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Seedbank dynamics after masting in mulga (*Acacia aptaneura*): Implications for post-fire regeneration

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ABSTRACT

Members of the arid Australian mulga (*Acacia aneura*) complex are fire-sensitive shrubs that produce mast seed crops after exceptionally high rainfall years. Such years also drive widespread wildfires in inland Australia, as high rainfall causes grassy fuels to accumulate, thereby enabling fuel contiguity to occur. Despite seedling regeneration playing an important role in mulga post-fire recovery, a dearth of information exists on the dynamics of its seedbanks. Here we examine the temporal and spatial dynamics of mulga seedbanks after a region-wide masting event at Laycock's Sandplain, central Australia. Masting had a profound effect on seedbanks, producing massive but short-lived pulses of seed in upper soil layers. After seed fall, seedbanks declined rapidly, and within 18 months had been reduced by predator depredations to low pre-mast levels. Our results suggest that mulga masting should enhance resilience to burning by providing transient seed pulses during periods of high flammability (i.e. after heavy rainfalls). The results also suggest that burn intensity will influence post-fire regeneration, by interacting with seed germination biology and post-mast seedbank dynamics. In our discussion, we examine possible evolutionary drivers behind mulga seeding periodicity, and hypothesize that rain-driven masting in mulga is a fire-related form of environmentally predictive masting.

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1. Introduction

Masting, the intermittent, synchronous production of large seed crops among plant populations, is generally interpreted as an adaptive syndrome used to maximize reproductive success (Janzen, 1971; Salisbury, 1942). There are several non-mutually exclusive hypotheses to explain masting: enhanced seedling establishment through satiation of seed predators (Janzen, 1976; Watt, 1925); improved pollination efficiency of normally outcrossing trees (Iwasa and Satake, 2004); wider propagule dispersal by scatter-hoarders (Christensen and Whitlam, 1991); and environmental prediction [the use of environmental cues such as precipitation, drought, or fire to predict future conditions favourable for seedling growth (Burns, 2012)]. The non-adaptive resource-matching hypothesis, which holds that masting is purely a response to fluctuating resources, has received little support in the literature, and is normally only accepted for 'putative' masting species with low inter-annual variation in seed output (Kelly, 1994).

Although masting is well studied in temperate [e.g. Fagaceae and Pinaceae (Koenig and Knops, 2000)] and tropical ecosystems [e.g. Dipterocarpaceae (Sakai et al. 2006)], it has received little attention in arid, fire-prone habitats. Previous studies from mesic fire-prone systems have shown that the timing of mast events in relation to fire can have important consequences for plant regeneration after burning. For example, fires that occur long after masting may result in poor post-fire recovery, owing to predator-induced seedbank declines (O'Dowd and Gill, 1984) and/or habitat deterioration (Peters et al. 2005). In addition, for species that are mast seeders and that also possess heat-stimulated seed germination, there are likely to be multifaceted interactions between fire intensity and fire timing in relation to masting, with concomitant impacts on post-fire stand regeneration (Wright, 2007).

The mulga species complex (*Acacia aneura* F. Muell. ex. Benth.) comprises mast seeding, woody shrubs with seeds that are stimulated to germinate by heat (Davies, 1976; Hodgkinson, 1991). They occur in monodominant stands over c. 20% of arid and semi-arid

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Australia, and extend in a broad band from the west Australian coastline nearly to the eastern coast. Masting in mulga is weather-mediated, and while flowering can occur even after relatively small falls of rain, irrespective of season, substantial fruit maturation normally only occurs when heavy summer falls are followed by wet winters (Preece, 1971). Hence, given the climatic unpredictability of arid Australia, masting in mulga is relatively strict, with little or no seed produced in most years, but with bumper crops produced occasionally (Davies, 1976; Davies and Kenny, 2013).

Like masting, fire cycles in mulga ecosystems are inextricably linked to climate, with fire being constrained most of the time by low fuel connectivity. However, when grassy fuels accumulate after heavy rain years, fuel contiguity increases and large lightning (and in modern times human) ignited fires are able to take place (Allan et al. 2003; Griffin et al. 1983). The onset of these fires normally occurs during spring or summer, as these are the main lightning seasons, and by this time fuels have fully cured and flammable conditions are at their peak. Widespread, ecologically severe wildfires are known to have taken place in mulga-dominated systems following high rain years in the early 1920s, the early 1950s, the mid-1970s, the early 2000s, and recently between 2011 and 2012 (Allan et al. 2003; Allan, G. pers. comm.). Whilst no records are available to indicate whether masting events occurred following the rains that caused the 1920s, 1950s or mid-1970s wildfires, widespread masting in mulga populations was observed after the rains that initiated the 2000 and 2011–12 fire events (Baarda, F., pers. comm.; Latz, P.K., pers. comm.).

Adult mulga mortality rates during fire are often high, and populations rely primarily on regeneration from seeds after high-intensity burning (Nano and Clarke, 2010; Wright and Clarke, 2007). However, whilst members of the species complex are habitat dominants with long-lived seeds [previous studies have shown 100% viability in 20 year old seed samples (Harrington, 1972)], previous seedbank studies have returned either no (Hodgkinson et al. 1980) or very low (Wright, 2007; Page, 2009) densities of soil-borne seed. This suggests that infrequent reproduction coupled with high rates of seed predation may prevent populations from accumulating large, persistent seedbanks. Nevertheless, given that 1) the high-rainfall conditions that drive wildfires in inland Australia are also the environmental cue used by mulga to synchronize mast events, and 2) anthesis and seed shed have normally been completed by the time fuels have cured and wildfires commence (Wright, B.R., pers. obs.), it appears likely that widespread fires in mulga vegetation will normally be accompanied by an abundance of available seed. Furthermore, as the seed of mulga is released from dormancy by heat during fire, there are likely to be important interactions between fire intensity and the depths at which seeds are buried following mast events [given the variable temperatures reached at different soil depths during mulga fires (Wright and Clarke, 2008)]. Unfortunately, no empirical data currently exist to verify these assumptions, and there are no demographic data available concerning the spatial or temporal dynamics of mulga seedbanks.

This paper analyzes vertical and temporal seedbank data collected from a central Australian mulga population following a widespread masting event that took place in central Australia in October 2010. In our analyses, we used statistical modelling techniques that accounted for dependencies, allowing us to analyse seed data collected from different depths of soil, and over different time periods from individual shrubs. There were several underlying ecological questions addressed by the research:

1. How long do mulga seedbanks remain elevated after a masting event?

2. Do post-mast seedbanks diminish as distance from parent plants increases?
3. How are seedbanks stratified across soil depths following masting?
4. Are mulga seedbanks influenced by phyllode litter accumulations that occur at the soil surface?

Our results are discussed in the context of post-fire regeneration, and the possible evolutionary causes behind reproductive periodicity in mulga are explored.

2. Methods

2.1. Study area

The study area was within Laycock's Sandplain, on the eastern edge of the Western Desert, Northern Territory, Australia. The region encompasses an approximately level sheet of Quaternary aeolian sand, with a semi-arid climate and a mean annual rainfall of approximately 280 mm (Nano and Clarke, 2010). Inter-annual rainfall variability is high, and the seasonal occurrence of rain is skewed towards summer months owing to the influence of the north Australian summer monsoon. Mulga associations within the study area occur either as large continuous belts of vegetation on relatively infertile loams or red earths, or as scattered islands on slightly heavier soils within prevailing matrices of spinifex (*Triodia* spp.) dominated sand. There are numerous varieties of mulga, and recent taxonomic revisions have designated the variety studied in this paper, which was formerly known as *A. aneura* var. *tennuis*, as a new species, *Acacia aptaneura* (Maslin and Reid, 2012) (Fig. 1a and b). Like the other varieties of mulga, *A. aptaneura* is a long-lived species [>50 years (Friedel et al. 1994)] that is easily killed by intense fire, but can regenerate profusely from seed after burning as its seeds are released from dormancy by heat.

2.2. Seedbank sampling

2.2.1. Study 1 — impacts of masting on seedbank distribution over time and parent plant effects

Soil seedbanks of *A. aptaneura* shrubs were monitored from 12 reproductively mature individuals across a 20 km transect over a period of 24 months. The sample times were: early October 2010 (immediately prior to seed shed), late November 2010 (c. 1 month after seed shed had commenced), July 2011 (9 months after seed shed), November 2011 (13 months after seed shed), March 2012 (17 months after seed shed) and September 2012 (23 months after seed shed). Seed fall in all shrubs had commenced in late October and was largely completed by late November 2010. The 2010 seeding event occurred in response to exceptional rains that had taken place during the 12 months prior to seed fall at the study area, with 651 mm of rain recorded during this period at Papunya Police Station, 30 km north of Laycock's Sandplain. This was the first region-wide mast event observed since the first author began observations in the study area in 2002.

The 12 shrubs were selected on the basis of being judged older than 25 years of age at the time of sampling, and were expected to have been of reproductive age during the previous known mast event in 2000/01. In this way, it was expected that data from the first sampling round would represent 'background' seedbank densities of mature mulga populations that had been exposed to approximately 10 years of seedbank-diminishing processes (e.g. predation, deterioration and germination). During the initial sampling round, various measurements were taken from each shrub, including height, canopy diameter, and trunk diameter at 20 cm above ground level. The shrubs ranged in size, with canopy
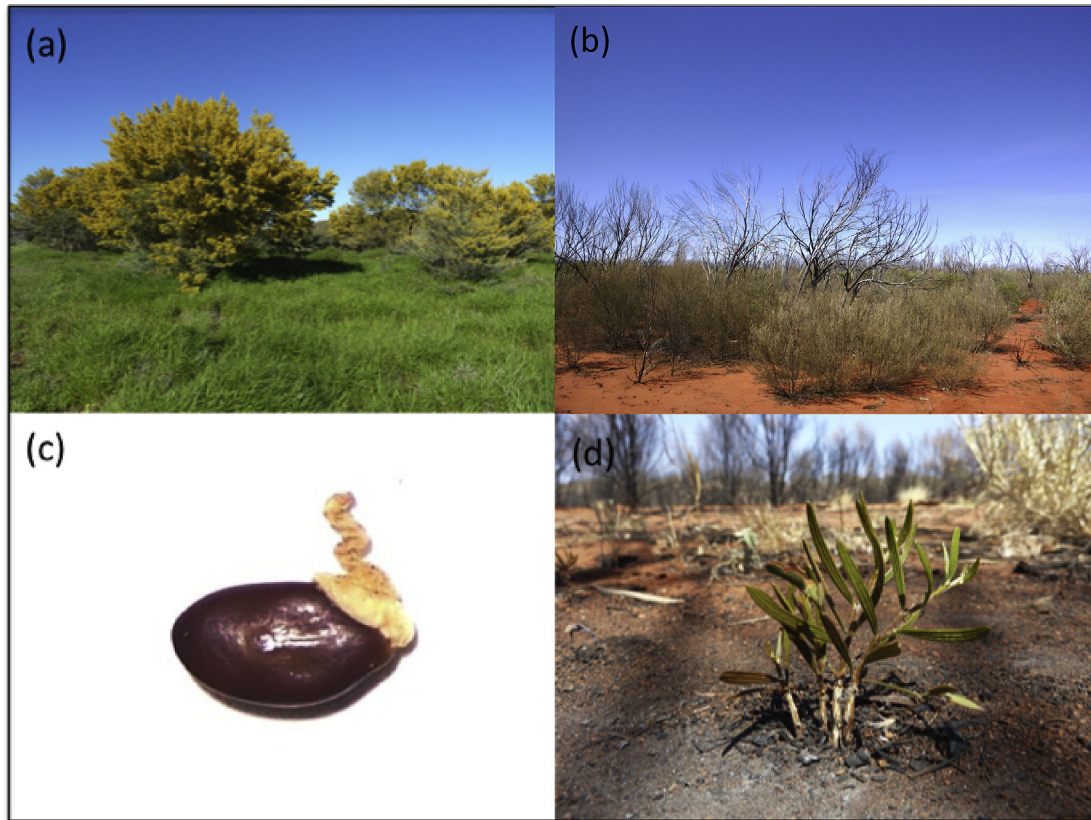
Fig. 1. (a) Synchronized mulga flowering event (March 2012) in the eastern MacDonnell Ranges in central Australia, following exceptional rains over the preceding summer; (b) profuse post-fire seedling regeneration at a mulga stand burnt in 2001, 200 km northwest of Alice Springs (December 2013); (c) mulga seed with prominent white eliasome; (d) clumped seedlings emerging after fire on Burt's Plain, 50 km west of Alice Springs (October 2012).

diameters ranging from 4 to 9.4 m (mean 5.2 m) and heights ranging from 2.8 to 7.5 m (mean 4.6 m).

The spatial (horizontal) distribution of mulga seedbanks in relation to parent plants was assessed for each shrub by sampling two adjacent spatial zones: 1) the zone directly beneath the shrub canopy (canopy zone); and 2) an annulus-shaped 'extended canopy zone' immediately adjacent to and surrounding the canopy zone, with an area exactly that of the canopy zone. In all except one case, shrubs were spaced >10 m from the nearest mulga shrub (with the two eastern most shrubs being spaced c. 5 m apart). Consequently, as mulga seeds are not adapted for wind dispersal, it was assumed that plants were spaced at sufficient distances to ensure that seeds recorded from beneath shrub canopies were seeds that had originated from those particular shrubs.

At each shrub four randomly sampled 20 × 20 cm wide × 1 cm deep quadrats of soil, plus any phyllode litter lying on top, were taken from each of the two zones. Sampling soils to 1 cm depth was considered appropriate, as previous studies have revealed that the majority of seeds tend to accumulate in upper soil layers in arid Australia (Simpson, 1999). A small pilot study also revealed that areas of heavy litter acted as seed traps, and hence soils covered by litter were more likely to have higher densities of seeds than bare areas. Consequently, prior to sampling an estimate was made of the proportion of litter to bare ground beneath each shrub. Quadrat samples were then collected in proportion to the level of litter cover/bare ground beneath each shrub. For example, if a shrub had 50:50 proportional cover of litter to bare ground, then two quadrats of soil were taken from litter covered areas, and two quadrats were taken from bare ground. This methodology would permit more accurate 'up-scaled' estimates of seed densities per m², and thereby

enable comparison of the observed mulga seedbank densities with those of other studies (that generally report findings in seeds/m²).

Whenever samples were collected, 15 cm flat-topped wire pins were inserted into the ground to mark the location where soil had been removed. This ensured that subsequent sampling avoided re-sampling from the same location. The soil samples were passed through 1.6 mm wire sieves and seeds of *A. aptaneura* were counted. When entire seedpods were present the sample was vigorously rubbed and winnowed to release seeds from pods. Once the seeds had been counted out, they were tested for viability by splitting and checking for intact, healthy endosperm (seeds averaged 84.9% viability among the 12 shrubs across all sampling times). Where large numbers of seeds were encountered in a sample, a representative sample of 20 seeds was collected and tested for viability. This enabled an estimate of the number of viable seeds for that sample, by multiplying the estimated viability percentage by the total number of seeds collected. Hereafter, in this paper whenever the term 'seed' is used we refer to viable seeds.

2.2.2. Study 2 − vertical seedbank distribution and litter effects

The vertical distribution of mulga seedbanks across soil depths was determined in December 2011, approximately 13 months after the 2010 mast event. Ten of the shrubs from study 1 were used. Seedbank densities were assessed by excavating four randomly located 20 × 20 cm soil columns to a depth of 4 cm across two microsite stratifications: 'litter' and 'bare ground'. Columns taken from the 'litter' zone had a surface layer that was covered by a thick mat of mulga phyllode litter. Columns taken from the 'bare' zone had an upper layer composed of minimal or no phyllode litter and generally had light cyanobacterial soil crusting at the soil surface.

Within each of the two microsite stratifications, mulga seed numbers were examined across the following four soil depth categories: surface, 0–1 cm, 1–2 cm and 2–4 cm. The red earth soil beneath the shrubs was free from rocks and root material, so it was possible to accurately excavate the necessary depths of soil using a paint scraper, and a steel ruler (which was used to measure the different depths). The soil levels were treated as categorical variables in subsequent statistical analyses, as the depth of the phyllode litter layer was somewhat inconsistent between shrubs, and could not be incorporated as a discrete variable. Identifying soil depth as a categorical variable also meant that subsequent analyses could allow for non-linear depth effects.

Seed densities of the surface layer were assessed by removing litter (in the case of the 'litter' zone) or any loose sand or organic material overlying the cyanobacterial layer at the soil surface (in the case of the 'bare ground' zone). These samples were then subject to thorough rubbing and winnowing to break up clumps and release stored seed. Seed densities of the 0–1 cm, 1–2 cm and 2–4 cm deep soil layers for both littered and bare areas were assessed by first rubbing the soil samples to break up soil aggregates, and then passing them through a 1.6 mm sieve and counting the seeds.

2.3. Data analysis

2.3.1. Study 1

Data from the canopy and extended zones were examined separately to investigate how long seedbanks remained elevated after mast seeding events. Prior to the two analyses, data explorations were applied following a protocol described by Zuur et al. (2010). For each analysis, we had multiple observations over time at each of the 12 shrubs, introducing dependency to the datasets. Therefore, to incorporate a correlation structure into the models, generalized linear mixed models (GLMM) with shrub as a random effect were applied (Zuur et al. 2009, 2013). As both datasets comprised count data, we initially used generalized linear mixed models (GLMM) with Poisson distribution. However, these models were overdispersed. Consequently, the following negative binomial GLMM was applied:

$$\text{Seeds}_{ij} \sim \text{NB}\left(\mu_{ij}, k\right)$$

$$\log\left(\mu_{ij}\right) = \text{Time}_{ij} + a_i$$
$$= \beta_1 \times T_{1ij} + \beta_2 \times T_{2ij} + \beta_3 \times T_{3ij} + \beta_4 \times T_{4ij} + \beta_5 \times T_{5ij} + \beta_6 \times T_{6ij} + a_i$$

Seeds_{ij} was the number of viable seeds from time j at shrub i, where $j = 1, .., 6$ and $i = 1, .., 12$. Time_{ij} was used as a categorical covariate and was split up into six dummy variables with values 1 (observation was taken at time j) or 0 (observation was not taken at time j). The six levels of Time_{ij} represented the six sampling times, from October 2010 through to September 2012. The random intercept a_i was assumed to be normally distributed with mean 0 and variance σ^2_{shrub}. Its inclusion introduced a compound correlation between observations from the same shrub.

Estimation of the regression parameters was done within a Bayesian framework using JAGS (Plummer, 2003) via the R2jags package in R (Yu-Sung and Masanao, 2012). Posterior distributions (using diffuse normally distributed priors) were calculated for each parameter using Markov Chain Monte Carlo (MCMC) simulations (see Appendix for MCMC specifications). Specifically, the MCMC iterations calculated the posterior distributions of $\beta_2 - \beta_1$, $\beta_3 - \beta_1$, $\beta_4 - \beta_1$, $\beta_5 - \beta_1$, and $\beta_6 - \beta_1$. Using the posterior distribution of these differences, 95% credible intervals were obtained, and by observing

the post-mast time point when the 95% credible interval contained 0, it was possible to estimate the time point when post-mast seed densities returned to pre-mast levels. Posterior mean Pearson residuals were extracted for both the observed data and the simulated data, and then compared using residual sum of squares to assess model fit (Ntzoufras, 2009; Zuur et al. 2013).

To investigate the effect of proximity to parent plant on seed densities at the different sampling times, we calculated the differences between seed numbers in the 'canopy' and 'extended' zones at each shrub at each of the six sampling periods. These differences were then analysed using a Gaussian linear mixed-effects model using the same covariates as in the temporal analysis.

2.3.2. Study 2

Exploration of the soil depth dataset followed a similar protocol to that used in the temporal analysis. Initial modelling using Poisson GLMM and zero-inflated Poisson GLMM indicated overdispersion. When we applied a zero-inflated negative binomial (NB) GLMM, the estimated value of π was equal to 0, indicating that an ordinary NB GLMM should be applied. This model was not overdispersed. The NB GLMM was of the form:

$$\text{Seeds}_{ij} \sim \text{NB}\left(\mu_{ij}, k\right)$$

$$E\left(\text{Seeds}_{ij}\right) = \mu_{ij} \text{ and } \text{var}\left(\text{Seeds}_{ij}\right) = \mu_{ij} + \frac{\mu_{ij}^2}{k}$$

$$\log\left(\mu_{ij}\right) = \text{intercept} + \text{Depth}_{ij} + \text{Strata}_{ij} + a_i$$

$$a_i \sim N\left(0, \sigma^2\right)$$

Seeds_{ij} was the number of observed viable seeds from soil strata j at shrub i, where $i = 1, …10$ and $j = 1, .., n_i$. The shrub identity (a) was used as a random intercept, and this automatically imposed a correlation between observations from the same shrub.

As in the temporal analysis, models were estimated using MCMC techniques using the same software packages (see Appendix for MCMC specifications). Once models were fitted, model validation was applied in which Pearson residuals were plotted versus fitted values, and versus all covariates in the model.

3. Results

3.1. Study 1

The mean density of viable seeds at each shrub was low prior to masting, at 1 seed per 0.16 m^2 sampling unit in the canopy zone (6.3 seeds/m^2), and 0.1 seeds per sampling unit in the extended zone (0.5 seeds/m^2). Mean seed densities increased sharply following seed fall, with the November 2010 sampling round indicating 206.8 seeds per sampling unit in the canopy zone (1292 seeds/m^2) and 36.4 seeds per sampling unit in the extended zone (227.6 seeds/m^2). For both the canopy and the extended zone datasets, the posterior distributions calculated by the MCMC estimations indicated that there were significant differences between the seed densities of time 1 and times 2, 3 and 4, but not between time 1 and times 5 and 6 (Fig. 2, see also Appendix 1). These results showed that seedbank densities in both zones were significantly higher than pre-mast densities for the first three sampling periods, but that seedbank densities had returned to pre-mast densities by approximately 18 months after initial seed rain.

Results of the Gaussian mixed effects 'zone comparison' model indicated that for times 1, 5 and 6 there were no differences in seed numbers between the two zones (Table 1 in Appendix). However,
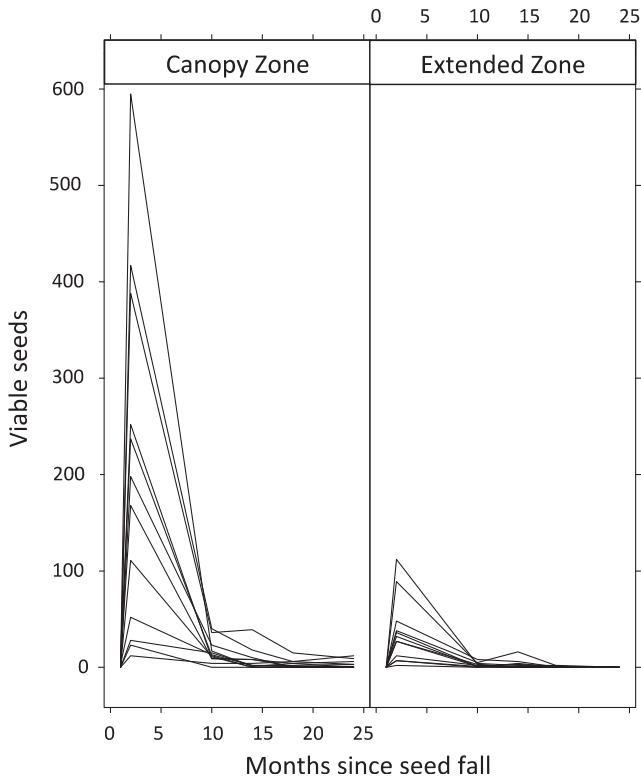
Fig. 2. Number of viable seeds observed (per 0.16 m² sampling unit) beneath canopies and in the extended canopy zone for each of 12 mulga shrubs, sampled at six time periods between October 2010 and September 2012. The *x*-axes indicate the number of months since sampling time 1 (October 2010).

for times 2 and 3 (and to a lesser extent, time 4) there were significant 'parent plant effects' with significantly more seed found in the canopy than the extended canopy zone (Fig. 3).

3.2. Study 2

There was a weak strata effect, showing that litter-covered soils had higher seed densities than areas with bare soil (Table 1, Fig. 4).
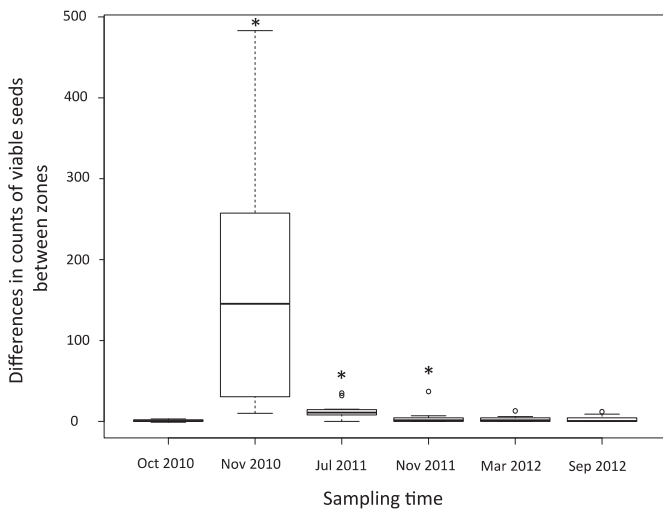

Fig. 3. Bar chart showing differences in viable seed numbers (per 0.16 m² sampling unit) between canopy and extended zones at each of the six sampling periods. Sampling periods with significant between-zone differences in seed numbers are indicated with (*).

Table 1
Results from the soil depth MCMC. The columns labelled 'Mean' and 'sd' indicate the mean and standard deviations of the posterior distributions from the MCMC. The columns labelled 2.5% and 97.5% define a 95% credible interval (the Bayesian equivalent of a confidence interval). If 0 is within this credible interval, then the corresponding parameter is not significant*. The Rhat and *n*.eff columns are for diagnostic purposes.**

	Mean	sd	2.5%	97.5%	Rhat	*n*.eff
Intercept	−1.90	0.75	−3.41	−0.49	1.001	8000
Depth 0−1	3.85	0.77	2.36	5.44	1.001	8000
Depth 1−2	2.99	0.77	1.51	4.57	1.002	8000
Depth 2−4	2.33	0.80	0.75	3.95	1.001	8000
Strata	0.92	0.47	0.007	1.83	1.001	8000
Sigma shrub	0.72	0.44	0.066	1.72	1.001	4300
k	0.42	0.11	0.239	0.69	1.001	8000

* For the three soil depth parameters, seed numbers were analysed against the baseline 'surface' parameter.
** The Rhat column is a diagnostic for mixing of the MCMC chains, and n.eff is the sample size of the chains corrected for auto-correlation in the chains.
The term *k* is used in the variance of the negative binomial GLMM.

There was also a clear non-linear depth effect, with few seeds contained in the surface layer, and with highest seed abundances occurring at the 0−1 cm level for both strata (19.3 seeds per sampling unit (120.6 seeds/m²) for littered areas, and 5.7 seeds per sampling unit (35.6 seeds/m²) for bare areas) (Fig. 4). Seed numbers for both the litter covered and bare areas declined sharply with increasing depth, reaching a mean of 4.3 viable seeds per sampling unit (26.9 seeds/m²) at the 2−4 cm level for littered areas, and 2.1 viable seeds per sampling unit (13.1seeds/m²) for bare areas.

4. Discussion

4.1. Seedbank dynamics

The current study indicated that mulga populations have sparse seedbanks in the absence of recent seed fall, but experience transient post-mast seedbank pulses that last approximately 18 months from the time of initial seed fall. This finding suggests that previous studies recording low mulga seed densities were conducted in the absence of any recent seed fall (Hodgkinson et al. 1980; Wright, 2007; Page, 2009). Rapid reduction in seed numbers after masting is consistent with studies elsewhere (Haase et al. 1995; Kelly and Sork, 2002), and in the current study, was likely to be driven by high levels of seed predation from the diverse granivore fauna in
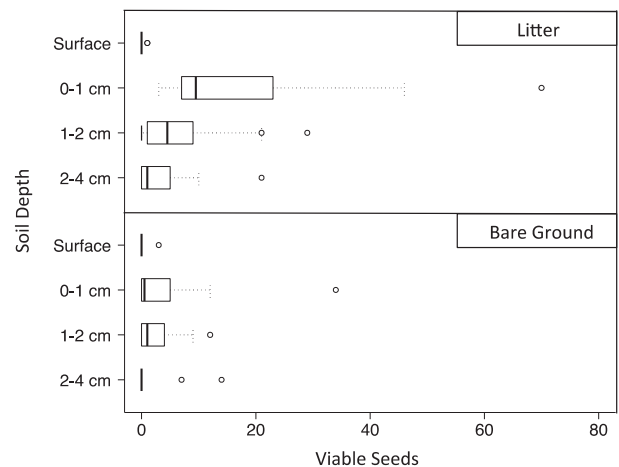

Fig. 4. Box plots of viable seed densities at four depth categories (surface; 0−1 cm; 1−2 cm; 2−4 cm) for bare ground and litter habitat zones. Sampling of depth categories was carried out in December 2011, c. 13 months after initial seed fall in November 2010.

arid Australia. Our results are also consistent with the findings of a previous field experiment at Laycock's Sandplain, where seed numbers in sites baited with mulga seeds were reduced by 39% over 14 days, and by 98% over a six month period (Wright, 2007). While this previous experiment was unable to determine the species involved in the removal of mulga seeds, common *Acacia* seed predators known to exist in mulga habitats include generalist seed-eating birds (e.g., *Poephila, Melopsittacus,* and *Ocyphaps* spp.) (Leavesly, 2008), highly mobile rodents (e.g., *Pseudomys, Notomys,* and *Rattus* spp.) (Dickman et al. 1999), and a high diversity of harvester ants (Morton, 1982).

At this stage it is unclear whether shed post-mast mulga seed is actually consumed by predators, or simply dispersed and discarded at spatially distant seed caches. Previous research would tend to support the former premise, as most granivorous birds and rodents, as well as many species of common arid ant genera such as *Pheidole* and *Iridomyrmex*, are known to be true seed harvesters (seed predators) rather than dispersers (Bridgewater, 1934; Ireland and Andrew, 1995). Nevertheless, it is likely that seed removal by ants may promote some level of either distance (away from parent plants) or depth dispersal (to lower, 'safer' soil depths), as white elaiosomes on mulga seeds indicate an adaptation to ant-assisted dispersal (Davidson and Morton, 1984) (Fig. 1c). Moreover, occasional observations of mulga seedling clumps after fire denote the presence (and potential importance) of sporadic, belowground seed aggregations (Fig. 1d).

Mulga seedbanks were found to be more concentrated beneath areas with litter compared to bare areas. This may indicate that mulga litter beds act as seed safe sites, providing mechanical protection against granivore removal following seed shed. Alternatively (or additionally), heavy litter may act as a physical barrier during rain events or windy weather, catching seeds that become entrained by overland water flows or wind during gusty conditions. Mulga seeds were also found to be more concentrated around the 'canopy' zone than in the adjacent 'extended' zone for approximately 12 months after masting. This suggests that dispersal away from parent plants is not high, and explains the commonly observed clusterings of seedlings around mature mulga shrubs that are killed during fires (Everist, 1949).

Exploration of the raw seedbank data revealed occasional collections of seed at greater soil depths. These seed clumps are assumed to be either seed caches of vertebrate or invertebrate fauna, or seeds that had descended to lower soil profiles via cracks in the soil surface. It is possible that deeply buried seeds may provide an important seed source for recovery after severe droughts, when adult mortality can be high (Everist, 1949) and volumes of seed at shallower soil depths may be low due to lack of recent seed input. In post-drought situations, extra water and nutrients that are available because mature adults died due to water deficits may facilitate increased seedling recruitment, irrespective of the absence of heat cues. This is because unheated mulga seeds may still achieve 5—50% germination rates in optimum temperature and moisture conditions [although there is high variation in the levels of exogenous dormancy in seeds from different mulga genotypes (Burrows, 1973; Fox, 1985)]. This finding may help to explain the ecological health of heavily stocked mulga ecosystems in Queensland and New South Wales, despite the absence of fire over long periods of time.

4.2. Implications for regeneration after fire

The presence of seedbank pulses shortly after seed shed shows that *A. aptaneura* masting is likely to have important consequences for populations that are burnt. Our results indicate that populations burnt within 18 months of seed fall should experience high levels of seedling regeneration, as seed predators are satiated during this period and there are excess seeds available to be released from dormancy by heat during fires. Conversely, populations burnt long after masting may experience comparatively poor seedling regeneration, as granivores will have had more time to reduce seedbank densities. Given the natural link between high rainfall and fire in arid Australia, most fires in mulga habitats occur after occasional exceptionally high rainfall years (Allan et al. 2003; Griffin et al. 1983). Consequently, because high rainfall stimulates masting in mulga, most rain-linked fires should elicit post-fire seedling regeneration sufficient to offset adult mortality during fire. However, whether or not post-fire recruits survive to replace fire-killed stands will still ultimately depend on the timing and quantity of post-fire rainfall.

Our findings also suggest that fire intensity will interact with fire timing (in relation to masting), as mulga seeds are concentrated in the upper 0—2 cm soil level. For example, low-intensity fires shortly after masting (i.e. fires that only singe upper layers of mulga litter beds and cause minimal soil heating) may stimulate little germination. This is because low soil temperatures during such fires would fail to reach the dormancy-breaking thresholds for the majority of buried seeds (Griffin and Friedel, 1984). Conversely, intense fires shortly after masting (i.e. fires that entirely consume mulga litter beds and cause high levels of soil heating) should stimulate strong seedling germination because: 1) after masting most seed is positioned in the upper 0—2 cm of the soil profile; 2) mulga seeds are stimulated to germinate by temperatures from c. 60—80 °C (Hodgkinson, 1991); and 3) soil temperatures during experimental summer fires have been found to reach approximately 400 °C at the soil surface, 80 °C at 1 cm depth and 60 °C at 2 cm depth (Wright and Clarke, 2008). Consequently, whilst intense fires may kill a proportion of seed that are very close to the soil surface [as mulga seeds are killed by temperatures ≥ 120 °C (Wright, B.R.; unpub. data)], they should stimulate germination of large numbers of seeds at soil depths exposed to temperatures of c. 60—80 °C.

The invasion of buffel grass (*Cenchrus ciliaris L.*) to some mulga communities may be having detrimental effects on mulga seedling recruitment after fire, as soil temperatures experienced during buffel grass fires are believed to be far greater than those experienced during fires where native grasses are the primary fuel source (Marshall et al. 2012). Buffel fires may therefore have negative impacts on seedling regeneration, regardless of whether recent seed fall has occurred or not, by eliminating high proportions of the seedbank with lethal heats. Similarly, occasional fires that take place when high wind and temperature conditions facilitate crown fires may also promote exceptionally high soil temperatures that kill off most of the shallow soil seedbank. Further research is therefore urgently required, to explore the impacts that introduced species and extreme weather conditions have on soil temperatures during fires, and to examine what effects they have on mulga seedling regeneration after fire.

4.3. Adaptive significance of masting in mulga

In arid environments, where rainfall is inherently low and resource availability is often pulsed, resource limitations due to soil moisture deficits are expected to put strong constraints on plant reproductive output (Noy-Meir, 1973). Nevertheless, it seems unlikely that masting in mulga is adequately explained by the resource-matching hypothesis (i.e. that periodicity in reproduction is purely a response to among-year variability in soil moisture resources). Rather, we propose that high levels of reproductive intermittency in mulga may be the result of selective pressures that have accentuated rainfall-induced fluctuations in seed crop size over evolutionary time.

Following the same lines of reasoning used to argue for the adaptive nature of masting in mesic environments (Kelly, 1994; Waller, 1979), the following observations point towards the possibility of masting being an evolved reproductive syndrome in mulga: 1) among-year variation in *A. aneura* reproduction is far more exaggerated than the annual precipitation patterns that exist in arid Australia (Davies, 1976; Preece, 1971); 2) many tree and shrub species occurring alongside mulga have relatively constant among-year seed production (Davies, 1976; Friedel et al. 1994); and 3) being a long-lived habitat dominant with large seeds that are attractive to predators, mulga has the necessary life history traits of a plant that Waller (1979) and Kelly and Sork (2002) predict should be vulnerable to selection for masting by high levels of seed predation.

The current study demonstrated that mulga seedbanks are strongly regulated by seed predators, with transient seed pulses occurring following high rainfall periods. As high rain years are inevitably followed by wildfires in arid regions such as inland Australia (Meyn et al., 2007), masting in mulga may represent a form of environmentally predictive masting (EPM), with populations using exceptionally high rainfall as an environmental cue to synchronize seeding among populations, because such rainfall conditions reliably portend periods of high fire danger. This syndrome satiates predators during periods when landscape-scale fires are likely, which in turn should increase the possibility that large numbers of seeds will be cued by heat to germinate and replace fire-killed stands (see Fig. 1b). Mulga masting may therefore be functionally analogous to other fire-related forms of EPM, such as pyriscent serotiny (the spontaneous, synchronous release of seed from woody fruits after fire) and fire-stimulated flowering, by permitting seedlings to take advantage of reduced competition and the more favourable environmental conditions that exist after fire (Kelly, 1994; O'Dowd and Gill, 1984).

4.4. Summary

This work has shown that mulga seedbank densities fluctuate strongly in response to masting, with maximum seedbank densities occurring shortly after seed shed, and with seed numbers declining rapidly as time-since-masting increases. We therefore predict that fire timing in relation to masting will have important impacts on post-fire seedling regeneration, with fires in close temporal proximity to seed fall having the highest likelihood of promoting profuse post-fire seedling growth. The finding that the majority of the seedbank occurs at the 0–2 cm soil depth was also important, and suggests that low-intensity fires that cause minimal soil heating may have little effect on seed germination, while high-intensity fires may stimulate increased germination. However, we do not suggest that high-intensity fires will be beneficial for mulga systems overall, as such burns invariably result in high levels of adult mortality, and presumably lead to declines in habitat condition for animals. Much further empirical research is required to quantify the impacts that mast years have on seedling regeneration after fire, and to explore the various selective forces that may have been involved in the evolution of masting in mulga. Nevertheless, given the benefits that rain-driven masting should afford a fire-sensitive shrub in environments subject to rain-linked fires and heavy seed predation, we conclude that masting in *A. aptaneura* is likely to be the result of adaptive factors overlaid on environmentally driven reproductive variability.

Acknowledgements

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jaridenv.2014.03.008.

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