Chapter 6

The influence of seed fate and germination ecology on seedling recruitment of *Acacia* spp. in spinifex grasslands

Introduction

Seedling recruitment events for woody species are extremely uncommon in the spinifex-dominated ecosystems of arid and semi-arid Australia (O'Donoghue 1916; Wellington and Noble 1985; Zimmer 1940). This rarity of natural recruitment was confusing to early naturalists, and led to speculations that the seed of certain inland trees and shrubs was non-germinable (Prescott 1941), and that the vegetation propagated entirely by vegetative means (Holland 1967). Over time, however, observations revealed that occasional regeneration from seed did take place, although it was found to occur almost exclusively after major disturbances, especially after fire (Burbidge 1943; Noble 1982).

There are now known to be many inter-related factors that account for the importance of fire on woody seedling recruitment in inland Australian ecosystems. Fire-associated changes to soil nutrient status (resulting from the release of nutrients from ash (Raison 1979)) and increased post-fire water availability (resulting from the temporary arrest in transpiration of standing vegetation (Wellington 1984)) both serve to improve the survival chances of establishing seedlings. The germination ecology of seeds of many species is also strongly dependent on fire, with heat shock and smoke both known to overcome dormancy and promote germination among a variety of leguminous arid species (Bradstock and Auld 1995; Nano 2005; Preece 1971). Fire is also recognised for its role in facilitating the establishment of temporary seed stores for serotinous tree species, by causing a massive synchronised release of canopy-held seed, which temporarily satiates seed harvesters (Wellington and Noble 1985). In other regions of Australia, post-fire seedling recruitment for non-serotinous tree species is strongly affected by interactions between the germination ecology of seeds and seasonal fluctuations in seed availability (Williams, Congdon *et al.* 2005). These studies have found that when fires coincide with seasonal seed bank peaks, more seedlings establish because more seed is available to be cued by fire.

The results of Chapter 4 revealed that a significantly higher number of non-serotinous woody seedlings (79.6% of which were *Acacia* seedlings) occurred in burned landscapes than in unburned landscapes. This finding suggested that fire was interacting with the germination ecology of seeds of these species, indicating that further investigation into potential links between fire and seed dormancy mechanisms should occur. The results in Chapter 4 also suggested that post-fire seedling recruitment was strongly dependent on season of fire, with higher seedling numbers occurring after summer compared to winter fires. When this finding is coupled with the observation from Chapter 5 that the seed banks of woody species appeared to be highly transient (but with field observations suggesting that peaks occurred after spring seed shed), it can be suggested that higher germination rates after summer fire are due to the synchrony of fire with increased summertime availability of seed. However, the precise mechanism/s behind the apparently transient nature of these seed banks (whether caused by harvesting of seed or decay of seed) remains unclear.

This chapter seeks to determine the mechanisms behind the observed increase in seedling recruitment after summer fires by investigating; a) biotic and abiotic factors that account for the apparently transient nature of woody seed banks; and b) how the dormancy of seeds of *Acacia* species interact with fire related germination cues. Specifically, the following hypotheses are addressed:

1. Seed removal of *Acacia* spp., rather than seed decay, regulate seed bank abundances when seed rain is held constant; and

2. The combination of heat shock and seasonal temperature regime regulate germination in *Acacia* spp.

Methods

Experimental design and study area

Three simultaneous experiments were implemented to test the two hypotheses posed about seed fate and germination. The first involved sowing seeds and testing for seed removal by predators; the second involved examining the deterioration of sown seeds in the absence of predation; and the third involved testing the affect of heat shock

and seasonal temperature regime on germination rates of seed that had been exhumed from the first and second experiments.

Seeds of the following four *Acacia* species were selected: *A. aneura, A. kempeana, A. maitlandii* and *A. melleodora*. All seeds were harvested locally and were not more than two years old at the time of the experiment's commencement. Individual seeds were selected on the basis of the following criteria: a) each seed had an intact aril, b) each seed was whole and not visibly damaged by insect borers and c) each seed was of normal shape and size.

The complete field experiment was replicated in two independent sites approximately 100 m apart, to test for any spatial effects that may have influenced the examined variables. The location of the experiment was adjacent to the site used for the soil temperature experiments (see Chapter 3 for a description of the vegetation and topographic characteristics of this location).

1. Removal experiment

The first experiment tested seed removal rates by imposing three exclusion treatments to ten surface-sown seeds of each *Acacia* species for the following three time periods: 1) one month during winter (July); 2) one month during summer (December); and 3) six months from July to December. The three exclusion treatments were as follows: full exclusion (FX – see Fig. 6.1 a), where exclosures were used to restrict predator access to sown seeds; cage control (CC – see Fig. 6.1 b), where an open exclosure was placed around the seeds to test for exclosure effects on seed removal; and no exclusion (NX – see Fig. 6.1 c) where free access was permitted to sown seeds. Each of these treatments was replicated three times in a random sequence in each of the two sites for each time period. Because the design of the removal experiment also involved the incorporation of cued (heat-shocked) and un-cued seeds from the germination experiment, the replication of the removal experiment was effectively doubled. A schematic depiction of the physical layout of the experiment is shown in Figure 6.2.
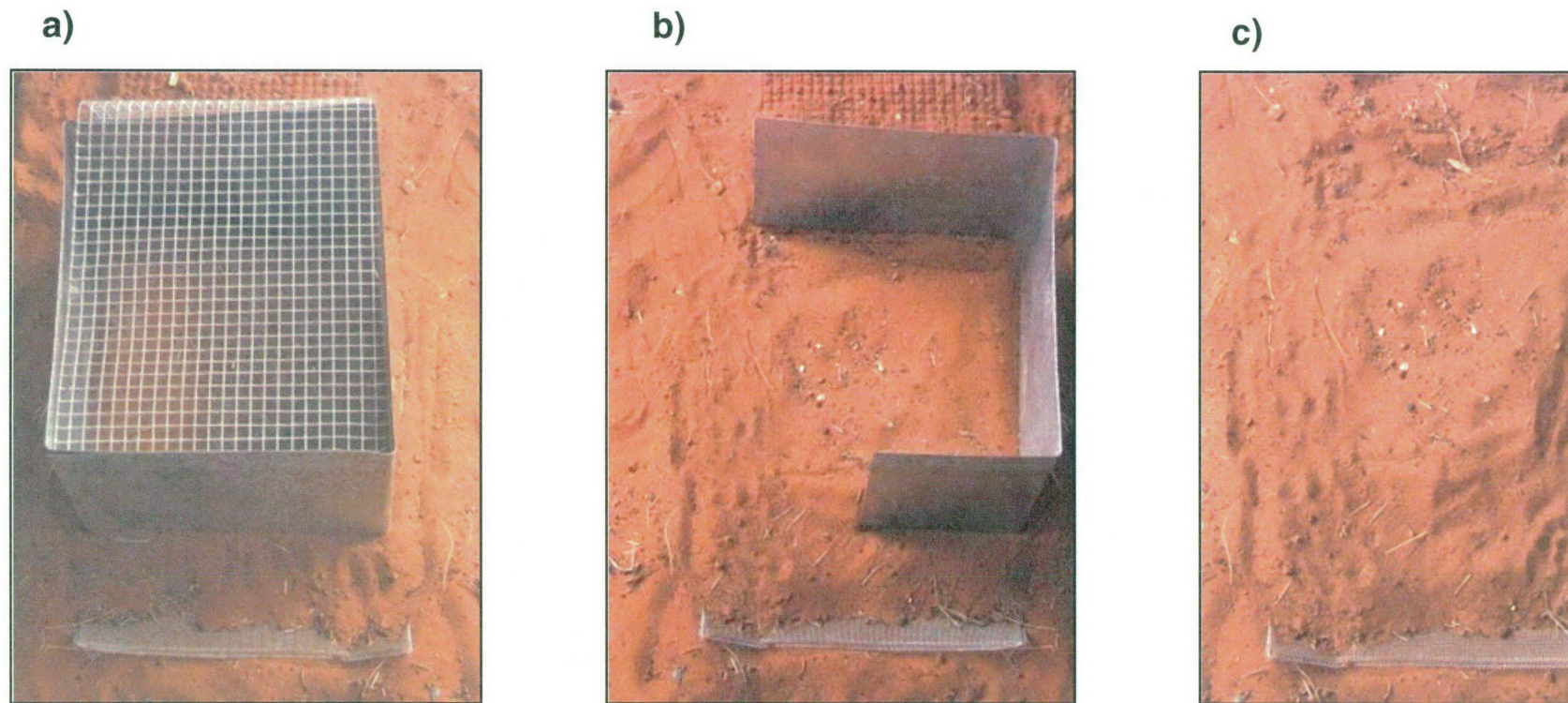
Fig. 6.1 Exclusion treatments used in seed removal experiment: a) full exclusion of seed predators (FX); b) cage control, whereby a sham exclusion was used to test for exclusion effects on seed removal rates (CC); c) no exclusion of seed predators (NX). A sheet of fly screen was also buried beneath the exclosures to restrict access from below.
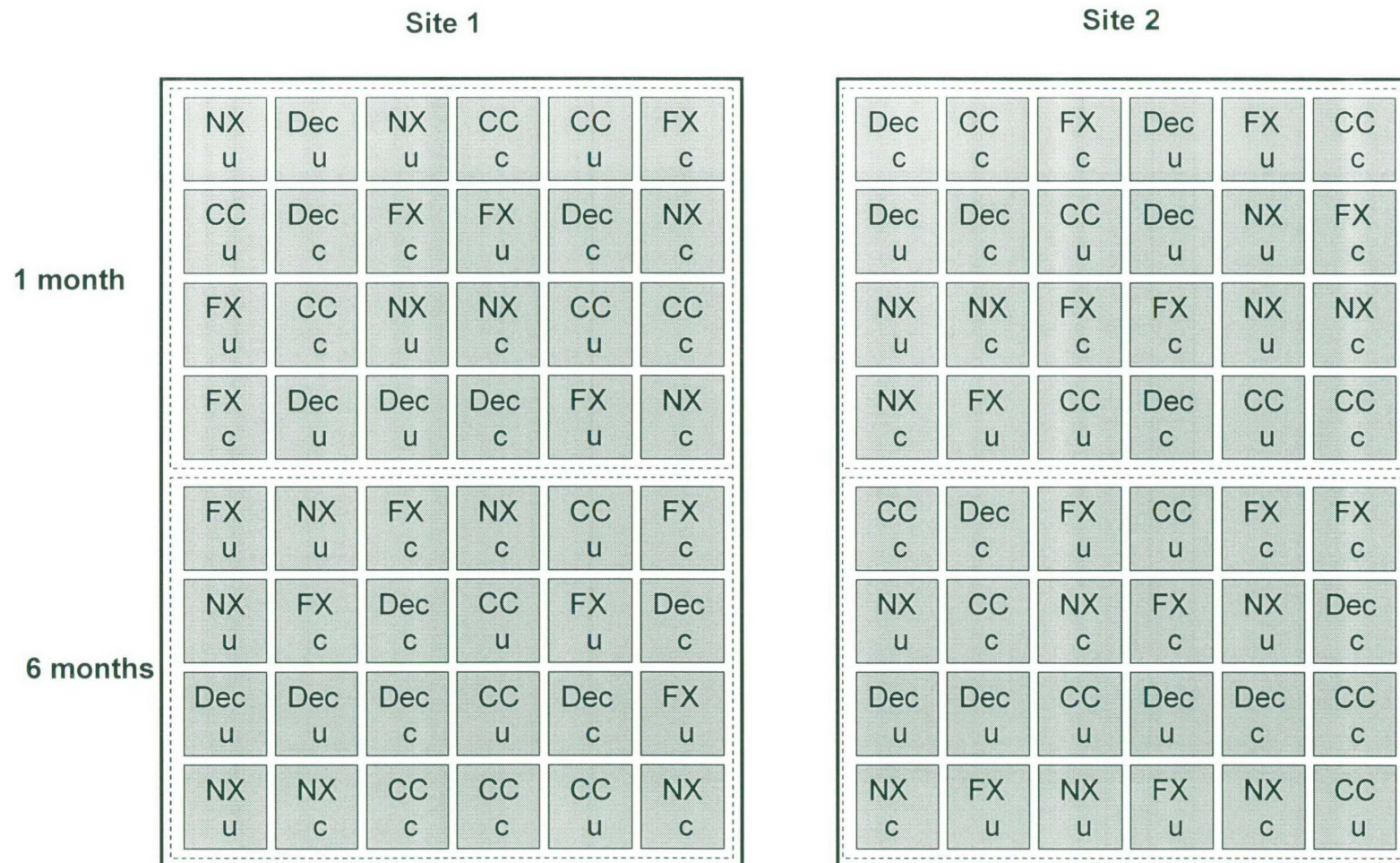
Site 1

1 month

NX u	Dec u	NX u	CC c	CC u	FX c
CC u	Dec c	FX c	FX u	Dec c	NX c
FX u	CC c	NX u	NX c	CC u	CC c
FX c	Dec u	Dec u	Dec c	FX u	NX c

6 months

FX u	NX u	FX c	NX c	CC u	FX c
NX u	FX c	Dec c	CC u	FX u	Dec c
Dec u	Dec u	Dec c	CC u	Dec c	FX u
NX u	NX c	CC c	CC c	CC u	NX c

Site 2

1 month

Dec c	CC c	FX c	Dec u	FX u	CC c
Dec u	Dec c	CC u	Dec u	NX u	FX c
NX u	NX c	FX c	FX c	NX u	NX c
NX c	FX u	CC u	Dec c	CC u	CC c

6 months

CC c	Dec c	FX u	CC u	FX c	FX c
NX u	CC c	NX c	FX c	NX u	Dec c
Dec u	Dec u	CC u	Dec u	Dec c	CC c
NX c	FX u	NX u	FX u	NX c	CC u

Fig. 6.2 Schematic representation of experimental design for seed removal and seed decay experiments. Levels of the removal treatment were FX (full exclusion of predators); NX (no exclusion of predators); and CC (cage control). Plots used to bury seed caches are indicated by 'Dec' (decomposition), while 'u' and 'c' indicate whether the seeds used in each plot were exposed to a heat shock (c) or not (u).

Prior to undertaking the experiment all standing vegetation was cleared to ensure consistent spatial conditions across all treatments and replicates. For the 'full exclusion' treatment, metal frames (50 cm x 50 cm x 10 cm) were constructed from galvanized sheet metal. These frames were placed onto the soil surface and a 2 cm band of Fluon ^{TM} was smeared around the upper lip of each frame to restrict ant access. Prior to the placement of the exclosures, 10 seeds of each species were randomly sown onto the soil surface. A layer of 1 cm chicken wire was then secured to the top of each exclosure to discourage bird and small mammal access, and a sheet of fly screen was buried beneath each exclosure to restrict access for ants and other invertebrates from below. For the 'exclosure control' treatment, 10 seeds of each species were randomly sown on the soil surface and open ended exclosures, identical to the ones used in the full exclusion treatment but with one side missing, were placed around the seed. No Fluon or chicken wire was used for this treatment, although fly screen was placed below the soil as this assisted in the collection of soil when it came time to exhume the seed. For the 'no exclusion' treatment, 10 seeds of each species were randomly sown on the soil surface, with a layer of fly screen beneath the soil to assist in soil retrieval when seeds were exhumed.

Once the seeds had been exposed for their allotted times, remaining seeds (together with a large quantity of soil) were shovelled from the soil surface, stored in plastic bags and brought back to the laboratory. The soil samples were then sifted using a 1.5 mm sieve and the sieved organic matter was placed under a low magnification bench microscope to extract and count the number of remaining *Acacia* seeds.

The effects of removal treatment, season of exposure, duration of exposure and heat shock on seeds remaining for each *Acacia* species were examined using orthogonal multi-factor generalised linear models in GLMStat. The significance of the models was tested using a Pearson's Chi-square function in GLMStat, and the response variable for each analysis was the number of seeds extracted from each soil sample. All analyses employed logistic models, and plots of residuals were examined prior to analyses to detect non-linear trends. As the models were multi-factored, orthogonal combinations were sequentially deleted from the models when they were found to be non-significant by

the Pearson's Chi-square analyses. Scheffé post hoc tests were employed to test for between treatment differences.

2. Decay experiment

The second experiment tested for decay of seed over time by comparing the mortality of seed buried in soil over one month with seed that was buried for six months. The sowing and collection dates for this experiment were synchronised with those of the first experiment. Ten seeds of each species were first placed in nylon purses and sealed using an Impulse Sealer [TM]. Holes of approximately 300 mm depth were then dug using a spade, and the purses were buried in them. Burying the seeds at this depth mimicked deep burial in an ant or rodent seed cache and ensured that successful germination or emergence could not occur. These holes were randomly interspersed among the previously laid out predation exclosures (see Fig. 6.2). The response variable for this experiment was the total numbers of viable seeds remaining after the purses were exhumed. This was calculated as the sum of the geminated seedlings (tested in the germination experiment) together with the number of ungerminated seeds that were deemed viable by tetrazolium tests (see germination experiment).

The effects of burial time on seed decay for each *Acacia* species were examined using orthogonal multi-factor generalised linear models in GLMStat. The significance of the models was tested using a Pearson's Chi-square function in GLMStat, and the response variable for each analysis was the number of viable seeds remaining after the seed caches had been exhumed after one and six months burial. All analyses employed logistic models, and plots of residuals were examined prior to analyses to detect non-linear trends. As the models were multi-factored (burial time and site), orthogonal combinations were sequentially deleted from the models when they were found to be non-significant by the Pearson's Chi-square analyses.

3. Germination experiment

The third experiment examined the affects of a heat cue and seasonal temperature regime on germination of exhumed seeds. The seeds used for this experiment had been previously incorporated into the removal and decay experiments (see Fig. 5.2). The effect of heat cue on germinability was examined by comparing the germination rates of seeds

that were exposed to a heat shock of 80 ^{0}C for 10 minutes to the germination rates of non-shocked seeds. The effect of seasonal temperature regime on germination was examined by comparing germination rates of exhumed seed sown under summer (day/night temperatures of 30/20 ^{0}C) and winter (day/night temperatures of 15/8 ^{0}C) temperature conditions. This experiment also investigated whether cued seeds entered secondary dormancy, by comparing the germinability of the seed that had been surface sown for one month in the removal experiment against the germinability of seed that had been surface sown for six months in the removal experiment.

Prior to being placed in the germination cabinets, the seeds were placed on anti-fungal germination pads. These were then positioned on top of moisture-retaining sponges and placed in 10x10 cm germination trays. Prior to running the trials all equipment was sterilised. Both the water and moisture-retaining sponges that were to be used for the experiment were autoclaved at 121 ^{0}C at 101 kPa for 30 minutes. Germination trays were also sterilised by being soaked overnight in 0.5% bleach solution. Seeds were placed into the germination trays using forceps, with seeds positioned approximately equidistant to avoid possible interactions between the seeds. The trays were then watered with the sterilized water and placed in random sequence in each of two, independent growth cabinets. Germination of the seeds was monitored every five days, with germination being defined by radicle emergence. The experiment concluded after 21 days in each season. A series of control seed trays were also run in conjunction with the main germination experiment. These control trials used seed that had not been sown in the field experiments, and this tested the viability of the unsown seed. Both cued and uncued seeds were used for these trials.

Following the germination trial, non-germinated seeds were tested for viability. First a simple 'squish test' was performed, with seeds that tested as soft being deemed not viable. The remaining firm, ungerminated seeds were tested for viability using the following tetrazolium test (Lakon 1949). The seeds were first cut longitudinally (but not in half) using a scalpel, to expose the centre of the embryo. The cut seeds were then placed in plastic vials containing 2 mL of 0.5% tetrazolium chloride salt solution, and stored in a dark room for three hours. Following storage, seeds that possessed completely coloured embryos were considered viable, while non-coloured embryos or embryos with

very minimal pink coloration were deemed not viable. A standard for interpretation of viability was worked out previously by boiling samples of seed of each species for one hour and observing how much colour was present in these dead seeds.

The effects of seasonal temperature regime and heat shock on seed germination for each *Acacia* species were examined using orthogonal multi-factor generalised linear models in GLMStat. The significance of the models was tested using a Pearson's Chi-square function in GLMStat[TM], and the response variable for each analysis was the number of seeds that had germinated after 21 days in the growth cabinets. All analyses employed logistic models, and plots of residuals were examined prior to analyses to detect non-linear trends. As the models were multi-factored (seasonal temperature, heat shock and site), orthogonal combinations were sequentially deleted from the models when they were found to be non-significant by the Pearson's Chi-square analyses.

Results

Removal experiment

Removal rates of seeds of *A. aneura, A. kempeana* and *A. melleodora* were all significantly affected by predation exclosures, with exhumed seed numbers being lowest in the 'no exclusion' treatment, and highest in the 'full exclusion' treatment (see Table 6.1). *Acacia maitlandii* was the only species whose seeds were not significantly reduced by seed predators over a one-month period; although this species did show increased removal of seed under summer compared to winter conditions. Over a six-month period, however, all *Acacia* species showed strong reductions in seed numbers in the 'no exclusion' treatment, with an overall average (of all species) of 2.3% seeds remaining (see Table 6.2).

Table 6.1 Summary of results for 4-factor generalised linear model (GLM) of seed predation experiment with exclosure, season and heat cue as factors.

| | GLM sequential model | | | | | | | | Mean seeds remaining (n/10) | | | | | | |
| | | | | | | | | | Exclosure | | | Season | | Cue | |
Acacia spp.	Exclosure	Cue	Season	Site	Exclosure x Cued	Exclosure x Season	Season x Cued	Exclosure x Cued x Season	CC	FX	NX	S	W	C	U
A. aneura	***	ns	***	ns	ns	ns	ns	ns	7.9^A	9.8^B	6.9^C	8	9.3	-	-
A. kempeana	***	ns	***	ns	ns	*	ns	ns	7.7^A	9.9^B	5.9^C	7.5	9.3	-	-
								Summer	6	9.9	4				
								Winter	9.5	9.8	7.8				
A. maitlandii	**	ns	***	ns	ns	*	ns	ns	8.6^{aB}	9.2^a	8.1^B	8.5	9.4	-	-
								Summer	7.9	9.3	6.9				
								Winter	9.2	9.2	9.3				
A. melleodora	***	ns	***	**	ns	***	ns	ns	7.7^A	9.7^B	4.9^C	7	9.2	-	-
								Summer	5.8	9.9	1.9	-	-	-	-
								Winter	9.5	9.4	7.9	-	-	-	-

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, not significant

* EC-exclosure Control (sham control), FX-full exclusion; NX- no exclusion;

* S-summer; W-winter

* C-seeds cued; U-seeds uncued

Table 6.2 Summary of results for 2-factor generalised linear model (GLM) of seed predation experiment according to exposure time.

Acacia species	Time	Mean seeds remaining (n/10)	
		Exposure time : 1 month	Exposure time: 6 month
A. aneura	***	6.9	0.25
A. kempeana	***	5.9	0.17
A. maitlandii	***	8.1	0.33
A. melleodora	***	4.9	0.17

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, not significant

Rates of seed removal were found to vary significantly according to season, with all species showing significantly higher rates of seed removal during summer (see Table 6.1). Seeds of *A. melleodora* were the most rapidly removed during this season, while those of *A. maitlandii* were the least rapidly removed. In winter, all species showed similar rates of seed removal, averaging 9.3 seeds remaining after one month. *Acacia melleodora* showed a significant site effect, indicating that there was some spatial variation in removal rates in these systems (see Table 6.1). In addition, *A. melleodora, A. kempeana* and *A. melleodora* showed significant interactions between treatment and season (see Table 6.1). Under these interactions, there were similar seed numbers exhumed from the 'full exclusion' treatment under both seasons, but lower seed numbers exhumed in the 'exclosure control' and the 'no exclusion' treatments in summer compared to winter. No species showed any significant effect of heat cue on seed removal rates, indicating that any heat-induced alterations to the chemical nature of eliasomes on seeds do not alter ant preferences for seed.

Decay experiment

The seed burial component of the experiment demonstrated that there was no significant decomposition of seed over a six-month period for *A. kempeana, A. maitlandii* or *A. melleodora* (see Table 6.3). Likewise, there was no significant effect of exposure to a heat cue on the viability of seed after six months for these species. Only *A. aneura*

showed any burial effects, with a significant reduction in viable seed from 9.4 after one month to 7.3 after six months (see Table 6.3).

Table 6.3 Summary of results for 4-factor generalised linear model (GLM) of viable seed remaining after decomposition experiment.

| | | | | Mean seeds remaining (n/10) | | | |
| | | | | Burial time | | Cue | |
Acacia spp.	Time	Cue	Time*Cue	1	6	Cued	Uncued
A. aneura	***	ns	ns	9.4	7.3	-	-
A. kempeana	ns	ns	ns	-	-	-	-
A. maitlandii	ns	ns	ns	-	-	-	-
A. melleodora	ns	ns	ns	-	-	-	-

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, not significant

Germination experiment

The effects of season, heat cue and duration of burial on the germination rates of viable seed were found to vary among the different species of *Acacia*. Seeds of all species showed strong increases in germination rates when exposed to heat shock, although the significance of the effect was marginally lower for *A. maitlandii* than for the other species. Season strongly influenced germination of *A. aneura* and *A. melleodora*, with seeds of these species being much more amenable to germination when imbibed under summer compared to winter-growing temperatures (see Table 6.4). In contrast, seeds of *A. kempeana* and *A. maitlandii* did not appear to show any seasonal preference for seed imbibition. The duration of burial had a significant effect on the germinability of seed for *A. maitlandii* and *A. melleodora*, with seed of both these species appearing to enter secondary dormancy after six months (showing far less germination after six months compared to one month burial) (see Table 6.5). Germinability of seed for *A. aneura* and *A. kempeana* was not affected by the duration of burial.

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Table 6.4 Summary of results for 2-factor generalised linear model (GLM) of germinated seed following germination experiment, according to season and heat cue.

Acacia spp.	Season	Cue	Season*Cue		Proportion of exhumed seeds that germinated			
					Summer	Winter	Cued	Uncued
A. aneura	***	***	***		0.3	0.05	0.39	0.04
				Cued	0.55	0.06		
				Uncued	0.05	0.03		
A. kempeana	*	***	ns		0.1	0.6	0.14	0.03
A. maitlandii	*	***	ns		0.07	0.03	0.09	0.02
A. melleodora	***	***	ns		0.16	0.03	0.19	0.04

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, not significant

Table 6.5 Summary of results for 2-factor generalised linear model (GLM) of germinated seed following germination experiment, according to time and heat cue.

Acacia spp.	Time	Cue	Time*Cue		Proportion of exhumed seeds that germinated			
					1month	6 months	Cued	Uncued
A. aneura	***	***	*		0.26	0.12	0.39	0.04
				Cued	0.49	0.19		
				Uncued	0.03	0.06		
A. kempeana	*	***	ns		0.11	0.04	0.14	0.03
A. maitlandii	**	***	ns		0.07	0.02	0.09	0.02
A. melleodora	***	***	**		0.17	0.01	0.19	0.04
				Cued	0.29	0		
				Uncued	0.05	0.02		

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, not significant

There were few interactions for the germination experiment, although *A. aneura* demonstrated a significant season by heat shock interaction, with a strong heat shock effect under summer growing conditions but virtually no effect under winter conditions (see Table 6.4). There was also a weakly significant time by heat shock interaction for *A. aneura* and *A. melleodora*, with much higher proportions of germinants for heat shocked compared to non-heat shocked seeds after one month burial, but no effect observed after six months burial (see Table 6.5).

Discussion

Seed removal

The factorial experiment identified seed removal as the main driving force causing the rapid depletion of seed of *Acacia* species in spinifex grasslands. This finding largely explains why seeds of woody *Acacia* species were almost completely absent from the seed bank study done in February 2005 (see previous chapter), despite the prolific fruiting of many *Acacia* species in late 2004.

Rapid removal of seed is not unique to spinifex grasslands, and several studies from other regions of Australia's arid zone have also reported rapid removal of seed of woody plants by native fauna. At Middleback, South Australia, near-complete removal of *Acacia papyrocarpa* by ants was rapid (< 12 hrs), and no soil seed bank could be detected for these trees, despite prolific fruiting of this species only six months earlier (Ireland and Andrew 1995). Likewise, at 'Oakvale' station near Nyngan in western NSW, seed bank studies from a mulga-dominated woodland failed to return a single *A. aneura* seed, and high rates of seed predation were also demonstrated for seeds of other woody flora in the area (Hodgkinson, Harrington *et al.* 1980). On 'Owen Springs' pastoral property, south-west of Alice springs, Nano (2005) also found rapid removal of seeds for a range of woody species. This study found a high degree of variability of the rates at which seeds of different species were removed, although no correlations could be detected between rate of removal, and factors such as seed size or seed type.

While the current study did not directly assess the type/s of fauna responsible for seed removal, there are several factors which point towards ants as being the primary removers of seed in these experiments. Firstly, studies from spinifex grasslands in the

nearby Gibson Desert Nature Reserve reveal that arid spinifex grasslands possess a high diversity of seed harvesting ant genera, such as *Melophorus, Monomorium, Phediole, Rhytidoponera* and *Iridomyrmex* (Gunawardene and Majer 2005). Secondly, visual inspection of the Haasts Bluff study sites revealed that ant activity was high, and on many occasions ants were observed carrying seeds away by their arils. Finally, *Acacia* seeds with small white arils, such as those found on three of the *Acacia* species in this study (*A. aneura, A. kempeana* and *A. melleodora*), are generally regarded to be adapted to dispersal by ants, as at least some ants are known to be attracted to white coloration against a dark background (Davidson and Morton 1984). Whilst this experiment identified ants as the main removers of seeds, it is quite likely that this was at least partly due to the choice of the eliasome-bearing *Acacia* seeds used in the experiment. It is possible that seed-harvesting rodents and birds would have had a bigger impact on seed removal rates if we had chosen larger, non-eliasome-bearing seeds such as those belonging to species of other locally common genera such as *Grevillea, Hakea, Brachychiton* or *Allocasuarina*.

At this stage it is impossible to speculate on the proportion of seed that is predated (with the seeds themselves being eaten), as opposed to simply transported and then discarded (with the eliasome only being eaten). If actual predation levels are low, then it is possible that seed bank abundances do not fluctuate over time as dramatically as was hypothesised in the previous chapter. Nevertheless, it would be expected that the spatial distribution of seed following seed shed (summer) would be far less clustered than at times long after seed shed (winter). This is because at times long after seed shed, ants and other seed harvesters would have had ample time to transport and discard/hoard seeds in and around their nests. Several pieces of evidence from this thesis suggest, however, that such seed stores/caches are not as important for seedling regeneration in spinifex deserts as they are in other regions of Australia (Hughes and Westoby 1992). Firstly, neither of the two seed sampling techniques in chapter 5 were able to detect even sparsely distributed seed banks for certain of these species (during autumn months) – although it could be argued that both techniques were still too coarse to detect a highly clustered seed distribution in seed caches/nests. Secondly, field observation showed that post-fire seedling recruits were always solitary, rather than clustered around ant nests; suggesting

they had not arisen from highly aggregated seed stores. Finally, many of the ant genera found in spinifex deserts, including *Phediole*, are known to be seed predators (Hughes and Westoby 1992). Thus, while some 'storage' of seed may occur in nests for short periods after seed shed events, over longer periods it is likely that much, if not most of the seed will be consumed.

The findings of the removal experiment also provided insight into why *A. maitlandii* was the only *Acacia* species to be detected in the seed bank at the time of sampling (see Chapter 5). Of the four *Acacia* species tested, *A. maitlandii* was the slowest to be removed, indicating that seed removers had a preference for seeds of the other three species over seeds of this species. It is likely that this was due in part to the small size of the aril on seeds of *A. maitlandii* (see Fig 6.3), as this would have considerably reduced the benefit for seed-harvesting ant species that rely on the eliasomes of seeds for their energetic reward (Berg 1975). Seeds of *A. maitlandii* also appear much harder and difficult to break than those of the other *Acacia* species (pers. obs.), and this may have further reduced the attractiveness of these seeds to ants, as well as to other seed predators such as birds and rodents.
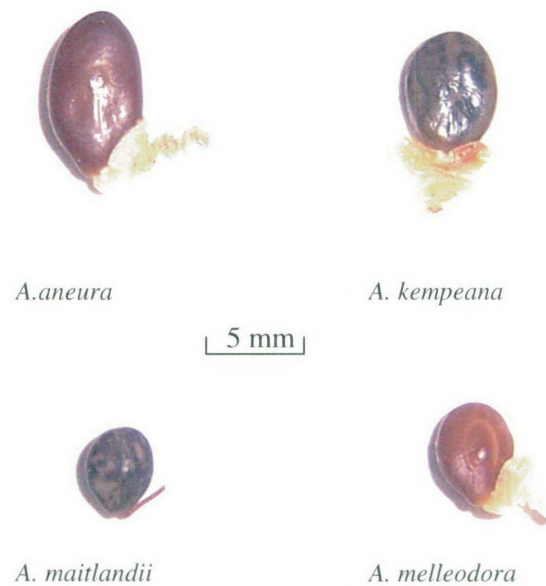

A.aneura   A. kempeana

⌐ 5 mm ⌐

A. maitlandii   A. melleodora

Figure 6.3 *Acacia* seeds used in removal, decay and germination experiments.

Seed decay

Decay of seed was found to play a minor role in the loss of seed from seed banks, and only mulga seed had any significant reduction in seed viability over time (after six months exposure, decay reduced buried seed numbers by 27% while predation reduced seed numbers by ~98%). That significant decay of mulga seed occurred over a period as short as six months was somewhat surprising, as it is generally assumed that diaspores of hard-seeded desert species such as mulga are very long-lived under natural conditions (Davison 1982). It is possible that the depth at which the seed caches were buried in the field experiment were deeper, and therefore moister, than would be experienced by *A.aneura* seeds in a 'natural' seed bank situation (in which seeds in the effective seed bank would have to remain in the relatively dry, top few centimetres of the soil). Consequently, seeds in the purses may have rotted or germinated and died at much faster rates than normal. Seeds of the remaining three species experienced no significant decay over the six months of burial, indicating that these species have the potential to form persistent seed banks should the seeds escape predation.

Seed germination

Not surprisingly there was a strong positive response of heat shock on germination among all of the examined *Acacia* species. This finding is consistent with results from previous studies on the effects of heat on seed dormancy, both among arid zone *Acacias* (Letnic, Dickman *et al.* 2000; Nano 2005), and among *Acacias* from more mesic regions of Australia (Auld and O'Connell 1991; Floyd 1966; Shea, McCormick *et al.* 1979).

The importance of heat shock on germination has two main implications for the recruitment dynamics of these species. Firstly, it suggests that fire is important in facilitating large-scale recruitment events. Secondly, it indicates that soil temperature intensities during fire will play an important role in the recruitment dynamics of these species. This means that factors that influence temperature regimes during fire – such as the proximity of fuel loads to seed, soil moisture and season of burn (see Chapter 3) – will all strongly affect the proportion of seed that become germinable.

Interestingly, heat-treated seeds of both *A. maitlandii* and *A. melleodora* entered a secondary dormancy after being buried in the soil for six months. Such a response has not been previously recorded among hard-seeded seeds of *Acacia* spp. in Australia, although

it is not an uncommon trait among seeds of weed species (Harper 1957). Return to dormancy by *Acacia* seeds suggests that the lens (which is generally the site of 'first water entry' when dormancy is broken in *Acacia* spp. (Morrison, McClay *et al.* 1998)) must cryptically become repaired over time, thus preventing future water penetration. The ecological significance of this rapid return to dormancy is difficult to interpret. It may represent a mechanism of ensuring that seeds only germinate during periods shortly after fire, when transpiration in the community has been temporarily arrested due to the loss of standing vegetative material, and competition for soil moisture is at a minimum (Wellington 1989). This hypothesis implies that conditions favourable for seedling establishment only exist for short periods after fire, and that post-fire domination of water reserves by resprouting vegetation occurs extremely rapidly. This hypothesis could be tested by observing temporal changes in leaf water potentials of seedlings (or other factors indicative of soil moisture availability) as time-since-fire increases.

Increased recruitment after summer fire

The findings of the predation/decay experiment revealed that ants, and to a much lesser degree seed decay, are driving forces in the removal of *Acacia* spp. seed in spinifex grasslands. This finding accounts for the apparently transient nature of the seed banks of regular seasonal fruiters, such as *A. melleodora,* which exhibit annual peaks in seed bank abundance (of duration < 2–3 months) after seeds are shed in late spring/early summer. The results of the germination experiment also indicated that, for mass recruitment of these species to occur, their seeds must be exposed to heat shock from fire. Therefore, the observed increase in seedling numbers after summer fires for these species can be explained by the synchrony of seed availability during summer with the heat shock from fire. This interaction between fire season and fruiting phenology is represented in the diagrammatic model in Figure 6.3 (model based on Bond 1984).
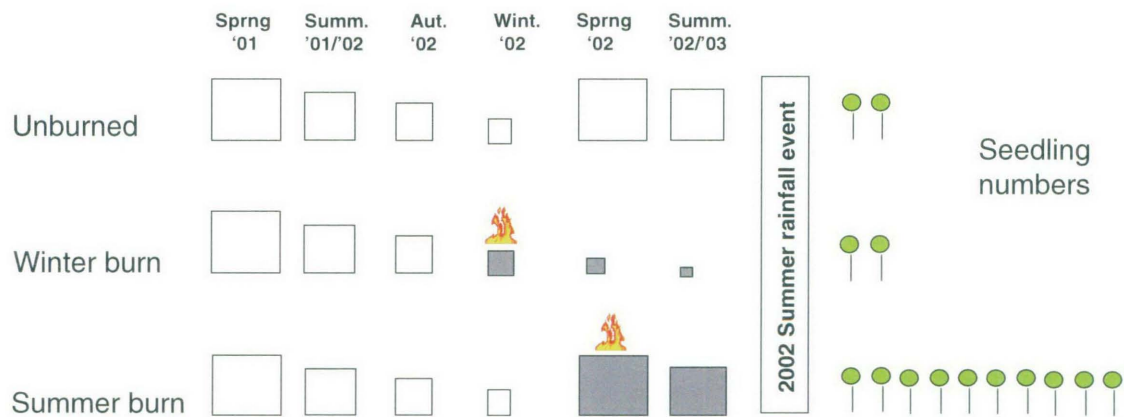
Figure 6.3 A model of the causes of variation in seedling recruitment between summer and winter fires for seasonal fruiting *Acacias* in spinifex grasslands. Squares represent relative seed bank sizes, which peak in spring following seed fall, but diminish rapidly due to predation. Shading in squares represents proportion of seed banks that are cued by fire. See text for further explanation.

This model also shows that that if fires occur during winter, seed predators have considerably reduced seed bank abundances since the previous spring's seed fall, so a comparatively small number of seeds remain to be cued by fire. Also, as the seeds of *A. melleodora* are more germinable under summer temperatures, a proportion of seeds cued by winter fire may re-enter dormancy by the time summer rains occur (thereby further reducing the seed population available to germinate). The model also shows that in the absence of fire some germination of seeds may still occur after summer rains (because a large number of seeds are available during this season, and as the germination trials in this chapter demonstrated, a small proportion of *Acacia* spp. seed do not possess innate dormancy and are still germinable in the absence of fire). However, not only will the proportion of seeds that germinate be less in these unburned areas, but the survival chances of recruited seedlings will also be lower, due to competition from the standing vegetation. Such low levels of recruitment are unlikely to be an issue in unburned areas, as plant populations are not relying on seedling recruitment to offset mortality of standing

vegetation. However, in burned vegetation, some seedling recruitment is essential to maintain plant populations, as some death of adult plants invariably occurs during fire.

The importance of synchronizing fire with spring-time peaks in *Acacia* seed availability can be considered a form of 'predator satiation' (Janzen 1971), whereby the soil becomes temporarily saturated with seed and increased numbers of seeds can 'escape' from predation and become cued by fire. This phenomenon is largely analogous to the predator satiation that is characteristic of serotinous tree genera in the spinifex grasslands, such as *Allocasuarina decaisneana, Eucalyptus* spp. and *Hakea* spp. (Noble 1982; Wellington 1989; Wellington and Noble 1985). However, for both satiation syndromes, seedling regeneration of populations is ultimately contingent on the occurrence of post-fire rain. If no rain occurs for a long period after seed rain, predators will have the opportunity to deplete seed supplies and recruitment potentials once again become limited.