Chapter 5

Effects of fire regime on seed banks in spinifex grasslands

Introduction

Fire regimes are primary drivers of seed bank dynamics in fire-prone ecosystems. Fire intensity affects seed banks directly by inducing mortality or breaking dormancy of seeds, while fire interval affects seed banks by interacting with seedling regeneration processes (Bell 1999; Cary and Morrison 1995; Lunt and Morgan 1999; Russel-Smith, Ryan *et al.* 2002). The season that a fire occurs in affects seed banks by influencing soil temperatures, which in turn affect seed germination and seed mortality processes (Hodgkinson and Oxley 1990; Keeley 1977; Williams, Congdon *et al.* 2005). Season of fire also influences seed bank dynamics through its interaction with the reproductive cycles of plants (Setterfield 1997; Whelan 1995), and with its interaction with seasonal rainfall patterns (Cohn and Bradstock 2000; Hodgkinson and Oxley 1990). Fire can also affect seed banks by stimulating flowering and fruit production in certain plant species (Lamont, Swanborough *et al.* 2000; Taylor, Monamy *et al.* 1998).

The results from Chapter 4 showed that spinifex grasslands possess a diverse assemblage of short-lived species that greatly increase in abundance after fire. Literature from other fire-prone ecosystems suggest that ephemeral species such as these exist during inter-fire periods via persistent seed banks, with seeds germinating after fire as the result of being released from dormancy by some fire-related cue, such as heat or smoke (Kemp; Planisek and Pippen 1984). These species generally produce a large 'pulse' of dormant, long-lived seed soon after fire, and their seed banks are normally not replenished until the next fire. Hence, it is expected that seed banks of ephemeral species in spinifex systems should peak with short time-since-fire.

Chapter four also demonstrated that large components of the spinifex flora are woody plants, with the majority possessing strong abilities to resprout after fire. Previous studies have shown that seed bank syndromes of woody species are often influenced by the response of adult plants to fire i.e. whether they are obligate seeders or resprouters (Auld 1995; Bell, Plummer *et al.* 1993; Enright and Goldblum 1999; Keeley 1977; Meney, Nielssen *et al.* 1994; Ne'eman and Izhaki 1999). Obligate seeders normally invest

heavily in maintaining persistent seed banks, because post-fire mortality is usually high. For these species, having a persistent seed bank maximizes the potential for at least some individuals to re-establish following fire. For resprouting species, mortality after fire is usually not as high and post-fire recruitment from seed is not as crucial. As a result, resprouters invest less heavily in seed production and instead allocate more reserves toward means of ensuring vegetative recovery in the event of fire or drought. Consequently, seed from resprouting species is generally lower in viability, smaller in size, shorter lived and produced in lesser quantities than those of obligate seeding species (Bell, Plummer *et al.* 1993; Enright and Goldblum 1999). Hence, in the spinifex grasslands it is expected that the seed abundances of obligate seeders such as mulga and certain *Triodia* species should be proportionately higher than those of resprouters.

Past studies have also shown that seed abundances of woody species with canopy-held seed banks (serotiny) increase in abundance shortly after fire (Bond 1984; Gill 1981; Wellington 1989). The woody fruits of these species release vast quantities of seed when dried by the heat of fire, and it is believed that this adaptation has been evoked over evolutionary time due to the high levels of seed predation that are characteristic of fire-prone ecosystems (Hodgkinson, Harrington *et al.* 1980; Wellington 1989). It may therefore be expected that seed numbers of serotinous species in spinifex grasslands will be higher at sites that have short times-since-fire.

At present, no data exist to verify the previous hypotheses regarding the effects of fire on seed bank dynamics in spinifex grasslands. To address this, the current study sought to examine the effects of fire interval and time-since-fire on the composition of seed banks within spinifex grasslands, and to relate fire-imposed variations in seed bank abundances to the life history traits of plant species. Two contrasting techniques were used to estimate the seed bank composition; 1) a seed extraction technique, hereafter called the flotation method, whereby seeds were physically removed from soil samples via flotation of organic matter that was subsequently sieved for seed; and 2) an emergence technique, hereafter called the germination experiment, whereby seedlings where germinated from soil samples in a greenhouse, and subsequently counted and identified. The germination experiment also sought to discern the roles that heat and smoke played in the germination of species within the seed bank. Such knowledge would

improve current understanding of the role of fire as a dormancy-breaking force in these systems, and provide insight into its role in maintaining the diversity of species within spinifex communities. To examine this issue, heat, smoke, heat/smoke and control treatments were also incorporated into the design of the germination experiment. The specific hypotheses tested in the two experiments were as follows:

1. Fire-cued ephemeral species have seed banks that increase in abundance in recently burned plots;
2. Obligate-seeding woody species maintain persistent seed banks;
3. Resprouting species possess lower seed bank abundances; and
4. Serotinous species will have higher seed bank abundances in recently burned plots.

Methods

Soil sampling

Soil samples for the two seed bank assessment techniques were collected from 35 sites within the Haasts Bluff Reserve. All sites had previously been sampled for vegetation to examine the effects of fire history on floristics (see Chapter 3). The design of the soil sampling was factorial, with four replicate sites being selected from each of the following three fire histories: unburned since 1985 (hereafter known as *Unburned*); burned once in 2002 but otherwise not since 1985 (hereafter known as *Burned once*); and burned twice between 2000 and 2002 but otherwise not since 1985 (hereafter known as *Short interval*). Within each replicate, soil was sampled from three plots, resulting in a total of 35 replicate plots (it was not possible to sample from one of the Short interval plots as it had been burned by local people for the third time in three years). All 35 sites had been burned twice between 1983 and 1985, thus ensuring that the long-term fire histories of the sites were similar.

At each plot, 100 random soil cores were sampled using a 2 cm deep x 5 cm diameter soil corer. These cores were sampled at 1 m contiguous intervals along five randomly placed 20 m transects within the vegetation sampling quadrats. The position and trajectory of each transect was determined by standing in the middle of each quadrat

and tossing a straight stick in the air. The transect's mid-point was then placed wherever the stick landed, and oriented with the direction of the stick. Following sampling, the 100 soil cores from each plot were bulked together according to plot and stored in polyethylene bags until processing. Soil samples for the germination experiment were collected during August 2004, while soil samples for the flotation experiment were collected during February 2005.

Flotation experiment

The flotation experiment commenced in March 2005 using the method of Malone (1967). The 100 soil cores from each of the 35 plots were initially pooled into 35 bulk samples, and representative samples of 1 kg were extracted from each bulk sample using a soil splitter. These samples were then immersed in 3.4 L of potassium carbonate solution (140 g potassium carbonate per 200 mL water) and stirred for 30 seconds using a spatula. After the soil solution had stood for five minutes, the organic material was extracted by pouring the solution through a series of three sieves (0.5 mm, 0.25 mm and 0.15 mm). The extracted organic material was then washed under running water to remove residual potassium carbonate solution, and the contents of the three sieves were examined separately under a binocular stereomicroscope. Any extracted seeds were then identified using a seed reference collection from the Alice Springs Herbarium. Viability of the seeds was tested by applying gentle pressure to the seeds with forceps: 'the squish test' (Whalley R.W.B., pers. comm., University of New England, 2005). If seeds resisted light pressure they were deemed viable and recorded. This viability testing procedure is less rigorous than other viability tests such as tetrazolium and germination-based tests, but it is much quicker and cheaper and is in common use in modern seed bank research (Ball and Miller 1989; Simpson 1999).

Germination experiment

The germination experiment was commenced in October 2004. As in the flotation experiment, the bulked soil samples were split into four 1 kg samples using a soil splitter and each of the samples was treated with one of the following four treatments: heat, smoke, heat and smoke, control. Samples that were given the heat treatment were put in aluminium trays and placed for five minutes in an oven pre-heated to 100 ^{0}C. Samples

that were given the smoke treatment were placed in plastic trays in an enclosed smoke chamber and exposed to smouldering mulga litter for one hour. One of the four samples was given both of these treatments (to test for any dual dormancy mechanisms that may exist in seeds) and one of the four samples was untreated and used as a control.

Once the soil samples had been treated, they were spread over a 3 cm layer of sterilized river sand in 30 cm x 40 cm black plastic seedling trays. The trays were then placed randomly under shade cloth and exposed to natural temperature and humidity conditions. The trays were watered three times daily using untreated Alice Springs town water, thus ensuring that the soil remained permanently moist and that desiccation of the seedlings did not occur. Seedling emergence was monitored every seven days over a three-month period. As seedlings emerged, they were marked using colour-coded pins so that they were not counted more than once. Where possible, seedlings were identified using seedling keys, but where this was not possible, seedlings were transplanted and moved into a growth chamber and grown to maturity or until positive identification was possible. By the end of the third month, seedling germination had slowed to almost nothing. Consequently, at this time a final census was taken and the experiment was terminated.

Data analysis

Variation in seed abundance in the flotation data set was analysed using Redundancy Analysis (RDA) in CANOCO (ter Braak & Smilauer 1998). Prior to analysis, the data were transformed in CANOCO using a log (10+1) transformation, but otherwise default options were employed. The overall significance of the model was also tested using Monte Carlo permutation tests with 499 unrestricted permutations under a reduced model. As with the RDA analyses used in Chapter 4, a series of supplementary variables (comprised of species from the fire response/life history groups used in Chapter 4) were plotted passively against the results of the ordination plot of the flotation dataset.

Statistical differences between sites of different fire codes were also tested using generalized linear models (GLIM) in GLMstat (Beath 2001). These analyses used a Poisson error structure with a log link function. Plots of residuals were examined initially to detect any non-linear trends. Where the models revealed significant differences in

seedling abundances, Scheffé post-tests with inbuilt Bonferroni correction were used to determine which treatments differed.

The germination data set was firstly analysed using Redundancy Analysis (RDA) in CANOCO (ter Braak & Smilauer 1998). This tested for any interpretable patterns that existed between seedling abundances and the four treatments imposed on the soil samples. As with the flotation data, the data were initially transformed in CANOCO using a log (10+1) transformation, and because of the paucity of seedlings in the dataset, the 'down weighting of rare species' option was used. Except for these alterations, default options were employed for the analysis. The overall significance of the model was also tested using Monte Carlo permutation tests with 499 unrestricted permutations under a reduced model (see ter Braak and Smilauer 1998 for technical details). Following the CCA, the effects of the four fire treatments on seedling emergence were analysed using generalized linear modelling and these analyses followed the same procedure as used in the flotation analyses. Scheffé post-tests were again used to determine significant differences between the different fire codes.

Results

Flotation experiment

A total of 1307 seeds, representing 61 different taxa, were extracted from the soil samples by the flotation experiment. This corresponded to approximately 320 seeds/m^2, with a richness of 7.4 species per plot. The majority of species extracted were short-lived species, with only a very small number of the standing woody vegetation actually represented in the seed bank. The only woody species present were one species of *Acacia* (*A. maitlandii*), several *Eucalyptus* spp., *Aluta maisseoneuvii* and *Micromyrtus flavifolia*.

As the result of the low numbers of seeds from woody species, further soil samples were taken in May 2005 to determine whether the seed banks of these species were in fact non-existent or whether they were simply sparsely distributed across the landscape. At each site of the 35 sites, 0.2 m^2 of top soil (top 2 cm) was shoveled and sieved from directly beneath the canopies of seven selected tree and shrub species: *Acacia aneura*, *A. kempeana*, *A. maitlandii*, *A. melleodora*, *Allocasuarina decaisneana*, *Brachychiton populneus* and *Grevillea juncifolia* (see Table 5.1).

Table 5.1 Mean seed counts per m^2 (standard error in brackets) of different tree and shrub species from sites of differing fire histories.

	Unburned	Burned once	Short interval
A. aneura	0	0.6 (0.03)	1.3 (0.03)
A. kempeana	0	4.4 (0.07)	0
A. melleodora	0	0.6 (0.03)	2.5 (0.06)
A. maitlandii	637.5 (218.9)	200 (78.7)	0
Allocasuarina decaisneana	0	0	0
B. populneus	0	0	0
G. juncifolia	18.8 (10.2)	4.2 (2.8)	0

This additional sampling reinforced the findings of the flotation experiment – that the seed banks of many woody species are absent or in very low densities (although certain species such *as A. maitlandii* and *G. juncifolia* appeared to maintain relatively persistent seed banks).

The ordination of the flotation data set demonstrated a strong relationship between seed bank composition and fire history ($P = 0.002$ with 499 permutations, see Fig. 5.1). The first axis of the ordination was determined primarily by fire interval, with *Short interval* occupying the right hand region of the axis, and sites that did not experience a short fire interval occupying the left-hand region of the axis. The second axis was determined by time-since-fire, with short time-since-fire occupying the top of the diagram (*Burned once* and *Short interval*) and long time-since-fire occupying the bottom (*Unburned*).
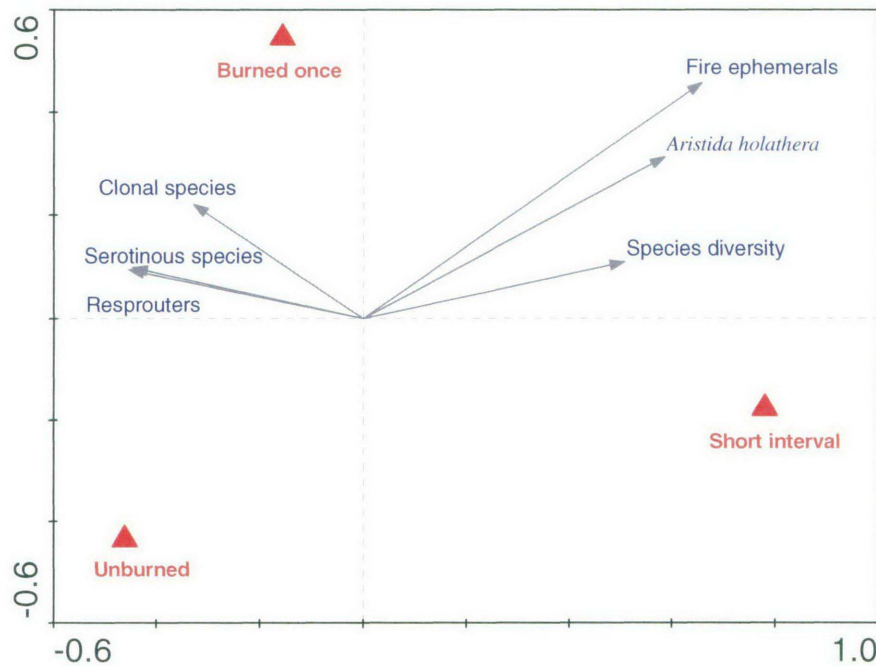
Fig. 5.1 Fire history and supplementary variable bi-plot of Canonical Correspondence Analysis (CCA) of species data from flotation experiment. Triangles represent the positioning of the nominal fire history variables in the ordination space, while the length and direction of the vectors indicate the strength of the (continuous) species/species group variables, as well as their relationships to other variables.

The length and direction of the fire ephemerals vector indicated that abundances of seeds of these species were higher at sites burned recently. Species diversity was also correlated with recent time-since-fire, although the direction of the vector indicated it was more closely correlated to *Short interval* sites than to *Burned once* sites. Clonal species, serotinous species and resprouting species were all more strongly associated with *Unburned* and *Burned once* sites, indicating that seeds for these species were more abundant at sites burned without a short fire interval.

Under the GLIM model, species richness of seeds was not significantly affected by fire history (see Table 5.2). Species diversity, however, was affected ($P < 0.05$), with the diversity of seed being significantly higher at *Short interval* sites than *Unburned* and *Burned once* sites.

Table 5.2 Summary of results for 1-factor generalized linear models (GLM) for counts of seeds within functional groups according to fire code.

			Fire treatment		
		P - value	Unburned	Burned once	Short interval	Grand mean
Resprouters		**	12^A	7^{AB}	1^B	7
Serotinous species		**	12^A	7^{AB}	$<0.05^B$	6
	Eucalyptus gamophylla	***	12^A	2^B	$<0.05^B$	5
	E. oxymitra	ns	-	-	-	2
Clonal species		#	5	6	<0.05	4
Non-fire ephemerals		ns	-	-	-	7
	Calandrinia balonensis	ns	-	-	-	5
Fire ephemerals		***	1^A	10^B	10^B	7
	Aristida holathera	***	1^A	5^{AB}	8^B	4
	Sida A86753 *pindans*	***	$<0.05^A$	3^B	$<0.05^A$	1
Species richness		ns	-	-	-	8
Species diversity		*	0.6^A	0.7^{AB}	0.8^B	0.7

#, $P <0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, not significant

Fire ephemerals were strongly affected by fire history, with seed abundances for this variable far more abundant at sites burned recently than at sites with a long time-since-fire (see Table 5.2). There were only two fire ephemeral species that were abundant enough in the seed bank to be statistically tested individually (*A. holathera* and *Sida* A86753 *pindans*), and both species were more abundant in sites burned recently than at sites with a long time-since-fire (see Table 5.2). Seeds of resprouters and serotinous woody species were both significantly more abundant at sites with long time-since-fire than at sites that had experienced a short fire interval, and these results were driven primarily by the high numbers of *Eucalyptus gamophylla* seed in these groups. The seed abundance of non-fire ephemerals was not affected by fire history and clonal species were only marginally affected, with higher abundances of clonal seed occurring at sites that did not experience a short fire interval than at sites that did (see Table 5.2).

Germination experiment

The germination experiment recorded a total of 1277 germinants across all seedling trays, representing 54 different taxa. This corresponded to approximately 45 seeds/m^2, with a richness of 4.1 species per plot. As with the flotation experiment, the majority of species extracted were short-lived species, and the seed bank of woody species was virtually non-existent, with one *Acacia maitlandii* seedling and one *Brachychiton populneus* seedling being the only evidence of seed from woody species.

The results of the germination experiment largely complemented those of the flotation experiment, by indicating that both fire interval and time-since-fire played strong roles in regulating the compositions of the seed banks (See Fig. 5.2).
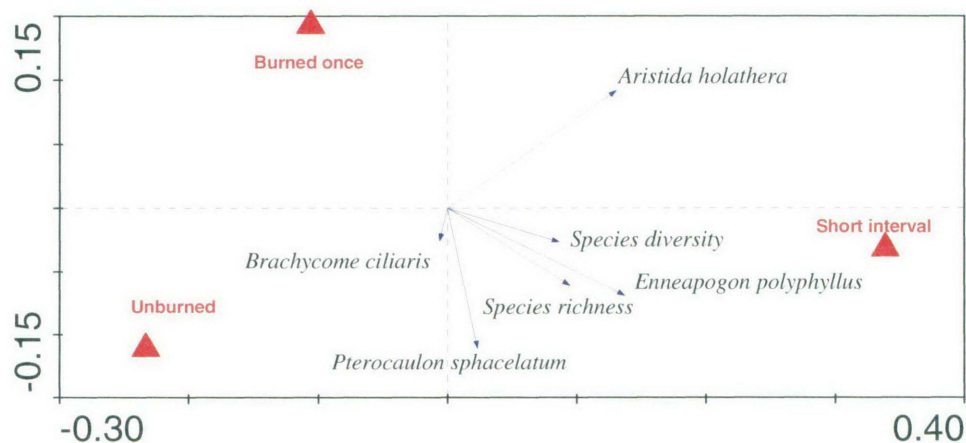

Fig. 5.2 Fire history and species bi-plot of redundancy analysis (RDA) from species data from germination experiment. Triangles represent the positioning of the nominal fire history variables in the ordination space, while the length and direction of the vectors indicate the strength of the (continuous) species variables, as well as their relationships to other variables.

The first axis of the ordination was determined primarily by fire interval, with *Short interval* occupying the right-hand region of the axis, and *Unburned* and *Burned once* occupying the opposite end of the axis. The second axis was determined by time-since-fire, with *Short interval* and *Burned once* occupying the top of the diagram and *Unburned* occupying the bottom.

The germination experiment also indicated that a proportion of variation in the seedling dataset (10.6%) could be attributed to the effects of the four fire treatments. The ordination diagram shows that the first axis was determined mainly by the differences between trays that had been treated with smoke/heat and smoke, and trays that were controls or had been treated with heat alone (Fig. 5.3).
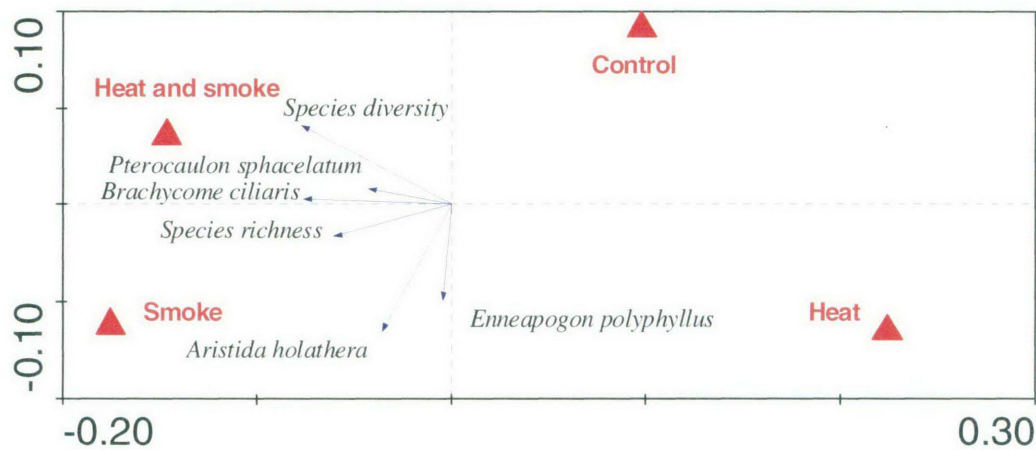

Fig. 5.3 Fire treatment – species bi-plot of redundancy analysis (RDA) from species data from germination experiment. Triangles represent the positioning of the nominal germination variables in the ordination space, while the length and direction of the vectors indicate the strength of the (continuous) species variables, as well as their relationships to other variables.

Species richness and species diversity were both correlated with sites that had received smoke or heat and smoke, but the increased length of the species diversity vector indicated that the association was stronger for this variable than for species richness. The direction and length of the *Aristida holathera* vector indicated that this species was strongly associated with the smoke treatment, suggesting that smoke enhances the germination of this species. *Brachycome ciliaris* and *Pterocaulon sphacelatum* were correlated with the smoke and 'heat and smoke' treatments, also suggesting that smoke was the primary factor promoting germination in these species.

Under single factor GLM models, it was found that fire treatment had a significant effect on species richness, although the effect was only marginal and the Scheffe's post-test failed to discern which variables differed significantly from each other

(see Table 5.3). There was a strong effect on species diversity, with significantly higher diversity of seedlings occurring in trays treated with smoke, and heat and smoke, compared to trays treated with heat alone. When the individual species were analysed, only *A. holathera* and *B. ciliaris* were affected by the fire treatments, both of which increased in abundance under the smoke, and the heat and smoke treatments.

Table 5.3 Summary of results for 1-factor generalized linear models for counts of seeds within functional groups according to germination treatments.

	P – value	Heat	Smoke	Heat and smoke	Control
Aristida holathera	*	1	2	2	1
Brachycome ciliaris	*	<0.05	1	1	0.6
Enneapogon polyphyllus	ns	-	-	-	-
Pterocaulon sphacelatum	ns	-	-	-	-
Species richness	*	3	5	5	4
Species diversity	***	0.46^A	0.66^B	0.68^B	0.55^{AB}

#, $P <0.1$;*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, not significant

Discussion

Seed bank densities

Seed densities of the spinifex grasslands in this study, which were estimated at 320 seeds/m^2 by the flotation experiment and 45 seeds/m^2 by the germination experiment, are low in comparison with seed banks from other inland Australian ecosystems. In more productive central Australian mulga woodland habitats, Kinloch and Freidel (2005) reported seed densities of 74 to 1493 seeds/m^2, while in the semi-arid *Eucalyptus* woodlands in western Queensland, seed densities of 13 207 +/- 4160 seeds/m^2 have been recorded (Navie, Cowley *et al.* 1996).

Comparisons of seed densities between these studies should be interpreted cautiously, however, as there was variation between studies in the depth from which soils were sampled. In the current study soil was sampled from a depth of 2 cm, in Kinloch and Friedel's (2005) study it was sampled to depths of 5 cm, and in the study of Navie,

Cowely *et. al.* (1996), soils were sampled to a depth of 3.5 cm. This discrepancy aside, the magnitude of the differences in seed density between our study and these others was quite large and suggests that actual differences do exist. These differences may reflect variation in seed addition and removal processes between the different ecosystems, with the spinifex grasslands in the Haasts Bluff region being hotspots for seed predator activity. Conversely, the higher seed densities of the more wooded habitats of the other studies may indicate that seed rain events are more extreme or more common in these more productive and better watered environments.

The higher seed numbers recovered by the flotation experiment compared to the germination experiment (as well as the considerably quicker times that were taken to carry out the flotation compared to the germination experiment) highlight the utility of the flotation technique in the estimation of seed banks in these arid systems. There are several factors that may have contributed to the low seed abundances that were detected by the germination experiment. Firstly, the heat and smoke treatments applied to seedling trays may not have been optimum for breaking the dormancies of a majority of seeds. Several studies have indicated that this can limit the effectiveness of such studies (Lloyd, Dixon *et al.* 2000; Thomas, Charles Morris *et al.* 2003). Secondly, by irrigating the seed trays with Alice Springs town water – which has a high mineral content – the pH of the soil was artificially raised. After three months of watering, it was found that the average pH of six randomly selected trays had risen from a mean of 5 to a mean of 9.5. This would undoubtedly have adversely affected the growth of seedlings and may also have affected germination rates. Thirdly, given that the experiment was carried out over the summer months, the winter-germinating component of the flora would have been unable to grow, and hence the overall richness of the seed bank would have been underrepresented in the germination trial. Finally, it is possible that the differences in seed banks between the flotation and germination experiments may be explained by variation in the timing of the soil sampling. Certain species may have been better represented in the flotation soil, which was sampled in February, while others may have been better represented in the germination soil, which was sampled in August.

Effects of time-since-fire on seed banks

Fire ephemeral species had seed bank populations that peaked at recently burned sites, presumably as the result of seed inputs by extant vegetation that had grown and set seed after the 2000–02 fires (see Chapter 4). At long unburned sites, however, these species possessed significantly lower seed bank abundances. This was probably due to the lack of recent seed rain, with seeds deteriorating over time, and/or having been preyed upon by vertebrate and invertebrate predators. Peak seed bank abundances of ephemeral flora have been observed with short time-since-fire in other fire-prone plant communities both within Australia and overseas (Bell, Plummer et al. 1993; Williams, Congdon et al. 2005; Zammit and Zedler 1988). In contrast to fire-cued ephemerals, seed abundances of clonal species remained constant under different times-since-fire. This probably reflects the longevity of these species, but may also show that these species have the ability to set seed in both recently burned and long unburned landscapes.

In contrast to more short-lived species, no seed was found for the majority of woody plants. Two hypotheses may explain this result. Firstly, seed predation in Australia's arid zone is very intense and complete relocation or destruction of seed can happen extremely rapidly (Ireland and Andrew 1995; Letnic, Dickman et al. 2000; Wellington and Noble 1985). Consequently, soil seed banks for most woody plants may only last a month or two after seed shed before they are removed by predators such as ants, birds or rodents. Secondly, the seeds of many arid Australian woody species are short lived and/or do not possess dormancy mechanisms (Auld 1995). This may result in seed banks that deteriorate quickly after seed shed, and/or that germinate completely following a substantial rainfall event (this issue is explored more fully in the next chapter).

The paucity of woody seed at the time of sampling supports the hypothesis from Chapter 4, that seed banks of most woody species in spinifex grasslands are transient, and that summer fires promote increased recruitment because of increased seed numbers during this season. It is suggested that sampling between October and December would have been more likely to detect higher abundances of woody seed, as it is during these months that the majority of central Australian tree and shrub species set seed (Friedel, Nelson et al. 1994 Greening Australia flowering and fruiting database).

It was interesting to find that despite the apparent rapidity with which seeds of most woody species were removed and/or decayed, there was still obviously a proportion of seed, albeit a very small one, that had remained in the soil and formed a persistent seed bank (see Table 5.1). By having at least some seed in the soil at all times, these woody populations would be provided with a buffer against the possibility that fire should occur out of synchrony with the timing of seed shed of the standing vegetation. This would allow populations to recruit from seed should standing plants suffer substantial mortality during fire. Nevertheless, the high levels of resprouting vigour that were observed among woody species after the 2000–02 fires (see Chapter 4) suggest that vegetative recovery is a primary means of post-fire recovery for these species.

This study also found a near complete absence of *Triodia* seed under all fire histories. This was an unexpected result, given that *Triodia schinzii* and *Triodia basedowii* (the two dominant grass species in the Haasts Bluff study area) are both obligate seeders, and regenerate primarily from seed after fire. The high abundance of *Triodia* seedlings observed in recently burned plots (see Chapter 4) indicates that seed must have been present in the soil shortly after fire. However, the absence of seed from the seed bank at the time of soil sampling – which was almost 3 years after the fires occurred – suggests that most viable seed had either germinated, deteriorated or been removed by seed predators.

It is proposed that, like the woody species of the spinifex grasslands, *Triodia* spp. possess transient seed banks, with seed populations that fluctuate over time in response to a dynamic interplay between seed addition (seed shed events) and seed removal processes (attrition, deterioration, predation and germination). It is suggested that in contrast to most of the woody species in these grasslands, the seed banks of *Triodia* spp. do not fluctuate in accordance to regular seasonal cycles, but instead follow irregular rainfall-driven cycles, with opportunistic flowering and fruiting occurring in response to above-average rain events (Westoby, Rice *et al.* 1988). This phenological syndrome provides the obligate-seeding *Triodia* spp. with a reliable means of persistence in these fire-prone systems, by ensuring that an abundant supply of seed is always present at times when the likelihood of fire is high i.e. when fuel continuity increases after extreme rain events (see

Chapter 2). Further long-term monitoring would be valuable here, to show that the seed banks of *Triodia* species do fluctuate in accord with these rain driven cycles.

Similar opportunistic flowering and fruiting patterns have been observed in several arid Australian shrub species, including *Acacia aneura*, *A. kempeana* and *A. estrophiolata* (Friedel, Nelson *et al.* 1994). For these trees, the synchrony of seed availability with fire is especially important, as all of them possess hard seeds, and the heat from fire is necessary to break seed coats and release them from dormancy.

Another unexpected finding from this study was the comparative increase in seed from serotinous *Eucalyptus* spp. at unburned compared to recently burned plots. This finding runs counter to models of the seed bank dynamics of these species, which hold that soil seed bank abundances of serotinous species should increase dramatically in recently burned country owing to the heat of fire causing fruits to dehisce and release large quantities of seed onto the soil (Noble 1993; O'Dowd and Gill 1984; Wellington 1989). The low seed numbers at recently burned sites could once again reflect the speed with which ants and other seed predators remove seed. In order to observe the post-fire flush of seed it may have been necessary to sample within a much shorter period after fire. This explanation also accounts for the absence of seed from other serotinous tree species from recently burned plots, including *Allocasuarina decaisneana* (Desert Oak) and *Hakea* spp. (Corkwoods).

Effects of fire interval on seed banks

The overall abundance of seed of fire-ephemeral species was unaffected by whether or not sites had been exposed to short fire intervals. This suggests that the recruitment failure following short fire intervals in Chapter 4 was more likely due to low rainfall or adverse climatic conditions after follow-up fires than due to seed bank exhaustion.

For woody species, seed was largely absent from plots that had received short fire intervals. In other systems, such a finding may have caused some concern, given that depletion of carbohydrate reserves by closely spaced fires is believed to reduce extant populations of resprouters (Hodgkinson 1986; Noble 1989a). In the Haasts Bluff dunefields, however, such concerns may not be well founded, as the majority of species probably do not rely strongly on seed regeneration in such situations, and are capable of vegetative resprouting even after very close fire intervals (see Chapter 4).

Effects of heat and smoke on seed germination

The germination trial demonstrated that the germination of at least a small component of the flora is enhanced by smoke, thereby alluding to the importance of fire as an environmental force in maintaining the richness and diversity of species within spinifex communities. However, it was also shown that a proportion of seed of all species was not dependent on fire for establishment, with at least some recruitment still occurring in the absence of smoke. This ability for a proportion of seed to germinate in the absence of fire-related cues may represent a mechanism to ensure persistence during extended periods without fire, where some between-fire recruitment/seed production would be essential to offset seed losses due to granivory, soil pathogens, germination and deterioration (Enright and Kintrup 2001).

The absence of any observed heat effect in the germination trial was curious, and deviates from the findings of seed bank studies from heathlands in south-eastern Australia (Enright and Kintrup 2001; Wills and Read 2002), and from forest ecosystems in the south-west (Tieu, Dixon *et al.* 2001) and east of Australia (Auld and O'Connell 1991; Read, Bellairs *et al.* 2000). It also differs from the findings of Simpson (1999), who demonstrated a strong positive heat effect on the germination of several forb species in the Tanami Desert, north of the Haasts Bluff reserve. The findings of the current study suggest that spinifex systems in the Haasts Bluff Reserve differ from these other systems in that it is not so much the intensity of fire that regulates the germination and seed bank dynamics of species (although exposure to lethal soil temperatures during fire is still likely to play an important role in seed mortality processes), but rather it is the chemical substances in smoke that are critical. However, had the soil sampling for the germination experiment taken place at a time when woody species were shedding seed, it is suggested that heat would have been indicated as a germination precursor for species such as *Acacia* and *Senna* (Hodgkinson and Oxley 1990).