles, post-fire recruitment may be contingent on the seedfall density of pre-fire masts, and  
24 on whether granivores are satiated at the time of fire.

25 **METHODS:** We conducted a longitudinal seedbank study and a mensurative field  
26 experiment in central Australia to examine whether fire and the variation in seedfall density  
27 across sites in a mast year interact to influence recruitment of slender mulga (*Acacia*  
28 *aptaneura*), an iteroparous masting shrub with heat-stimulated germination.

29 **KEY RESULT:** The seedbank study showed seedbank pulsing after masting, with mean  
30 seed counts in the upper 4-cm soil layer being 132.8 seeds/m<sup>2</sup> 12-months after a dense  
31 seedfall, but only 3.8 seeds/m<sup>2</sup> following a year with no seed production. Consistent with  
32 this, recruitment increased post-fire at sites where denser seedfall had occurred during the  
33 pre-burn mast year, whereas little recruitment occurred at unburnt populations, irrespective of  
34 pre-fire seedfall density.

35 **CONCLUSIONS:** We attribute our findings to 1) elevated soil temperatures during fires  
36 stimulating germination of heat-cued seeds, and 2) granivore satiation following masting  
37 facilitating assimilation of seeds into the soil seedbank. These results provide the first  
38 example of an interactive effect between fire and seedfall density during a mast a year on  
39 recruitment in an arid biome, and highlight the importance of rare seed-input events for  
40 regeneration in fire-prone systems dominated by masting plants.

41 **Key words** Aridity; Bayesian statistics; Fabaceae; fire ecology; mass flowering; mast  
42 seeding; predator satiation; recruitment; reproductive ecology; seedbank

43 Fire is an important driver of recruitment processes for plants with soil-stored seedbanks and  
44 seeds that are triggered to germinate by heat (Gill, 1981; Keeley et al., 2011; Chamorro et al.,  
45 2017). Another important process known to impact recruitment patterns is mast seeding,  
46 which is the synchronous but highly variable production of seed crops by plant populations  
47 (Salisbury, 1942; Borchert and DeFalco, 2016; Zwolakl et al., 2016). Despite that masting  
48 during pre-fire periods may facilitate post-fire recruitment by satiating predators and  
49 bolstering pre-fire seedbanks, the effects of variable seedfall densities during pre-fire masts  
50 have rarely been examined (Peters et al., 2005). We carried out a mensurative field  
51 experiment to investigate whether seedfall density during a pre-fire mast year drives seedling  
52 regeneration of slender mulga (*Acacia aptaneura* Maslin & J.E. Reid [Fabaceae]) (hereafter  
53 mulga), a desert Australian masting shrub with heat-stimulated germination.

54 Several non-mutually evolutionary hypotheses have been evoked to explain mast  
55 seeding, including predator satiation (Janzen, 1971; Meyer and Pendleton, 2015), improved  
56 wind pollination efficiency of outcrossing plants (Smith et al., 1990; Kelly et al., 2001), and  
57 wider propagule dispersal by scatter hoarders (Xiao et al., 2013). In some instances, masting  
58 is unrelated to evolutionary factors, but purely a response to inter-annual fluctuations in  
59 resource availability (i.e. the resource-matching hypothesis [Kelly and Sork, 2002; Monks  
60 and Kelly, 2006]). However, documented examples of resource-matching masting plants are  
61 rare (Snook et al., 2005; Pearse et al., 2016). With regards to the proximate triggers that  
62 synchronize masting, some plants mast in response to cues associated with increased resource  
63 levels (e.g. elevated temperatures or high precipitation [Davies, 1976; Norton and Kelly,  
64 1988; Koenig et al., 1996]), whereas others mast in response to cues that are associated with  
65 reduced resources (e.g. drought [Espelta et al., 2008]) or that are unrelated to resource levels  
66 (e.g. barometric pressure [Williamson and Ickes, 2002]).

67 Mast seeding plants are common in fire prone habitats, with well-known examples  
68 including species of Northern Hemisphere temperate forest tree genera such as *Fagus*, *Picea*,  
69 and *Pinus* (Peters et al., 2005; Ascoli et al., 2013; Buechling et al., 2016), certain Australian  
70 *Eucalyptus* species (O'Dowd and Gill, 1984; Franklin et al., 2016), and semelparous masting  
71 bamboos from fire-prone subtropical forests (Brandis, 1899; Keeley and Bond, 1999). Similar  
72 to non-masting plants, post-fire recruitment dynamics of masting plants can relate to factors  
73 such as the size of the pre-fire seedbank, seed mortality during fire, and the proportion of the  
74 seedbank released from dormancy during fire (Moreno and Oechal, 1991; Whelan, 1995;  
75 Bond and van Wilgen, 1996). For species with long masting cycles, and/or that are subject to  
76 high levels of seed predation, fire-timing in relation to masting may be an important  
77 determinant of pre-fire seedbank levels. This is because long intervals between mast events  
78 and fire may allow predators more time to reduce the size of the pre-burn seedbank (Whelan,  
79 1995; Wright and Fensham, 2017). Additionally, the seedfall density (i.e. the total viable seed  
80 production [Nakajima, 2015]) of a mast crop prior to a fire may be important, as a significant  
81 positive relationship usually exists between seed crop size and the proportion of a seed crop  
82 that escapes predation (Silvertown, 1980; Tsvuura et al., 2011; Borchert and DeFalco, 2016).

83 Mulga is a fire-sensitive single- or multi-stemmed masting shrub that dominates  
84 woodlands in arid and semi-arid climate zones across c. 20 % of Australia (Maslin and Reid,  
85 2012). It is easily killed by high-severity fire, though juveniles and adults may resprout from  
86 epicormic buds if burnt under low-severity conditions (Griffin and Friedel, 1984; Hodgkinson  
87 and Oxley, 1990). Mulga recruitment is typically enhanced by fire, as its seeds are stimulated  
88 to germinate by temperatures between 80 and 100 °C, and such temperatures are often  
89 achieved in upper soil layers during fire (Fox, 1985; Hodgkinson and Oxley, 1990). In  
90 addition, fire severity influences recruitment patterns, as high-severity fires with high soil

91 heating trigger increased recruitment compared to low-severity fires that only partially  
92 combust dense understory litter layers (Hodgkinson and Oxley, 1990; Wright et al., 2015).

93 Masting in mulga is rainfall mediated (Preece, 1971a; Davies and Kenny, 2013), and  
94 in the Australian arid zone wildfires naturally occur after mast years because the high rainfall  
95 periods that trigger masting also drive fuel accumulations and wildfires (Griffin et al., 1983;  
96 Allan and Southgate, 2002; Bastin and Allan, 2012). The seeds of mulga are subject to  
97 predation from chalcid wasps (*Mesopolobus* sp.), birds such as galahs (*Eolophus roseicapilla*  
98 Vieillot) and emus (*Dromaius novaehollandiae* Latham) (Preece, 1971b; Davies, 1976),  
99 rodents, beetles, and possibly ants and termites (Preece, 1971b; Davies, 1976; Leavesly,  
100 2008). Presumably as a result of the seeds being favored by granivores, previous seedbank  
101 studies have found mulga seedbanks to be very sparse (Page, 2009; Wright and Clarke,  
102 2009), or non-existent (Hodgkinson et al., 1980). However, short-lived seedbank pulses in  
103 upper soil layers do occur following mast years, apparently because seed predators are  
104 satiated during such periods, which allows a fraction of the seed crop to disseminate into the  
105 soil (Wright and Zuur, 2014; Wright et al., 2015).

106 We conducted a mensurative field experiment across 14 central Australian sites to  
107 examine whether post-fire mulga recruitment is dependent on the density of seedfall during a  
108 pre-burn mast event. The study took place following an exceptionally high rainfall period that  
109 led to widespread but variable (in terms of output and synchrony) masting in late 2010 and to  
110 subsequent extensive wildfires in 2011. The use of widely dispersed study sites across our  
111 study area permitted access to a range of population-level seedfall densities during the 2010  
112 mast year. This in turn allowed testing of the effects of pre-fire mast seedfall density on  
113 recruitment. We measured seedfall from the mast year indirectly, by estimating the density of  
114 pods in the litter layer of each population at each site. This method was used because of its  
115 efficiency, and because prior studies have found similar indirect measures of seedfall (e.g.

116 flowering intensity or visual seed surveys) are strongly correlated with sound seedfall density  
117 during mast events (Perry and Hill, 1999; Suzuki et al., 2005; Nakajima, 2015).

118         The 2010 mast year was the first time synchronized, population-wide mulga seeding  
119 had been observed in 8 years of fieldwork on Aboriginal and pastoral station land in central  
120 and west-central Australia (Latz, P.K., pers. comm. 2017; B.R.W. pers. obs.). It was also the  
121 first time since 2000 that the Yuendumu Mining Company had been able to purchase mulga  
122 seed for rehabilitation purposes from Aboriginal seed collectors in north-west central  
123 Australia (Baada, F. pers. comm, 2017) (Fig. 1 A, B). We predicted a strong relationship  
124 between seedfall densities during masting and recruitment after the 2011 fires, because  
125 overall recruitment potentials should have been contingent on whether predators were  
126 satiated prior to fire, which in turn would have determined whether seedbanks were dense at  
127 the time of fire. We also predicted there would be little recruitment beneath unburnt plants,  
128 irrespective of pre-burn seedfall density, owing to the absence of the necessary heat cue to  
129 trigger germination. In addition to the recruitment study, we conducted a longitudinal 7 yr.  
130 seedbank study to quantify temporal changes in the depth distribution of mulga seedbanks in  
131 response to masting. Data provided by this study enumerated 1) whether periods shortly after  
132 high output mast years are associated with higher seedbank densities than inter-mast periods  
133 when seed production is low or absent, and 2) the vertical distribution of seed in the soil  
134 seedbank - important for understanding how temperatures at different soil depths interact  
135 with the germination biology of seeds during fire.

## 136 **MATERIALS AND METHODS**

### 137 *The study system*—

138 The 14 study sites were located across a roughly east-west trending transect from Alice  
139 Springs in the east, to Newhaven Conservation Reserve, approximately 300 km to the west

140 (Table 1). Soils at all sites were red earths, or kandosols, and detailed descriptions of the sites  
141 have been published previously by Wright et al. (2015). The vegetation at all sites was  
142 dominated by stands of slender mulga, interspersed with other members of the mulga  
143 complex, including *A. ramulosa* W.V.Fitzg., *A. aneura* var. *intermedia* Pedley and *A. minura*  
144 Randell. The understorey vegetation of all sites was dominated by native pasture grasses  
145 belonging to genera such as *Aristida* L., *Eragrostis* Wolf, *Panicum* L. and *Urochloa*  
146 P.Beauv..

#### 147 *Seedling recruitment study*–

148 Recruitment beneath 10 randomly selected burnt and unburnt *A. aptaneura* shrubs (20 shrubs  
149 in total), each from a population with a unique pre-fire mast seedfall density, was assessed in  
150 late 2012 at each of the 14 study sites (the dates of fires are given in Table 1). Unburnt shrubs  
151 were sampled at each site from the edges of burnt areas. Fire severity was variable at each  
152 site, presumably owing to pre-fire spatial heterogeneity of fuel loads and variation in wind  
153 speed, humidity and air temperature as fires had proceeded. Given that fire severity is a  
154 known driver of mulga recruitment patterning (Wright et al., 2015), we restricted our  
155 sampling of burnt plants to high-severity-burnt shrubs only. The quantitative criteria for  
156 inclusion as a high-severity burnt shrub were: 1) mean minimum diameter of 10 randomly  
157 chosen stem tips at 1-m height > 5 mm (Moreno and Oechal, 1991); and 2) >50 % bare  
158 ground (a surrogate measure for the proportion of the litter layer consumed during fire). Both  
159 burnt and unburnt shrubs were randomly chosen at each site by initially identifying and  
160 numbering a cohort of 60 shrubs that satisfied the criteria for inclusion as either high-severity  
161 burnt or unburnt (30 in each category). Subsequently, computer-generated random numbers  
162 were used to select a subsample of 10 individuals from each burn category (Harding, 2012).  
163 Inventories of seedling numbers were taken in late 2012 at each site by counting out  
164 seedlings from the zone directly beneath shrub canopies.



165 For each population at each site, data were also obtained on seedfall density during  
166 the 2010 mast year by counting pod numbers in four 20 × 20 cm quadrats of phyllode litter  
167 beneath 10 randomly selected unburnt shrubs. This estimate of dispersed pods from the 2010  
168 mast year was used as a surrogate measure for sound seedfall density of the mast year, and  
169 was utilized in the data analysis on post-fire recruitment as a continuous site-specific  
170 variable. To examine whether high pod densities would be accompanied by increased soil  
171 seedbank densities, at a single site (see seedbank study below) we compared seedbank  
172 densities in the year following the 2010 mast year, when pod production at the site was high  
173 (303.8 pods/m<sup>2</sup>) with seedbank densities during an inter-mast year in 2017, when pod  
174 production at the site was nil. In addition to the seedfall data, we also collected information  
175 on shrub size (measured by the basal diameter at 300 mm above ground), and 12-month post-  
176 fire rainfall at each site (Australian Government Bureau of Meteorology, 2017).

#### 177 *Seedbank dynamics study*–

178 Changes in the vertical distribution of *A. aptaneura* seedbanks over time were assessed by  
179 sampling soil cores from 10 randomly selected unburnt shrubs at the Pultitjaiti site (Table 1)  
180 in October 2010, December 2011, October 2015 and June 2017. The mulga population at this  
181 site masted in November 2010, with mean pods/m<sup>2</sup> in the litter layer following this event  
182 being 303.8 (Table 1). Following the 2010 mast event, no subsequent seed production was  
183 observed in this mulga population between 2011 and 2017. The vertical distribution of the  
184 seedbanks was determined across the following two microsites: ‘litter’ and ‘bare ground’.  
185 Columns from the ‘litter’ microsite were taken from areas that were covered by a thick mat of  
186 phyllode litter, whereas the ‘bare ground’ microsite had minimal or no litter. For each  
187 microsite, we excavated four randomly located 20 × 20 cm columns of soil beneath each  
188 shrub to a depth of 4 cm. Once the sides of the soil columns had been trenched away, the  
189 following four layers were carefully extracted using a paint scraper and a steel ruler: surface

190 litter, 0-1 cm, 1-2 cm, 2-4 cm. For the October 2010 sampling round, samples were collected  
191 only from the 0-1 cm layer as this sampling round was initially part of a seedbank study  
192 concerned only with seed populations in the very uppermost soil strata (Wright and Zuur,  
193 2014). Seed densities were assessed by passing the samples through a 1.6 mm sieve and  
194 counting the seeds. After the seeds were counted, their viability was assessed by splitting  
195 them and checking for an embryo that appeared intact and healthy.

### 196 *Statistical analysis*–

197 All analyses were conducted in the statistical environment R (R Core Team, 2016).  
198 Exploration of the seedling recruitment dataset followed the protocol of Zuur et al. (2010)  
199 (Appendix S1: see the Supplementary Data with this article). A mixed modelling approach  
200 was used to model the number of seedlings as a function of the categorical covariate ‘fire’  
201 (with the levels ‘burnt’ and ‘unburnt’) and the continuous variables ‘seedfall density’ (i.e.  
202 pods/m<sup>2</sup>), basal trunk diameter, and 12-month post-fire rainfall. We also tested all two-way  
203 interactions between the ‘basal diameter’, ‘fire’ and ‘seedfall density’ covariates. The  
204 variable ‘site’ was used in the model as a random intercept, which allowed observations from  
205 different shrubs at the same site to be correlated. We applied a negative binomial (NB)  
206 generalized linear mixed model (GLMM) to avoid overdispersion. Markov chain Monte  
207 Carlo (MCMC) techniques were used to estimate the parameters of the model using JAGS  
208 (Plummer, 2003) via the R2jags package (Yu-Sung and Masanao, 2012). We used diffuse  
209 normal priors, 3 chains, a thinning rate of 10, a burn-in of 10,000, and 50,000 iterations for  
210 each posterior distribution. Model validation was carried out subsequent to model fitting  
211 (Appendix S1). The Splines package (R Core Team, 2016) was used to create a 3-  
212 dimensional perspective plot to illustrate the relationship between the response variable  
213 ‘seedling count’ and the two continuous explanatory variables ‘shrub basal diameter’ and  
214 ‘seedfall density’.

215 Exploration of the seedbank dataset followed the protocol of the seedling recruitment  
216 analysis. The number of *A. aptaneura* seeds in the soil seedbank was modelled as a function  
217 of the fixed covariates ‘microsite’, ‘depth’ and ‘sampling time’ and all two-way interactions  
218 between the covariates. In order to account for dependencies due to observing seed counts at  
219 different depths from the same soil core at each mulga shrub, an NB GLMM framework was  
220 used with ‘shrub identity’ employed as a random intercept nested within ‘depth’. Parameters  
221 of the model were again estimated using MCMC techniques, and the MCMC methodology  
222 and model validation procedures were the same as for the seedling recruitment GLMM.

## 223 **RESULTS**

224 The ‘seedling recruitment’ MCMC indicated a significant interaction between fire and  
225 seedfall density during the pre-fire mast year (Fig. 2A - zero not contained in the credible  
226 interval of the ‘seedfall density: unburnt’ interaction parameter estimate). This indicated that  
227 the relationship between seedfall density and recruitment differed between burnt and unburnt  
228 shrubs. To visualize this result, we plotted the predicted number of seedlings versus seedfall  
229 density (i.e. pods/m<sup>2</sup>) for the two burn categories (Fig. 3). This showed that a strong positive  
230 relationship existed between seedfall density and seedling number for burnt mulga, with  
231 burnt shrubs at sites with higher seedfall densities experiencing increased recruitment  
232 compared to sites with lower pre-fire seedfall densities. In contrast, there was no relationship  
233 between seedfall density during masting and seedling number for unburnt shrubs. Across all  
234 seedfall densities, mean recruitment for burnt shrubs was 13.2 seedlings/shrub (SE = 2.0),  
235 and ranged from 0.3 to 60.9 seedlings/shrub across the 14 sites (Fig. 3, Table 1). In contrast,  
236 for unburnt shrubs, mean recruitment across all seedfall densities was 0.8 seedlings/shrub (SE  
237 = 0.2) and ranged from 0 to 2.1 seedlings/shrub across the sites (Table 1).

238 No interaction was detected between ‘fire’ and ‘basal diameter’, or ‘seedfall density’  
239 and ‘basal diameter’. The absence of an interaction between shrub size and pre-fire seedfall  
240 density indicated there were positive and equal slopes for these continuous covariates. This  
241 showed that increasing values for both variables were associated with increasing recruitment  
242 levels, with maximum recruitment occurring for larger-sized shrubs from populations that  
243 had dense seedfalls prior to fire (Fig. 4). The interactions were removed from the final  
244 analysis to allow testing of the main effect of the ‘basal diameter’ term (Engqvist, 2005).  
245 There was a significant effect of basal trunk diameter on post-fire recruitment (Fig 2A - zero  
246 not contained in the credible interval of the ‘basal diameter’ parameter estimate), with the  
247 positive slope estimate for this covariate indicating that plants with larger trunk diameters  
248 were associated with higher seedling numbers than plants with smaller trunk diameters (Fig.  
249 4). No effect of 12- month post-fire rainfall on recruitment was observed (Fig. 2A).

250 The seedbank pulsed strongly after the 2010 mast event, though the post-mast  
251 seedbank was patchily distributed, with seed clumps evident at all soil depths in the 2011  
252 sampling round (Figs 2B, 5). Across both microsites (litter and bare ground) mean viable  
253 seed density in 2011 in the upper 4 cm was 132.8 (SE = 35.1) seeds/m<sup>2</sup>. Subsequent to initial  
254 pulsing, seed populations in the soil declined to very low levels by 2015 and 2017 (Fig. 5). In  
255 2017, mean viable seed density in the upper 4 cm was 3.8 (SE = 1.4) seeds/m<sup>2</sup>. In addition to  
256 the sampling time effect, there was a strong soil depth effect on seed densities, with the  
257 MCMC indicating mean seed numbers across all microsites and sampling times were lower at  
258 the surface (0.6 (SE = 0.35) seeds/m<sup>2</sup>) compared to the 0-1 cm (26.8 (SE = 9.5) seeds/m<sup>2</sup>), 1-  
259 2 cm (12.9 (SE = 4.1) seeds/m<sup>2</sup>), and 2-4 cm (7.9 (SE = 2.9) seeds/m<sup>2</sup>) depths (Figs. 2B, 5).

260

261 **DISCUSSION**

262 Previous studies have identified fire intensity and post-fire rainfall timing and quantity as  
263 proximate drivers of mulga post-fire recruitment patterning (Griffin and Friedel, 1984;  
264 Harrington, 1985; Hodgkinson, 1991; Wright et al., 2015). Our study provided an alternative  
265 explanation for variability in post-fire mulga regeneration, by identifying variation in seedfall  
266 density across sites during the pre-burn mast year as a key determinant of mulga recruitment  
267 after fire. Specifically, we observed high levels of recruitment at burnt shrubs from  
268 populations that had dense seedfalls prior to fire, and we attribute this result to seedbank  
269 pulsing after masting, coupled with the influence of high soil temperatures during fire  
270 triggering mass germination from the heat-cued seedbank. Other evidence for the beneficial  
271 effects of masting on post-fire recruitment comes from temperate Northern Hemisphere  
272 forests (Peters et al., 2005; Ascoli et al., 2013). However, to our knowledge, the current  
273 central Australian study is the first to demonstrate such an effect in an arid fire-prone biome.

274 We did not detect a relationship between pre-fire seedfall density and recruitment for  
275 unburnt shrubs. This finding probably reflects that soils under these shrubs had not been  
276 heated sufficiently to break seed dormancy, irrespective of seedbank densities at the time of  
277 fire. In addition, it is likely that even if a fraction of the seedbank of unburnt shrubs had  
278 germinated without heat-stimulation (as usually occurs in mulga seeds [Fox, 1985]), seedling  
279 emergence would have been impeded by the dense phyllode litter mats that characteristically  
280 occur on the ground layer of unburnt mulga stands (Burrows and Beale, 1969; Winkworth,  
281 1973).

282 It was somewhat unexpected that our results indicate that seedfalls during the pre-fire  
283 mast year contribute strongly to recruitment dynamics after burning. This is because in many  
284 systems, if shed seeds are transferred to soil seedbanks primarily via abiotic processes (e.g.  
285 water-assisted movement during rainfall events), then seeds would likely still be very  
286 shallowly buried (or unburied) in the year after seedfall (Chambers and Macmahon, 1994;

287 Westerman et al., 2009). Such shallow or unburied seeds would therefore be unlikely to  
288 contribute to recruitment following a post-mast fire, as direct heat during fire would usually  
289 kill them. Nevertheless, in mulga systems, rapid entrainment of shed seed into deeper soil  
290 profiles could be facilitated by ants of the genera *Iridomyrmex*, *Rhytidoponera*, and/or  
291 *Camponotus*, which are attracted to the carbohydrate-rich eliasomes of *Acacia* seeds  
292 (Anderson, 1982, 1983; Bonney et al., 2017). The possibility of ant-assisted dispersal after  
293 masting is supported by observations from our seedbank study of a highly patchy seed  
294 distribution across the soil profile, which suggests ants had abandoned seeds in clumps in  
295 nests following consumption of eliasomes.

296 Further research is required to test whether the decline in seedbank densities we  
297 observed after initial post-mast seedbank pulsing was related to seed decay processes or to  
298 biotic factors such as seed predation. Harrington (1972) reported little loss of mulga seed  
299 viability over a 20-year period of dry storage in a laboratory. Additionally, Morris (1966)  
300 estimated that mulga seeds in soils in western New South Wales could remain viable for at  
301 least 30 years. Hence, if decay rates are slow, seed consumption by granivores subsequent to  
302 initial caching may be a plausible explanation for rapid seedbank declines after initial post-  
303 mast pulses. Rodents can detect buried seeds using olfaction (Jenkins et al., 1995; Wall,  
304 1995, 2003), and could have depredated seed clumps that ants had left behind in nests  
305 following initial dispersal. Alternatively, ants themselves could have been caching the seeds  
306 in nests and then eating them. However, this explanation seems unlikely to explain the overall  
307 reduction process we observed, as the only record we are aware of indicating ants consuming  
308 *Acacia* seeds in Australia comes from the Sydney region by *Rhytidoponera metallica* Smith  
309 (Hughes and Westoby, 1992). This ant species does not usually form a major component of  
310 ant assemblages in arid Australian systems (Anderson, 1983; Bonney et al., 2017).

311 A significant driver of post-fire recruitment levels in mulga was the size of the shrub,  
312 as estimated by basal diameter. Within a mast event, larger shrubs would be expected to  
313 produce more seeds than smaller shrubs, as has been demonstrated in Northern Hemisphere  
314 masting forest trees (Davi et al., 2016; Minor and Kobe, 2017). Hence, given that mulga  
315 seedbanks are exceptionally sparse in the absence of recent masting, higher post-fire seedling  
316 numbers for larger shrubs most likely indicates larger injections from such trees into the  
317 seedbank during the pre-fire mast year. An alternative explanation would be a plant age  
318 effect, with larger, presumably older, shrubs having had more time to grow and slowly  
319 accumulate a denser, more persistent seedbank over time. The finding of a significant shrub  
320 size effect has important management implications. If bigger shrubs have better recruitment,  
321 then older stands composed of larger shrubs should have increased resilience to fire than  
322 stands composed primarily of young cohorts. Given that mulga stands are typically even-aged  
323 and often composed primarily of recruited individuals since previous fires (Lange, 1966),  
324 longer fire-free intervals should therefore benefit mulga, as has been suggested by previous  
325 studies (Nano, 2005; Ward et al., 2014).

326 Our research did not examine evolutionary controls behind masting in slender mulga.  
327 Nevertheless, the predator satiation hypothesis could be relevant. Under the predator satiation  
328 hypothesis, mulga masting could have been selected for because 1) years of heavy seed crops  
329 satiate seed predators with an overabundance of food (i.e. causes a predator functional  
330 response (Moreira et al., 2016)), or 2) because seeding intermittency drives reductions in  
331 predator populations via starvation during successive low-production years (i.e. causes a  
332 numerical predator response (Pesendorfer and Koenig, 2017)). Although irruptions of some  
333 granivorous bird and rodent species have been linked to high rainfall years during which  
334 mulga masting is known to have occurred in arid Australia (Letnic and Dickman, 2006;  
335 Pavey and Nano, 2013), it seems unlikely that starvation of consumers would occur during

336 low output mulga inter-mast years. This is because most Australian granivores are ‘diet  
337 generalists’ (Predavec, 1994, 1997), and can probably switch to alternative food sources  
338 during periods when mulga is not seeding. A functional predator response to mulga masting  
339 is possible, and our observations of a short-lived seedbank pulse after masting suggest  
340 transitory satiation of granivores during post-mast periods. Nevertheless, formal testing of the  
341 hypothesis that masting evolved in mulga in response to benefits associated with predator  
342 satiation would require following the methodology outlined by Janzen (1976), whereby field  
343 examinations are conducted to compare the fraction of the seed crop that escapes predation  
344 during mast versus inter-mast years (Tsvuura et al., 2011; Zwolakl et al., 2016).

345         Another evolutionary hypothesis that may be relevant to mulga masting is the  
346 environmental prediction hypothesis (Williamson & Ickes 2002; Burns 2012). Under this  
347 hypothesis, large reproductive episodes are timed to coincide with periods of increased seed  
348 germination likelihood and/or improved seedling establishment conditions. To test the  
349 importance of this hypothesis in a study species, it must be demonstrated that the climatic or  
350 environmental stimulus that triggers masting is statistically associated with future periods of  
351 improved establishment likelihood. In the case of mulga, it has previously been shown that  
352 mast seeding is associated with periods of exceptionally high precipitation (Preece 1971a;  
353 Davies 1976), and such rainfall conditions are statistically associated with wildfires in mulga  
354 habitats because they trigger biomass accumulations (Griffin et al. 1983; Bastin and Allan  
355 2012). As fire cues mulga seeds to germinate and post-fire environmental conditions are  
356 favourable for seedling establishment (Whelan, 1995; Bond and van Wilgen, 1996), masting  
357 after exceptionally high rain periods could have been selected for in mulga because  
358 individuals that do so are likely to be fitter because they will be more likely to coincide seed  
359 availability with the passage of fire. Other environmentally predictive masting syndromes in  
360 which mast events are triggered to pre-empt periods with favourable post-burn seedling



361 establishment conditions include pyriscent serotiny in Alpine Ash (*Eucalyptus delegatensis*  
362 R.T. Baker) from South-eastern Australia (O'Dowd and Gill 1984), and post-fire flowering in  
363 members of the Xanthoreaceae (Kelly 1994).

364

## 365 **CONCLUSIONS**

366 Our results indicate that mulga stand composition after high-severity fires that raze  
367 populations can be dramatically altered depending on variation in seedfall during mast  
368 seeding years pre-fire. Specifically, sites with denser seedfalls elicit stronger post-fire  
369 recruitment compared to those with low seedfall during the same pre-fire mast year. This  
370 effect is presumably because denser seedfalls during pre-fire masts satiate predators, which  
371 bolsters the pre-fire seedbank by facilitating the entry of higher numbers of seeds into the soil  
372 prior to fire. Overall, the current research highlights the importance of quantifying seedbank  
373 responses to reproductive events of masting plants, and demonstrates that mass recruitment  
374 can occur when peaks in natural seedbank rhythms coincide with appropriate environmental  
375 stimuli for dormancy release.

376

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387

388 **DATA ACCESSIBILITY**

389 Data from this study are to be located at DRYAD digital repository

390 ([http://dx. doi.org/10/5061/dryad.kq67v](http://dx.doi.org/10/5061/dryad.kq67v))

391

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605 **TABLE 1.** Fourteen sites in central Australia monitored for seedling regeneration following wildfires in 2011. Sites are listed together with land  
606 tenure, location, (latitude and longitude), date of fires, mean pods/m<sup>2</sup>, 12-month post-fire rainfall, and mean seedling counts/shrub (and standard  
607 error) according to fire class.

Site	Tenure	GPS location	Fire date	Pods/m <sup>2</sup>	Rainfall	Mean seedling counts /shrub (and SE)	
					(12-month)	High-severity burnt	Unburnt
Aileron	Pastoral	-22.83017 S, 133.44796 E	19 Sep 2011	558.1	410	20.5 (7.1)	0.9 (0.5)
Amburla	Pastoral	-23.29615 S, 132.97792 E	25 Oct 2011	38.8	327	4.0 (1.5)	1.3 (0.7)
Hamilton Downs	Pastoral	-23.49035 S, 133.35419 E	5 Aug 2011	410.6	152	10.3 (3.5)	0.8 (0.4)
Bond Springs (Nth)	Pastoral	-23.39828 S, 133.72819 E	9 Oct 2011	8.1	410	6.3 (3.2)	1.0 (0.4)
Bond Springs (Sth)	Pastoral	-23.39897 S, 133.81666 E	23 Sep 2011	53.1	245	2.6 (0.9)	2.1 (1.7)
Deep Well	Pastoral	-23.75149 S, 133.99766 E	30 Aug 2011	69.4	195	6.6 (2.6)	0.2 (0.1)
Indukumanu	Aboriginal	-23.4558 S, 131.81033 E	17 Aug 2011	115	333	29.5 (7.5)	0.7 (0.6)
Mt Everard	Military	-23.53509 S, 133.68501 E	17 Jun 2011	23.1	152	0.9 (0.5)	0.5 (0.3)
Narwietooma (east)	Pastoral	-23.18791 S, 132. 82779 E	25 May 2011	207.5	315	15.9 (3.9)	0.3 (0.3)
Narwietooma (west)	Pastoral	-23.29981 S, 132.39506 E	5 Sep 2011	61.3	324	1.7 (0.7)	1.5 (1.5)

New Haven (east)	Conservation	-22.67799 S, 131.38176 E	6 Sep 2011	502.5	308	10.5 (3.5)	0.0 (0)
New Haven (west)	Conservation	-22.70527 S, 131.17006 E	12 Oct 2011	211.3	308	14.3 (6.5)	0.2 (0.2)
Pulitjaiti	Aboriginal	-23.51185 S, 131.87801 E	19 Sep 2011	303.8	333	60.9 (16.0)	0.9 (0.4)
Yamba	Pastoral	-23.05159 S, 133.72039 E	6 Oct 2011	33.1	348	0.3 (0.2)	0.9 (0.4)

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609 **FIGURE 1 (A)** Mixed bar and line chart indicating the relationship between 12-  
610 month rainfall and mass (kg) of mulga seed purchased by the Yuendumu Mining  
611 Company from Aboriginal seed collectors in the period 1999-2016; and **(B)** % area  
612 burnt in the period 1999-2016 across the Burt Plain (the bioregion within which most  
613 of the 14 slender mulga sites of the recruitment field study were located).

614 **FIGURE 2** Parameter estimates (means and 95% credible intervals) for MCMC  
615 analyses. If '0' is within the credible interval, the corresponding parameter estimate is  
616 not significant. **(A)** 'Seedling recruitment' MCMC. For the interaction parameter  
617 estimate ('Seedfall density: Unburnt'), seedling numbers were analyzed against the  
618 baseline 'Seedfall density: Burnt' parameter estimate. **(B)** 'Seedbank' MCMC. For  
619 the 'sample time' parameter, seed counts from 2015 and 2017 were analyzed against  
620 the baseline 2011 sampling time. For the 'bare ground' microsite parameter, seed  
621 counts were analyzed against the baseline 'litter' parameter. For the 3 soil depth  
622 parameter estimates (0-1 cm, 1-2 cm, 2-4 cm), seed counts were analyzed against the  
623 baseline 'surface' parameter.

624 **FIGURE 3** Seedling counts/shrub and relationships between the expected number of  
625 seedlings/shrub and seedfall density during masting (estimated by pod number/m<sup>2</sup>) for  
626 high-severity burnt and unburnt mulga shrubs (for average values of other covariates).  
627 Shaded areas in the figure show the 95% credible intervals around the posterior mean  
628 (fitted) values from the 'seedling recruitment' MCMC.

629 **FIGURE 4** Perspective plot showing a representation of the 'seedling recruitment'  
630 regression surface. Model included shrub basal diameter and seedfall density plus  
631 interaction term. The data were combined from across unburnt and burnt fire  
632 categories to produce the plot.



633 **FIGURE 5** Viable *A. aptaneura* seed counts/m<sup>2</sup> (and means and standard errors)  
634 across four soil depths. At each depth, soils were sampled from litter-covered areas  
635 and bare patches. Sampling occurred in October 2010, December 2011, September  
636 2015 and June 2017. The 2011 sampling round occurred 14 months after a mast-  
637 seeding event in October 2010, whereas the 2015 and 2017 rounds took place c. 5 and  
638 7 years after masting respectively.

639