



Spatially variable recruitment response to fire severity in golden-top wattle (*Acacia mariae*, family: Fabaceae), a thicket-forming shrub of semi-arid forests

Boyd R. Wright^{A,B,C,*} , Damien D. Andrew^A , Michael Hewins^A, Claire Hewitt^{A,D} and Roderick J. Fensham^{E,F}

For full list of author affiliations and declarations see end of paper

***Correspondence to:**

Boyd R. Wright
Department of Botany, School of
Environmental and Rural Science, The
University of New England, Armidale,
NSW 2350, Australia
Email: bwright4@une.edu.au

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ABSTRACT

Context. Investigations into the life history strategies of organisms in ecosystems prone to fires are essential for effective fire impact management. In Australia, fire severity is expected to increase under anthropogenic climate change (ACC), therefore understanding plant responses to this fire regime element is essential for developing conservation-focused burning practices. **Aims.** Assess the recruitment response of golden-top wattle (*Acacia mariae*) to varying fire severities (high, low and unburnt) in the semi-arid Pilliga forest in Northern Inland New South Wales. Investigate seedbank dynamics and germination biology to inform post-fire recruitment patterning. **Methods.** Longitudinal seedbank studies were performed to understand seedbank dynamics and the associated influence on post-fire regeneration. A laboratory trial was conducted to assess the effects of heat shock and incubation temperature on seed germination. Field surveys were conducted at four sites to assess fire severity impacts and evaluate spatial variability in post-fire recruitment after the 2018 Gibbican Rd wildfire. **Key results.** Recruitment varied among sites but was highest in shrubs burned by high-severity fire (5.8 seedlings/shrub), followed by low-severity fire (0.8 seedlings/shrub) and unburnt shrubs (0.1 seedlings/shrub). Over 5 years, seedbank densities fluctuated markedly, peaking in 2021 following a major seeding event but declined rapidly thereafter. Germination was optimised when seeds underwent heat shock at temperatures between 100 and 140°C and incubated at warm temperatures. **Conclusions.** *Acacia mariae* germination is promoted by heat stimulation, explaining why high intensity burns with higher soil temperatures enhance recruitment. Differences in seedbank densities at the time of fire may account for varied recruitment across landscapes. Overall, *A. mariae* regenerates well after high-severity fires but poorly after low-severity fires, indicating that the species may be resilient to increased fire severity under ACC but struggle under current widespread low-severity prescribed management burning regimes.

Keywords: Acacia, burn severity, climate change, fire regime, granivore, recruitment, seedbank, semi-arid.

Introduction

Wildfires play a pivotal role in shaping the dynamics of ecosystems worldwide, with many Australian forested and woodland landscapes particularly prone to large-scale, intermittent fire events (Bradstock 2010; Bowman *et al.* 2021a; Fensham *et al.* 2024). Despite the long evolutionary history of fire in Australia, the current rise in global temperatures and shifts in atmospheric conditions under anthropogenic climate change (ACC) are fundamentally reshaping the environmental context in which fires occur (Bowman *et al.* 2020; Pausas and Leverkus 2023; Di Giuseppe *et al.* 2024). Given these changing conditions, the resilience of many Australian plant species is speculated to be challenged, with biodiversity risks from wildfires heightened by anticipated increases in fire frequency, fire intensity (the energy output of a fire, measured as heat released per unit area) and fire severity (the ecological impacts of a fire, including effects on vegetation and soil) (Keeley 2009; Bowman *et al.* 2020; Bousfield *et al.* 2023; Cunningham *et al.* 2024a, 2024b).

The genus *Acacia*, comprising c. 1084 species worldwide, dominates the Australian flora and is integral to the biodiversity and ecological functioning of many fire-prone environments. In common with other obligate-seeding (i.e. fire-killed) species, many *Acacia* species exhibit a range of adaptations to fire, including fire-stimulated germination, seed dormancy strategies and post-fire resprouting (Sabiiti and Wein 1987; Tozer 1998; Gordon *et al.* 2017; Cruz *et al.* 2021; Le Breton *et al.* 2023). Reflecting a resilience to burning, numerous studies have shown that recruitment of *Acacia* species responds positively to high severity burning, with high-intensity fires enhancing soil heating and leading to increased recruitment by stimulating germination from heat-primed seedbanks (Hodgkinson and Oxley 1990; Gibson *et al.* 2011; Ooi 2012; Gordon *et al.* 2017; Palmer *et al.* 2018). Additionally, for *Acacia* species with transient seedbanks due to high seed predation (e.g. *A. aptaneura*, *A. melleodora*), the timing of fires in relation to soil seedbank density fluctuations plays a crucial role in post-fire regeneration (Wright and Clarke 2018; Wright and Fensham 2017). High-severity fires following large-scale seeding events,

when seed populations pulse, can trigger prolific recruitment from heat-activated seedbanks for these species.

A widespread but poorly researched *Acacia* species in semi-arid western New South Wales (NSW) is *Acacia mariae* Pedley (family: Fabaceae, subfamily: Mimosoideae; syn. *A. tindaleae* Pedley), commonly referred to as golden-top wattle (Fig. 1a–d). This *Acacia* species is an obligate-seeder and thicket-forming, and in our previous experiments in which we used a plant ignitability unit, results showed that the plant matter has fire-retardant properties, such as lower burn temperatures and slower ignition than coexisting plants (Supplementary Appendix Fig. S1). This reduced flammability appears to be crucial for preventing fire from penetrating the central areas of thickets during high-intensity fires, allowing shrubs in the interior to either remain unburnt or experience lower burn severities, thereby aiding the persistence of stands post-fire.

Despite the low flammability of *A. mariae* vegetation that seems to prevent fire incursion, our field observations suggest that the species uses a bet-hedging strategy, also



Fig. 1. (a) golden-top wattle (*Acacia mariae*) inflorescence/vegetation. (b) Dense post-fire *A. mariae* regeneration after 2018 high-severity wildfire at Rocky Rd site. (c) Unburnt *A. mariae* thicket in recently burnt eucalypt forest. (d) Rare *A. mariae* seedling among unburnt *A. mariae* shrubs. (e) Unburnt eucalypt forest, central Pilliga. (f) Burnt forest after high-severity Gibbican Rd wildfire in 2018 (photos T. Shalldoom, D. D. Andrew and B. R. Wright).

demonstrating strong seedling regeneration after fire. Although no ecological studies have focused on this species, we propose that fire likely promotes *A. mariae* recruitment by raising soil temperatures and breaking the physical seed dormancy common to many hard-seeded *Acacia* species. Our preliminary field observations also indicate significant spatial and temporal variability in *A. mariae* seedbanks. Therefore, as with other arid *Acacia* species, the timing of fire relative to seedbank fluctuations may play a crucial role in shaping recruitment responses within shrub populations.

Our study aimed to quantify the proposed relationship between fire severity and recruitment in *A. mariae*, and to test whether this relationship is spatially consistent. In addition, to test the prediction that recruitment patterning is driven by seedbank transience and/or heat-stimulated germination, longitudinal seedbank studies and a germination trial were carried out. The following experiments were conducted for this study: (1) a quantitative field survey across four shrub populations to monitor *A. mariae* recruitment after high and low severity burning and no fire; (2) a germination trial to determine the effects of heat shocking and incubation temperature on seed germination; and (3) seedbank studies at three sites to examine changes in seedbank densities at different spatial locations and soil depths over time.

Methods

Study area

The Pilliga forest spans more than half a million hectares and is located in the Northern Inland region of NSW. Mean annual precipitation varies across the forest, averaging 750 mm at Coonabarabran in the forest's south (Australian Government Bureau of Meteorology 2024a) and 626 mm in Baradine in the central region (Australian Government Bureau of Meteorology 2024b). The forest's soils originate primarily from non-marine Jurassic Pilliga sandstone, with widespread outcrops of this geological formation, along with associated skeletal soils, common in the southern regions of the forest (Arditto 1982; Dodson and Wright 1989). Dendritic streams drain from these outcrops in northward and westward directions, and this has led to the development of extensive areas of sediment-rich outwash soils in the northern and western sectors of the forest.

The forest is usually divided into two main areas for management purposes: a western zone, comprising numerous river valleys and extensive areas of productive white cypress pine (*Callitris glaucophylla*) woodland; and an eastern zone, characterised by eucalypt-dominated ridgetop forests and woodlands interspersed with creekline woodlands. Our preliminary field observations indicate that the vegetation of the ridgetop forests is usually dominated by eucalypts such as *Corymbia trachyphloia*, *Eucalyptus crebra* and *E. rossii*. The creekline woodlands in both the east and west are dominated by *E. blakelyi*, *E. melliodora*, *E. crebra* and *Angophora*

floribunda. Vegetation throughout the forest is characterised by a dense shrub layer, dominated by genera such as *Acacia*, *Allocasuarina*, *Daviesia*, *Dodonaea*, *Eremophila* and *Phebalium*. Grasses are typically sparse in the Pilliga, though the high rainfall in 2021–2022 that followed the 2018–2020 drought (Fig. 2) triggered the growth of a lush grassy understorey layer. This layer largely comprised grasses of the genera *Aristida*, *Eragrostis* and *Enteropogon*.

Fire regimes

Eucalypt-dominated systems in the Pilliga forest are prone to high-severity wildfires, driven by continuous fuel loads that extend from sparse grassy understoreys (<1 m) through dense shrub layers (1–5 m) to low tree canopies (<30 m) with oil-rich foliage (Norris *et al.* 1991; Cohn *et al.* 2011; Murphy *et al.* 2021). These systems feature a high diversity of obligate-seeding *Acacia* species, most of which germinate densely after intense fires, mature rapidly and have short lifespans (<15 years). Large-scale (sometimes >300,000 ha), high-severity wildfires are an intrinsic component of the forest's fire regime, and the incidence of these wildfires is closely associated with precipitation and fuel/soil moisture availability (Brookhouse *et al.* 1999). As in other semi-arid regions, fires often occur after successive high-rainfall seasons that promote plant growth and the accumulation of ground-cover and shrub-layer fuels (Fig. 2) (Brookhouse *et al.* 1999). Additionally, wildfires can also occur following drought periods, presumably because such conditions increase fuel dryness and heighten vegetation flammability (Fig. 2). Wildfires are mostly started by lightning during electrical storms that occur between the months of November and February.

There are no quantitative data on Aboriginal fire management before European colonisation of the region. However, studies from other arid systems and the 2019–2020 Black Summer fires in eastern Australia suggest that large-scale, high-severity fires are a natural part of woodland and forest ecosystems during extreme climatic conditions and that management/patch burn fires have low influence in preventing these (Sakaguchi *et al.* 2013; Bowman *et al.* 2021a, 2021b; Wright *et al.* 2021). Therefore, large wildfires likely occurred before European arrival during periods of climatic extremes, despite any active fire management by Aboriginal peoples in the Pilliga. Climate-linked fires also almost certainly existed over much longer evolutionary timescales in the prehuman era.

Study species

Acacia mariae is an erect or spreading shrub that grows to 2 m in height and is native to central NSW. The bark is smooth and grey, and the small (0.4–1.3 cm long) phyllodes are covered in fine silvery-grey appressed hairs (Fig. 1a). The geographic distribution encompasses the western slopes and plains of NSW, and the species grows on well-drained, sandy soils in

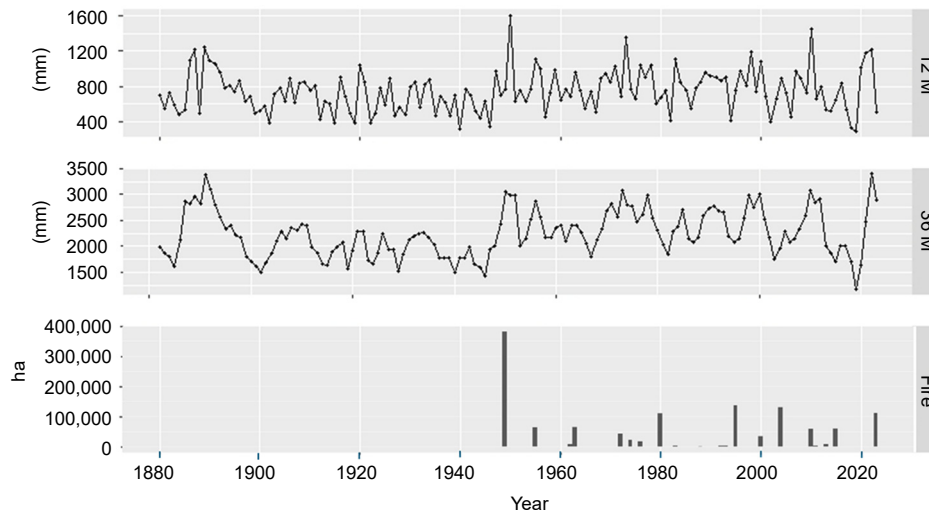


Fig. 2. Cumulative 12-month (12 M – top panel) and 36-month (36 M – middle panel) antecedent rainfall, and total annual area burnt in the Pilliga forest (Fire – bottom panel). Rainfall data are from 1880 to the present and were recorded at the Coonabarabran Showground weather station on the southern edge of the Pilliga forest. Fire records span the duration of recorded fire events and run from 1949 to 2024. No data are available for pre-1949 fire occurrence.

Eucalyptus–Callitris woodland, forest and mallee communities. Throughout the range, *A. mariae* often forms dense thickets (Fig. 1c) but can also occur as isolated individuals. Flowering occurs during winter months, while pod maturation and subsequent seed dispersal take place from mid to late spring (October–November). Field observations suggest that interannual reproductive output is highly variable and flower abortion rates are high (BRW, DA unpubl. data – Appendix Fig. 2). The species is closely related to *A. conferta* A.Cunn. ex Benth. that is widespread in a similar rainfall zone in NSW and Queensland, also thicket-forming and likely ecologically equivalent (Maslin 2001).

Recruitment study

The impacts of fire severity on *A. mariae* seedling recruitment were assessed in July 2021 at the following four sites: Gibbican Rd, Timmellallie Creek, No. 1 Break Rd and Rocky Creek Rd. At each site, fire severity during the 2018 wildfires had been patchy. This site-level variability in fire severity facilitated systematic stratification of shrubs into three distinct fire severity categories: high severity burnt, low severity burnt and unburnt. High severity burnt shrubs were classified based on burnt twigs/branches having a ‘mean minimum burnt tip diameter’ (MMBD) exceeding 3 mm (Moreno and Oechal 1991). In contrast, shrubs in the low severity burn class exhibited vegetation that had undergone scorching but displayed twig/branch MMBDs measuring less than 1 mm. Unburnt shrubs were classified as having remained unburnt during the wildfires.

At each site, 20 shrubs from each of the three burn severity categories were systematically tagged and numbered using the stratified random sampling methodology of Harding

(2012). Subsequently, a random number generator was used to select 10 shrubs for each burn severity category. A circular quadrat with a 1 m radius with the base of the shrub as the centroid was used to quantify the number of seedlings directly beneath shrub canopies for each shrub. Exclusion criteria for the shrubs included ensuring that the radii of any two sampling quadrats did not overlap and that sampled shrubs were not directly adjacent to mature trees. This was done to reduce the potential competition between established trees and seedlings which could affect the likelihood of seedling establishment.

Seedbank study

Acacia mariae seedbank dynamics were monitored over a period of 60 months from four reproductively mature shrubs at the Rocky Creek Rd site of the recruitment study. The sampling timeframe encompassed a widespread seed production event that occurred in the spring of 2020. Selection of the four shrubs for sampling was based on reproductive maturity at the time of assessment and the absence of any fire damage during the 2018 summer wildfire event. Seedbank sampling was also carried out at the Timmellallie Creek and Number 1 Break Rd sites of the recruitment study. However, resource constraints meant that only three rounds of sampling occurred at these two sites over a period of 20 months between January 2021 and August 2022.

At each sampling site, the seedbanks of four shrubs were sampled. At each of these shrubs, two randomly selected 20 × 20 cm square by 6 cm deep columns of soil were excavated from beneath the shrub canopy. Following the trenching of column sides, the surface litter layer and the deeper 5 × 1 cm

layers were removed from the column using a paint scraper and steel ruler. Seed populations in these various layers were assessed in the field by passing the soil/litter materials through 1.6 mm sieves and enumerating the seeds. Post-extraction, seed viability was evaluated by splitting the seeds and inspecting for intact white embryo tissue. When large numbers of seeds were encountered in the samples, viability testing was conducted on a representative sample of 20 seeds. The overall percentage viability for these larger samples was subsequently calculated by multiplying the total seed count by the estimated percentage viability of the representative sample. To prevent resampling the same location during successive sampling rounds, 15 cm long steel camping pegs were inserted into the ground whenever a soil column was extracted.

Germination study

A germination trial was conducted in 2021 in a laboratory at the University of New England, Armidale. Seeds for the trial were sourced from five randomly chosen *A. mariae* shrubs located at the Number 1 Break Rd and Timmellallie sites of the 'recruitment study'. Seed samples were stored in paper bags for 3 months after collection at room temperature. The experimental design of the trial used a two-factor orthogonal design, with the primary objective being to test the impact of heat shock and incubation temperature on seed germination. Heat shock effects were assessed by comparing the germination of untreated (control) seeds with the germination of seeds that were heat shocked for 5 min at temperatures of 60, 80, 100, 120 and 140°C. The effects of incubation temperature on seed germination were examined by comparing germination of seeds incubated in darkness at 25°C (intended to represent a mean summertime soil temperature at 2 cm depth), with seeds incubated at 10°C (intended to approximate a mean wintertime soil temperature at the same depth).

Five replicates of 20 seeds were used for each combination of the heat shock and incubation temperature treatments, resulting in a total of 100 seeds tested for each of the 12 treatment combinations. After the heat shock treatment, the seeds were arranged on Whatman No. 1 germination pads (Advantec, Dublin, California, USA) that had been placed on moisture-retaining sponges positioned within 100 mm petri dishes. The dishes were sterilised in boiling water, and sponges were placed in these and moistened with water sourced from the Armidale town water supply. The dishes were randomly distributed in the 10 and 25°C incubators. The incubation period spanned 21 days, and the trays were checked daily and kept moist for the duration of the trial. A final count of germination was conducted at the termination of the incubation period, with germination being defined as the emergence of the radicle from the testa. Tetrazolium testing of the unviable seeds was not conducted at the closure of the study and we acknowledge this as a limitation of the study.

Statistical analysis

Recruitment study

Statistical analyses were conducted using R statistical software (R Core Team 2023). Prior to each analysis, the datasets underwent exploration following the protocols outlined by Zuur *et al.* (2010). To model the relationship between *A. mariae* seedling recruitment and fire severity, a negative binomial (NB) generalised linear model (GLM) was employed using the R base package with fire severity as a fixed factor with three levels: 'high-severity', 'low-severity' and 'unburnt'. In this analysis, the inclusion of site as an additional fixed factor facilitated the assessment of variation in the relationship between recruitment and fire severity across sites. Following model fitting, a *post hoc* comparison with a Bonferroni correction was conducted using the 'emmeans' package (Lenth 2016) to assess recruitment differences among the three fire severity categories and among the four sites. Model validation, including graphical model validation procedures, and overdispersion and zero inflation testing, was performed to ensure compliance with the underlying assumptions of the model.

Seedbank study

The temporal dynamics and soil depth distribution of the Rocky Creek Rd seedbank dataset were examined using an NB generalised linear mixed model (GLMM) in the 'lme4' package (Bates *et al.* 2015). 'Soil depth' and 'sampling time' were incorporated as fixed effects and initial modelling tested for an interaction between these terms. 'Shrub' was modelled as a random factor to address temporal dependencies stemming from the repeated sampling of soils from the same shrubs over time. Upon establishing non-significance, the DEPTH × TIME interaction term was removed, and the model was re-run to assess the main effects of soil depth and sampling time. As with the recruitment analysis, graphical validation procedures were employed to verify the NB GLMM's underlying assumptions.

Intersite variability in soil seed populations through time and across soil depths was also assessed for the Timmellallie Creek and Number 1 Break Rd sites using an NB GLMM. In this model, 'Site', 'Soil depth' and 'Sampling time' were incorporated in the model as fixed effects and modelling tested for an interaction between these terms. As with the other analyses, graphical validation procedures were employed to test the underlying assumptions of the model.

Germination study

The interactive effects of heat shock temperature and incubation temperature on *A. mariae* seed germination were modelled using a GLM with a binomial distribution. A likelihood ratio test was applied to test the significance of the interaction between these two variables. After model fitting, graphical validation procedures were carried out to

assess the underlying assumptions of the model (i.e. fitted values were plotted against residuals etc.).

Results

Recruitment study

There was a strong association between seedling recruitment and fire severity (deviance = 230.26, d.f. = 2, $\text{Pr}(> \text{Chi}) < 0.0001$), with *post-hoc* testing revealing significantly higher seedling counts at shrubs burnt at high severity than those burnt at low severity and that were unburnt ($P < 0.0001$) (Fig. 3). The model also demonstrated strong variation in seedling densities between sites (deviance = 151.68, d.f. = 3, $\text{Pr}(> \text{Chi}) < 0.0001$), with significantly more recruitment at Rocky Creek compared to the Timmellallie Creek and Number 1 Break Rd sites, and significantly less recruitment at the Timmellallie Creek site than all other sites (Fig. 4).

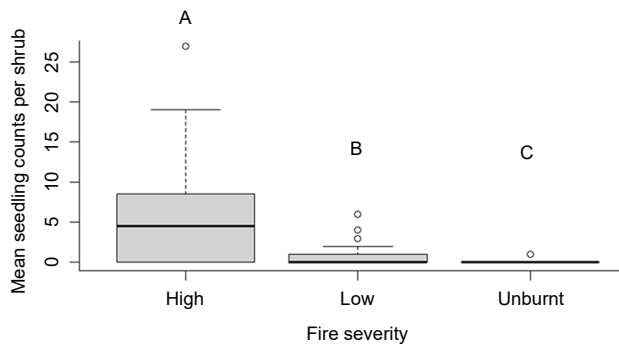


Fig. 3. Boxplot showing median seedling counts (and interquartile ranges) under *A. mariae* shrubs across four sites in the Pilliga forest, stratified according to whether plants had experienced high- or low-severity fire or remained unburnt during the January 2018 Gibbican Rd wildfire. Boxes denoted by different lettering indicate significant differences between fire severities under *post-hoc* testing ($P < 0.05$).

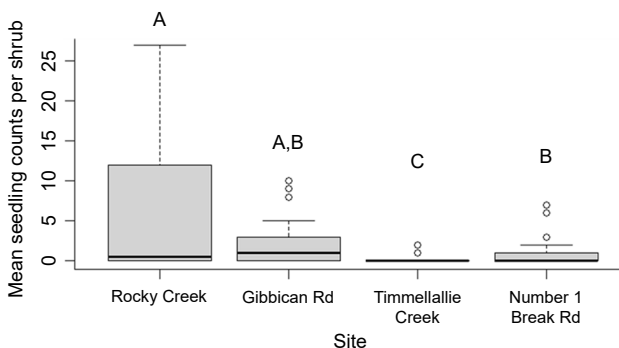


Fig. 4. Boxplot showing median seedling counts (and inter-quartile ranges) beneath *A. mariae* shrubs observed across four sites in the Pilliga forest (results are pooled across fire severities). Boxes denoted with different lettering indicate significant differences between sites under *post-hoc* testing ($P < 0.05$).

Seedbank study

Seed numbers exhibited no significant variation across the different soil depths over 60 months at Rocky Creek Rd (Likelihood Ratio Test (LRT) statistic = 4.046, $\text{Pr}(\text{Chi}) = \text{n.s.}$). Nonetheless, the NB GLMM analysis demonstrated a significant time effect (LRT statistic = 68.97, $\text{Pr}(\text{Chi}) < 0.0001$), with mean seed densities low across all soil depths during the 2018, 2019 and 2020 sampling rounds (0 (s.e. = ± 0), 1 (s.e. = ± 1) and 1 seeds/m² (s.e. = ± 1) respectively) (see Fig. 5) but with a significant increase in seed densities during the January 2021 sampling round (138.54 seeds/m² (s.e. = ± 51.36)) (Fig. 5). In the mid-2021 and 2023 sampling rounds, seed numbers experienced a rapid decline from the January 2021 densities, with mean seed numbers across all soil depths of 95.8 (s.e. = ± 34.4) and 13.5 (s.e. = ± 6.2) seeds/m² in August 2021 and July 2023, respectively (Fig. 5).

The analysis of the 18-month seedbank data from the Timmellallie and Number 1 Break Rd sites detected a significant three-way interaction between site, soil depth and sampling time. This indicated that the relationship between seed densities at different soil depths and sampling times differed between sites (Fig. 6). *Post-hoc* testing indicated that, like the Rocky Creek dataset, seed numbers at the Timmellallie Creek site declined through time from the initial January 2020 sampling time. In contrast, seed numbers were low at all soil depths and sample times for the Number 1 Break Rd site and *post-hoc* testing indicated no significant differences through time at this site.

Germination study

There was a significant interaction between heat shock temperature and incubation temperature on the proportion of germinated *A. mariae* seeds (deviance = 84.226, d.f. = 5, $\text{Pr}(> \text{Chi}) = 0.00302$) (Fig. 7). This indicated that the relationship between germination and ‘heat shock’ varied between the two different incubation temperatures. This effect is illustrated in Fig. 7, which shows that in the 10°C incubation cabinet not a single seed germinated, regardless of heat shock temperatures. In contrast, in the 25°C cabinet, a strong positive relationship existed between heat shock temperature and the proportion of seeds that germinated. In the 25°C cabinet, minimal (<5%) germination occurred for the control, 60 and 80°C heat shock temperatures. However, a strong increase in germination occurred for the 100 (mean = 72%, s.e. = ± 1.2), 120 (mean = 80%, s.e. = ± 0.3) and 140°C (mean = 70%, s.e. = ± 1.3) heat shock temperatures (Fig. 7).

Discussion

Our quantitative field experiment supported the hypothesis that a positive relationship exists between increasing fire

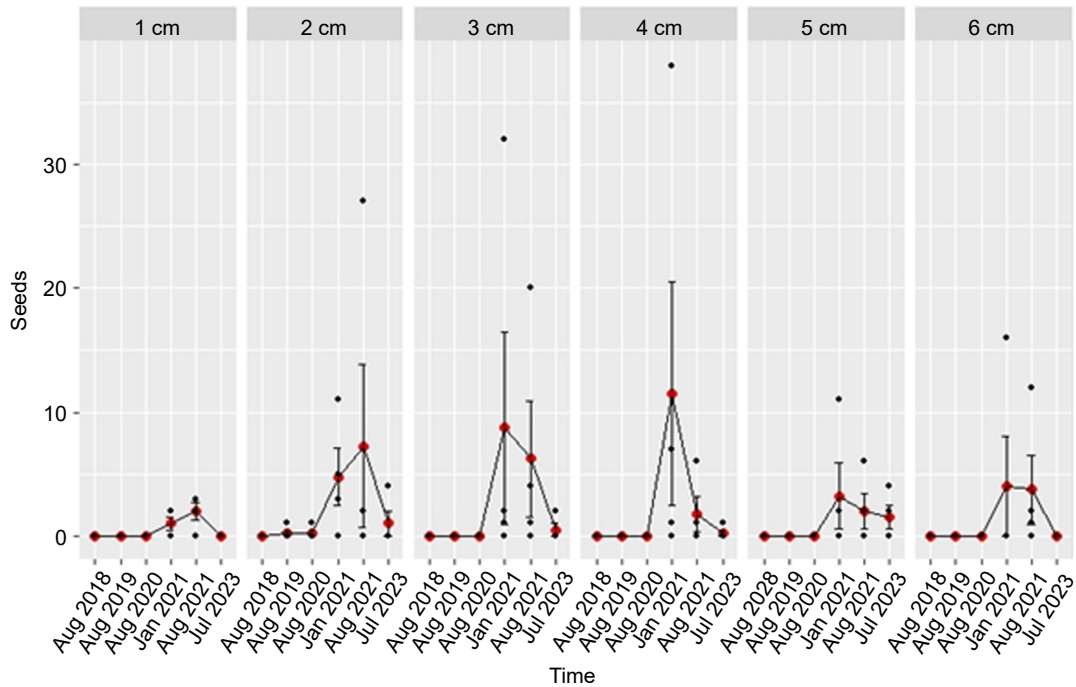


Fig. 5. Viable *A. mariae* seed counts/sampling unit (0.4) m² (including raw data (black dots), mean values (red dots) and standard errors of means (bars)) at Rocky Creek site in the Pilliga forest. Seedbanks were sampled at six time periods between 2018 and 2023, with sampling stratified across six soil depths.

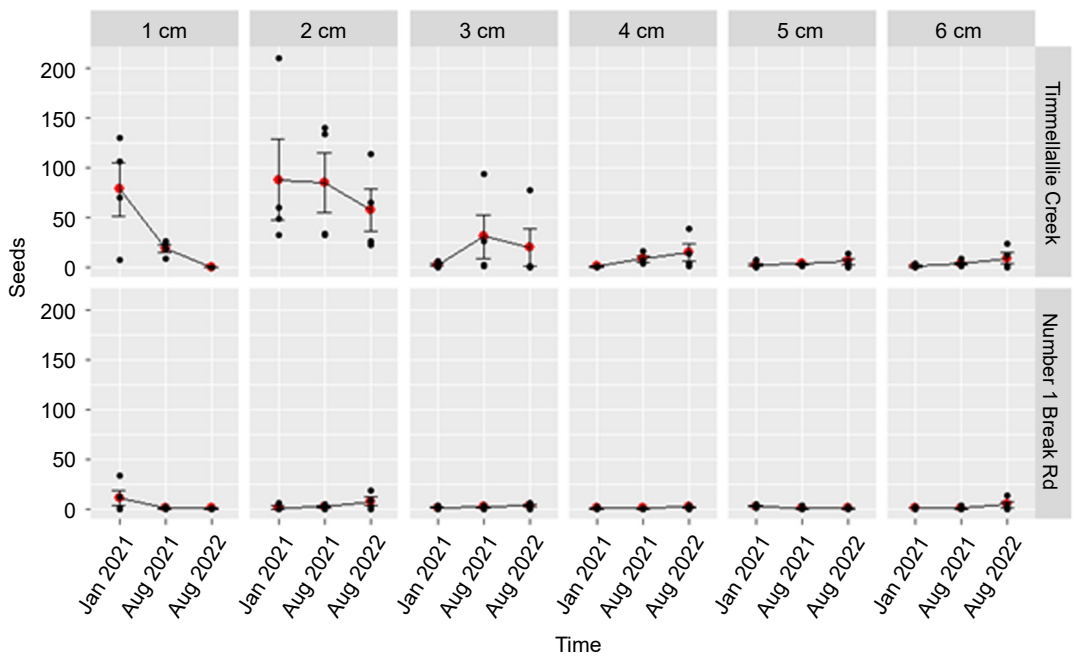


Fig. 6. Viable *A. mariae* seed counts/sampling unit (0.4) m² (including raw data (black dots), mean values (red dots) and standard errors of means (bars)) at Timmellallie and Number 1 Break Rd sites in the Pilliga forest, sampled between January 2021 and August 2022. Sampling was stratified across six soil depths.

severity and *Acacia mariae* recruitment. However, the strength of this relationship was also found to have varied across shrub populations. Observations of strong recruitment

after high severity burning are consistent with earlier studies by Gordon *et al.* (2017), who observed positive recruitment responses in twelve of sixteen *Acacia* species after the

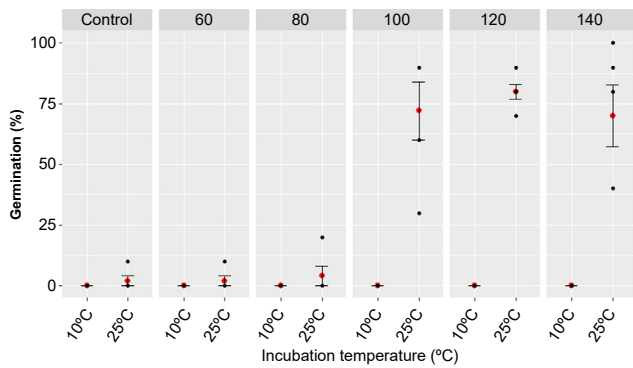


Fig. 7. Percentage germination of *A. mariae* seeds treated under different combinations of incubation temperature (10 and 25°C) and heat shock temperature (control, 60, 80, 100, 120 and 140°C). Five replicates (20 seeds per replicate) were tested for each combination of heat shock and incubation temperature treatments. No artificial lighting was supplied during incubation (i.e. the seed trays were incubated in darkness). Red dots in the figure are mean number of seeds that germinated, bars are standard errors of means and black dots are raw data points.

high-severity ‘Wambelong’ wildfire of 2013 in Warrumbungle National Park, slightly south of the Pilliga. In a separate study within the same park, Palmer *et al.* (2018) documented a nearly four-fold increase in the mean density of live woody *Acacia* stems under high compared to low severity-burnt shrubs. Similar positive associations between fire severity and seedling regeneration have been reported by Knox and Clarke (2012) in the New England Tableland Bioregion, Le Breton *et al.* (2023) in wet sclerophyll forests of south-eastern Australia, and Wright *et al.* (2016) and Wright and Fensham (2018) in arid central Australia.

The generally positive effect of high-severity fires on *A. mariae* recruitment likely relates to physical dormancy in hard-coated seeds, with elevated soil temperatures during ‘hot’ fires priming the seeds for germination via heat stimulation (Baskin and Baskin 2004; Ooi *et al.* 2014). Most hard-seeded *Acacia* species require heat to break dormancy, as strophioles (lenses) on the seeds must be ruptured by heat to allow water imbibition to initiate germination (Letnic *et al.* 2000; Pound *et al.* 2015; Gordon *et al.* 2017; Burrows *et al.* 2018). Our hypothesis that *A. mariae* seeds possess physical dormancy and require heat shock for germination was supported by the germination experiment that demonstrated that seeds exposed to heat shocks between 100 and 140°C germinated well when incubated at 25°C. In contrast, seeds subjected to the same heat shock but incubated at 10°C did not germinate, indicating that lower incubation temperatures are unsuitable for growth. These findings suggest that *A. mariae* recruitment is most likely to succeed following intense summer fires that should provide optimal soil temperatures for heat-shocking seeds and would be

followed by warm post-fire soil conditions that would be conducive to the germination of heat-primed seeds.

In addition to promoting greater soil heating, high-severity fires may trigger increased recruitment because these are more likely to fully consume litter layers on the forest floor than low-severity fires. Heavy litter layers can impose mechanical impedance to seedling emergence, and this has been demonstrated in some *Allocasuarina* species (Crowley 1986). Allelopathic chemicals in *A. mariae* litter may also possibly inhibit seed germination in unburnt areas and studies have shown that high soil temperatures during high-intensity fires can neutralise such chemical barriers to germination (Calviño-Cancela *et al.* 2018). However, further research is needed to test this hypothesis for *A. mariae*.

Although there was a generally positive effect of high fire severity on *A. mariae* recruitment, the effect was spatially variable, with shrubs at the Timmellallie Creek site experiencing minimal recruitment after the 2018 wildfire, irrespective of fire severity. This spatial variability in recruitment could relate to several factors, including between-site differences in post-fire rainfall, variable seedbank densities at the time of fire, and/or post-fire herbivory on seedlings. Limited studies have quantified the relationship between post-fire rainfall and plant recruitment, with notable exceptions including the works of Erickson *et al.* (2023) on arid Australian spinifex grasses, Wright *et al.* (2019) on the Gibson desert shrub *Aluta maisonneuvei*, and various studies on Mediterranean shrubs (Parra and Moreno 2018; Chamorro and Moreno 2019). Nevertheless, considering the intrinsic small-scale patchiness of rainfall in Australia, intersite variations in post-fire rainfall volume may conceivably have contributed to intersite differences in the recruitment of *A. mariae* seedlings.

Our seedbank studies supported the possibility that variations in seedbank density at the time of fire could also have affected the recruitment responses of *A. mariae* shrubs. The observed surge and subsequent decline in *A. mariae* soil seed populations of shrubs at the Rocky Creek and Timmellallie Creek sites following the high seed production year of 2020 indicate that the seedbanks of *A. mariae* are transient rather than persistent, and that an association likely exists between sporadic seed fall events and seedbank dynamics. In light of this finding, the shrub populations at sites that had higher levels of recruitment in our quantitative field survey may have had more recent and/or higher volume seed production events prior to fire than sites that had minimal recruitment. Similar associations between intermittent seed input events, seedbank pulses and enhanced post-fire seedling recruitment have been documented in the arid Australian shrubs, *Acacia aptaneura* (Wright and Zuur 2014; Wright and Fensham 2017) and *Acacia melleodora* (Wright and Clarke 2018), and experimentally tested in the arid zone masting grass, *Triodia pungens* (Wright and Fensham 2018). Fig. 8 illustrates this proposed relationship in *A. mariae*, with optimal recruitment from the heat-activated seedbank expected when intense fires with high soil heating occur

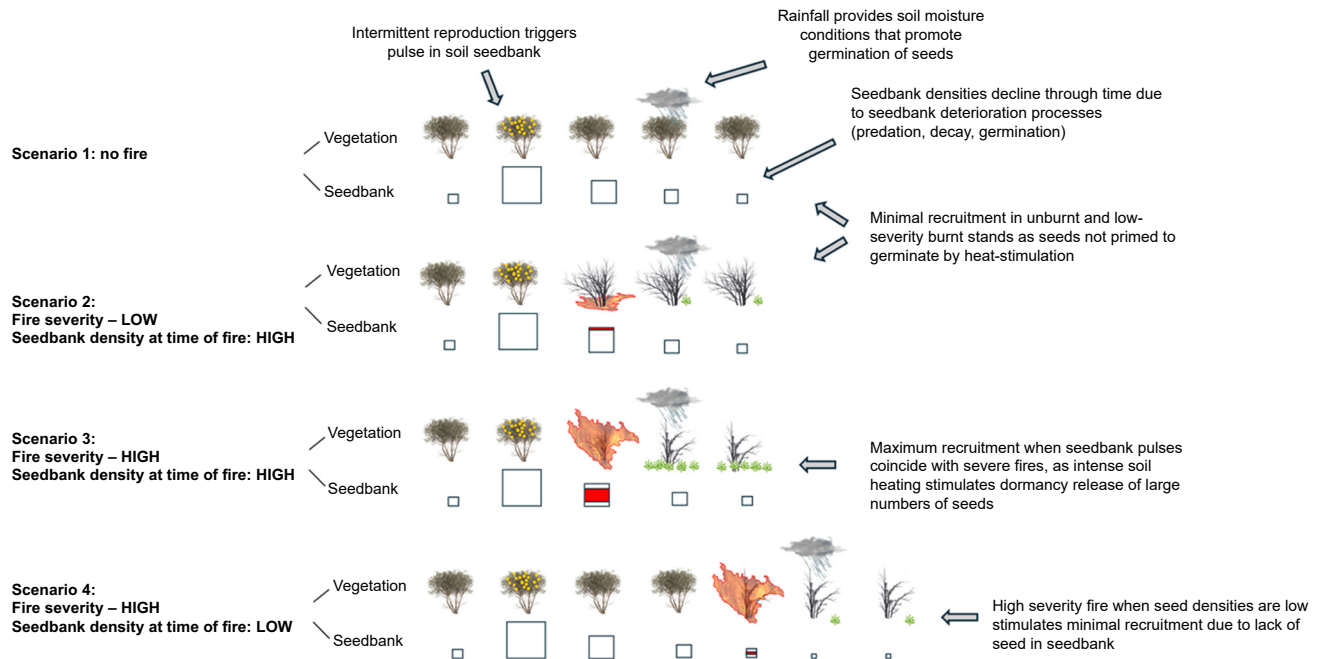


Fig. 8. Proposed dynamics of post-fire recruitment of *Acacia mariae* under four scenarios involving differing fire severities (unburnt, low-severity, high-severity) and differing seedbank densities at time of fire (high, low). Upper illustrations for each of the four scenarios (shrubs' line) depict seedling recruitment response to differing burn/seedbank scenarios (more seedlings (*) corresponds to more recruitment). Lower illustrations (boxes' line) depict changes in seedbank densities over time, with box size indicating relative seedbank density. After seed production events, seedbank densities are expected to decrease over time due to processes such as predation, decay and germination. Red shading within the seedbank boxes indicates the proportion of the seedbank that has been cued to germinate by soil heating during fire.

during periods of elevated seedbank density (Fig. 8 – scenario 3).

Further research is needed to formally evaluate the proposed regeneration model in Fig. 8. Specifically, studies should experimentally test the relationship between seedbank density at the time of fire and post-fire recruitment. Similar studies have been undertaken on the arid-zone masting grass *Triodia pungens*, in which reproductive output was manipulated by clipping inflorescences before burning and applying watering treatments post-fire (Wright and Fensham 2017). A comparable approach could be used for *A. mariae* as its small size would make the species amenable for controlled manipulation of reproductive output.

Several factors could explain *A. mariae* seedbank transience, including high levels of seed predation, rapid seed deterioration, pathogen attack and/or germination of seeds from the soil seedbank. Several Australian studies have shown that while ants are significant dispersers of *Acacia* seeds, few consume the embryo, with most instead attracted to the lipid-rich eliasomes on *Acacia* seeds (Hughes and Westoby 1990; Ireland and Andrew 1995). Predation of the seedbank by vertebrate fauna seems a more likely explanation for *A. mariae* seedbank transience, with species such as the Pilliga mouse (*Pseudomys pilligaensis*), cockatoos (*Cacatua* spp.) and some marsupials all known to consume the entirety

of *Acacia* seeds (Jefferys and Fox 2001; Irlbeck and Hume 2003; Tokushima and Jarman 2010). Senescence (death from old age) or lethal pathogen attack on *A. mariae* seeds would be unlikely to have occurred quickly enough to explain the rapid decline in seedbank densities that we observed. Most *Acacia* seeds are remarkably resilient and can survive for decades under optimal storage conditions (Leino and Edqvist 2010).

Conclusion

Fire-dependent obligate-seeder *Acacia* species are key components of many fire-prone Australian landscapes, yet research on the intricate fire ecology and life history of these species remains limited. Fire management in reserves dominated by these fast-growing species typically focuses on low-intensity, cool-season burns aimed at decreasing fuel loads and minimising ecological damage (Etchells *et al.* 2020; Landesmann *et al.* 2021; New South Wales National Parks and Wildlife Service 2023). Our research suggests that such fuel reduction burns may hinder the regeneration of *A. mariae*, as such burns could be sufficiently intense to kill shrubs but of insufficient intensity to generate the heat required to stimulate recruitment from heat-cued seedbanks.

Acacia mariae may instead be well-adapted to the current 'natural' regime of intermittent high-severity fires during summer. The species employs a bet-hedging strategy, forming fire-retardant thickets that reduce fire severity during extreme fire conditions and also shows strong seedling recruitment after high-severity fires. Although long-term fire exclusion beyond the lifespan of individual trees could result in population decline, the species still demonstrates low-level recruitment in the absence of fire and is likely to persist under various burning (or non-burning) scenarios.

While *A. mariae* seems likely to be resilient to the high-severity fires expected under ACC, the question remains of whether thickets could be at risk if fire frequency increases significantly. This study did not investigate the ideal fire return interval for *A. mariae* but this would likely depend on the time required for plants to reach reproductive maturity and the persistence of seeds in the soil seedbank. We observed *A. mariae* plants that recruited after the 2018 wildfires to be flowering and fruiting by 2023, indicating a primary juvenile period of less than 5 years (BRW, DDA pers. obs. 2023). Given the semi-arid conditions of the Pilliga, characterised by moderate to low rainfall and slow fuel accumulation, it seems unlikely fire frequencies could drop below 5 years, even with climate change. Overall, *A. mariae*'s rapid growth to reproductive maturity, ability to withstand both high- and low-severity fires, and tendency to form fire-retardant thickets suggest that the populations can likely tolerate a wide range of fire frequencies and intensities, and may be resilient to expected changes to fire regimes under ACC.

Supplementary material

Supplementary material is available [online](#).

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Data availability. The data that support this study will be shared upon reasonable request to the corresponding author.

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Author affiliations

^ADepartment of Botany, School of Environmental and Rural Science, The University of New England, Armidale, NSW 2350, Australia.

^BSchool of Agriculture and Food Sustainability, University of Queensland, Saint Lucia, Qld 4072, Australia.

^CThe Northern Territory Herbarium, Department of Lands, Planning and Environment, Alice Springs, NT 0871, Australia.

^DEnvironmental Resources Management Australia Pty Ltd, Level 14, 207 Kent Street, Sydney, NSW 2000, Australia.

^EQueensland Herbarium, Mt Coot-tha Road, Toowong, Qld 4066, Australia.

^FSchool of the Environment, University of Queensland, Saint Lucia, Qld 4072, Australia.