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Seed predation limits post-fire recruitment in the waratah (*Telopea speciosissima*)

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Abstract Seed predation may reduce recruitment in populations that are limited by the availability of seeds rather than microsites. Fires increase the availability of both seeds and microsites, but in plants that lack a soil- or canopy-stored seed bank, post-fire recruitment is often delayed compared to the majority of species. Pyrogenic flowering species, such as *Telopea speciosissima*, release their non-dormant seeds more than 1 year after fire, by which time seed predation and the availability of microsites may differ from that experienced by plants recruiting soon after fire. I assessed the role of post-dispersal seed predation in limiting seedling establishment after fire in *T. speciosissima*, in southeastern Australia. Using a seed-planting experiment, I manipulated vertebrate access to seeds and the combined cover of litter and vegetation within experimental microsites in the 2 years of natural seed fall after a fire. Losses to vertebrate and invertebrate seed predators were rapid and substantial, with 50% of seeds consumed after 2 months in exposed locations and after 5 months when vertebrates were excluded. After 7 months, only 6% of seeds or seedlings survived, even where vertebrates were excluded. Removing litter and vegetation increased the likelihood of seed predation by vertebrates, but had little influence on losses due to invertebrates. Microsites with high-density vegetation and litter cover were more likely to have seed survival or germination than microsites with low-density cover. Recruitment in pyrogenic flowering species may depend upon the release of seeds into locations where dense cover may allow them to escape from vertebrate predators. Even here, conditions suitable for germination must occur soon after seed release for seeds to escape from invertebrate predators. Seed production will also affect recruitment after any one fire, while the ability of some juvenile and most adult plants to resprout after fire buffers populations against rapid declines when there is little successful recruitment.

Keywords Fire · Proteaceae · Pyrogenic flowering · Seed predators · Seedling establishment

Introduction

In habitats where fire is a common occurrence, the importance of post-fire recruitment may be underestimated for plant species in which many individuals survive fire (resprouters). This is due to the presence

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of resprouting individuals in the post-fire environment. However, as for fire-sensitive (non-sprouting) species, recruitment is necessary after some fires to counteract mortality due to fire or other causes in its absence. The initial requirement for seedlings of resprouting species is that they reach a fire-resistant size before the next fire. Ultimately they must flower before they can contribute to the population. Establishment soon after fire increases the probability that recruits will meet these requirements.

In some resprouting species, however, recruitment occurs more than a year after fire. They have no persistent seed bank and take time to resprout after fire, flower and mature fruit before seeds are available for germination. These pyrogenic flowering plants include species of *Angophora*, *Doryanthes*, *Lomatia*, *Telopea*, and *Xanthorrhoea* in Australia (Gill and Ingwersen 1976; Auld 1986; Denham and Whelan 2000; Denham and Auld 2002), *Brodiaea, Marah*, *Sabal*, *Serenoa* and *Zigadenus* in the USA (Stone 1951; Parker and Kelly 1989; Keeley 1991; Abrahamson 1999; Tyler and Borchert 2002; Borchert 2004) and *Cyrtanthus, Watsonia* and other geophytes in South Africa (Le Maitre and Brown 1992; Keeley 1993; Bond and van Wilgen 1996). It is unlikely that these species receive the benefits of early post-fire recruitment that most species obtain, although they may benefit from amelioration of some harsh post-fire environmental characteristics with the regeneration of vegetation and litter cover.

Seed predation is likely to be a key factor in determining levels of recruitment when populations are limited more by seed availability than by microsite availability (Eriksson and Ehrlen 1992; Turnbull et al. 2000; Orrock et al. 2006). In fire-prone habitats, fires are expected to increase both the availability of microsites and the availability of seeds. The consumption of plant material and litter by fire increases the availability of microsites (Christensen and Muller 1975; Zammit and Westoby 1988; Keith 1996; Purdy et al. 2002), while heat and other fire-related cues increases the availability of seeds by releasing them from dormancy in species with soil seed banks (Keeley 1987; Auld and O'Connell 1991) and from fruits in species with canopy seed banks (Lamont et al. 1991). Fires are also expected to reduce populations of many seed predators through direct mortality and emigration (Whelan et al. 2002). In conjunction with this, the release of seeds from canopy seed banks may lead to satiation of the remaining predators (Wellington and Noble 1985; O'Dowd and Gill 1984; Andersen 1988). The vast majority of plant species in fire-prone habitats have persistent soil or canopy seed banks. Thus for seedling establishment, they benefit from the combined effects of increased microsite availability and the likely reduction in the impact of seed predation that occurs soon after fire.

For many pyrogenic flowering species, flowering is restricted to the first few seasons after fire. Hence, in the absence of a persistent seed bank protected in the soil or in cones, seed predation has the potential to greatly affect recruitment in these species. Few studies have examined the population dynamics of pyrogenic flowering species (Auld 1986; Bradstock 1995; Denham and Auld 2002; Borchert 2004, 2006) and the impacts of microsite limitation and seed predators on seedling establishment are poorly understood.

In this study, I followed the fate of seeds of *Telopea speciosissima* (Sm.) R. Br. (Proteaceae), a southeastern Australian pyrogenic flowering species, over 2 years in a manipulative seed planting experiment. Since ants and other invertebrate seed predators are largely subterranean, it was impractical to attempt to exclude them. However, using exclosures to manipulate the access of vertebrate predators to seeds, I was able to assess the relative impact of vertebrate and invertebrate post-dispersal seed predators on the size of the potential pool of post-fire recruits. The importance of litter and vegetation cover to seedling establishment by modifying its combined density within experimental microsites was also examined. Studies in other habitats have demonstrated that the ability of seed predators to locate seeds is affected by the amount of litter and vegetation cover (e.g. in North American prairies—Clark et al. 1991; Reed et al. 2006). Using the interaction of cover manipulations and predator access in this study allowed an assessment how cover influences the abilities of predators to find seeds in Australian fire-prone habitats.

Methods

Study sites

Three sites were selected within a 10-km radius in Royal National Park, approximately 35 km south of

Sydney (34°03′151°03′) that had identical recent fire histories (all burnt in 1994 and 2001). All sites were located on soils derived from the Triassic Hawkesbury Sandstone Formation with Sites 1 and 2 in Sydney Coastal Dry Sclerophyll Forest (Keith 2004) and Site 3 in Sydney Coastal Heath vegetation (Keith 2004). For detailed descriptions see Denham and Auld (2002) for Sites 1 and 3, and Denham (2007) for Site 2.

Study species

The NSW waratah, *T. speciosissima* (Sm.) R. Br. (Proteaceae) is a shrub, generally 2–4-m tall, common in dry sclerophyll forest and woodlands on the central coast and central and southern tablelands of New South Wales in southeastern Australia (Harden 2002). The species survives fire by having dormant buds protected in an underground lignotuber (Bradstock 1995). Aerial stems are completely regrown after each fire. After resprouting, mature individuals usually flower between the second and fourth spring after the fire. Flowering in subsequent years is reduced, with a few plants flowering a second time after each fire (Pyke 1983; Goldingay 2000; Denham and Auld 2002). Fruits mature and dehisce in autumn, with seed release occurring through late autumn and winter. Seeds have wings facilitating wind dispersal over short distances (Denham and Auld 2002). The seeds are non-dormant and germinate as soon as soil moisture is adequate (Bradstock 1995). After fire in 2001 in Royal National Park near Sydney, seeds were released 3 and 4 years after fire. These were the only years in which substantial fruiting occurred at the study sites between 2001 and 2007. Seed production by *T. speciosissima* within plots varied from approximately 0.31 seeds/m^2 at Site 1 in 2004 to 0 seeds/m^2 at Site 2 in 2005 (Table 1).

Experimental methods

A 30 m by 30 m plot was marked out within each site. The experiment was run separately in each of two fruiting seasons (2004 and 2005) using seeds collected in the year of the experiment from plants fruiting within 200 m of the plot, but not from inside it. Random grid points (experimental microsites) within plots (with *x* and *y* coordinates ranging from 1 to 29 m), were located and subjectively placed into one of three microhabitat classes (Low, Medium or High) according to the amount of litter and vegetation cover within 50 cm of the microsite. These microsites were marked until a maximum of 16 per site for any microhabitat class was reached. After reaching the maximum for any of the microhabitat classes, additional microsites that corresponded to these classes were passed over until all microhabitat classes had 16 microsites per site. Each microsite was randomly assigned to one of two vertebrate exclusion (caged, no cage) and clearing treatments (cleared, not cleared), resulting in total of 48 microsites per site, each in one of 12 treatment combinations. At each microsite, a short plastic cylinder, approximately 35 cm in diameter and 7 cm in height was bedded into the soil to a depth of 1 cm and pegged into place. These cylinders were used to prevent further dispersal of seeds or confusion with seeds already in the plot and to define the experimental microsite. For the clearing treatment, litter from within the cylinder was removed, rooted vegetation was clipped to 1 cm, and overhanging vegetation was cleared to 50 cm above it. At the end of the 2004 experiment, litter was collected from all experimental microsites, oven-dried at 80°C for 24 h and weighed to allow comparison of microhabitat classes. For the exclusion treatment, wire mesh with a 1-cm grid was fastened

Table 1 Background fecundity and pre-dispersal seed predation of *Telopea speciosissima* within the 30 × 30 m plot at each study site

Site	Year of flowering[a]	Adult plants[b]	Fruits matured	Fruits lost to predation	Estimated seed density[e] (per m^2)
Site 1	2003	30	25	6[c]	0.31
	2004	30	14	3[c]	0.17
Site 2	2003	19	20	0	0.24
	2004	19	0	0	0
Site 3	2003	38	19	1[d]	0.23
	2004	38	19	0	0.23

[a] Fruits ripen in the following year

[b] Assessed through evidence of previous flowering or on height exceeding 50 cm

[c] Whole fruits removed prior to ripening, presumably by parrots

[d] Whole fruit destroyed by an insect borer

[e] Calculated by assuming 11 seeds per fruit (Denham and Auld 2002)

onto the top of the plastic cylinder to exclude vertebrate seed predators from the microsite. Once treatments had been applied, 10 seeds (five in the exclusion treatment in 2004) were scattered into the microsite. Following the rapid loss of most seeds in some microsites in 2004, additional seeds were placed in some plots up to a maximum of 20 per microsite. Seeds were placed in July and August of 2004 (1,290 in total) and in July of 2005 (1,450 in total), within the time span of natural seed fall.

The survival of seeds and seedlings was monitored until April 2005 for the 2004 experiment, and until June 2006 for the 2005 experiment. Initial monitoring was twice weekly, tapering to every 3 weeks after 5 months. I observed the timing of germination (emergence of a radical) and seedling emergence (a raised hypocotyl and green cotyledons), and collected the remains of eaten seeds or shed seed coats when they were visible. I also collected representative samples of ants that were observed eating seeds for later identification. At the termination of the experiment, I sieved the litter to locate any surviving ungerminated seeds or remaining seed coats. I classified the remaining seed coats into those that had been eaten by invertebrates (indicated by damage consistent with bite marks) and those that had germinated and then died before being established as seedlings. Remaining intact seeds were placed on moist filter paper in petri dishes, with germination used as an indication of viability.

Analysis

I used ANOVA to compare the oven-dried mass of collected litter across microhabitat classes and sites from the 2004 data. These data were square root transformed to improve heteroscedasticity. I analysed the survival of seeds across treatment levels in the experiment for the first 5 months in each year of planting using repeated measures ANOVA (factors comprised Site, Microhabitat class, Clearing treatment, Cage treatment and Year, with two-way and three-way interactions included). In this analysis, I examined seed predation, so the sum of the remaining seeds, seedlings or dead seedlings were included at each time point. In other words, even though some seedlings may have died, these were considered to have escaped from predators. Thus only losses due to seed predators were considered, allowing comparison of the rate of loss of seeds to predators over the test period. Using data from approximately 7 months after the start of the experiment, I used ANOVAs to examine the proportion of seeds that had germinated and died or were still alive (as either seeds or seedlings), and the proportion of seeds or seedlings that were still alive. I used ANOVA with the same design to analyse the proportion of damaged seed remains found to seeds added in each microsite. I assumed that where damaged seed remains were found, these seeds had been eaten by invertebrates, whereas where entire seeds were gone, this was most likely due to predation by vertebrates. Thus I was able to estimate the relative importance of vertebrate to invertebrate predation. For multiple comparisons, I used the Tukey test. In all cases, the data were non-normal and heteroscedastic, and were not greatly improved by transformation. As a result, I used a conservative threshold probability ($\alpha = 0.01$) to determine the significance of factors.

Results

Litter and the classification of microhabitats

The mass of litter in microsites was significantly affected by Microhabitat class ($F_{2,118} = 10.24$, $P < 0.001$) and Site ($F_{2,118} = 16.56$, $P < 0.001$), while the interaction between these factors was not significant ($F_{4,118} = 0.27$, $P = 0.89$). Post hoc tests indicated that the litter content of each microhabitat class was distinct (mean ± standard error of 435 ± 46, 628 ± 46 and 1036 ± 157 g/m^2 for Low, Medium and High respectively). However, there was significantly less litter overall at Site 3 (486 ± 48 g/m^2) than at Site 1 (942 ± 136 g/m^2), while Site 2 (659 ± 92 g/m^2) was intermediate and not significantly different from the other sites.

Seed survival

Seed loss was substantial and rapid with most seeds removed from some experimental microsites within 2 weeks of placement. Many seeds disappeared from within uncaged microsites or were observed being eaten in situ by ants. Ants collected while eating seeds were from the genera *Crematogaster*, *Monomorium* and *Pheidole* (Shattuck 1999).

Germination was first observed after 4 weeks, while seedlings had not emerged until after 8 weeks. By this time, approximately half of the seeds in uncaged microsites had been removed or eaten (Fig. 1).

For the proportion of genets (seeds or seedlings) remaining, the repeated measures ANOVA revealed significant site × cage, site × year and clearing × cage interactions for between subject comparisons (Table 2). The site × cage interaction was caused by differences in the magnitude of the caging effects at different sites, with caging reducing predation at all sites, but causing a greater reduction at Site 1 than at the other two sites (Fig. 1a). The clearing × cage interaction indicates that the seed losses in uncaged microsites were greater when litter and vegetation were removed than when they were left intact (Fig. 1b). The site × year interaction was the result of much higher predation losses at Site 2 in 2005 than in 2004, while the reverse, but to a lesser degree, was apparent for Site 1 (Fig. 1c, d). These same factors were significant in within-subject comparisons, indicating that their effect on the *rate* of seed loss varied over the time-scale of the experiment. In addition, there was a significant clearing × year interaction (Table 2). This indicates that the *rate* of seed loss in the different clearing treatments depended on the year of the experiment. This effect is most apparent between months 3 and 4 where losses from uncleared plots in 2005 exceeded losses from all other combinations (Fig. 1e).

Approximately 7 months after the start of the experiment, it was apparent that few seeds ever had the opportunity to become seedlings (average less than 8%) and even fewer remained alive as either seeds or seedlings (average less than 4%). The microhabitat classification, the level of caging and a site × year interaction (Fig. 2) significantly affected the proportion of seeds that ever had the opportunity

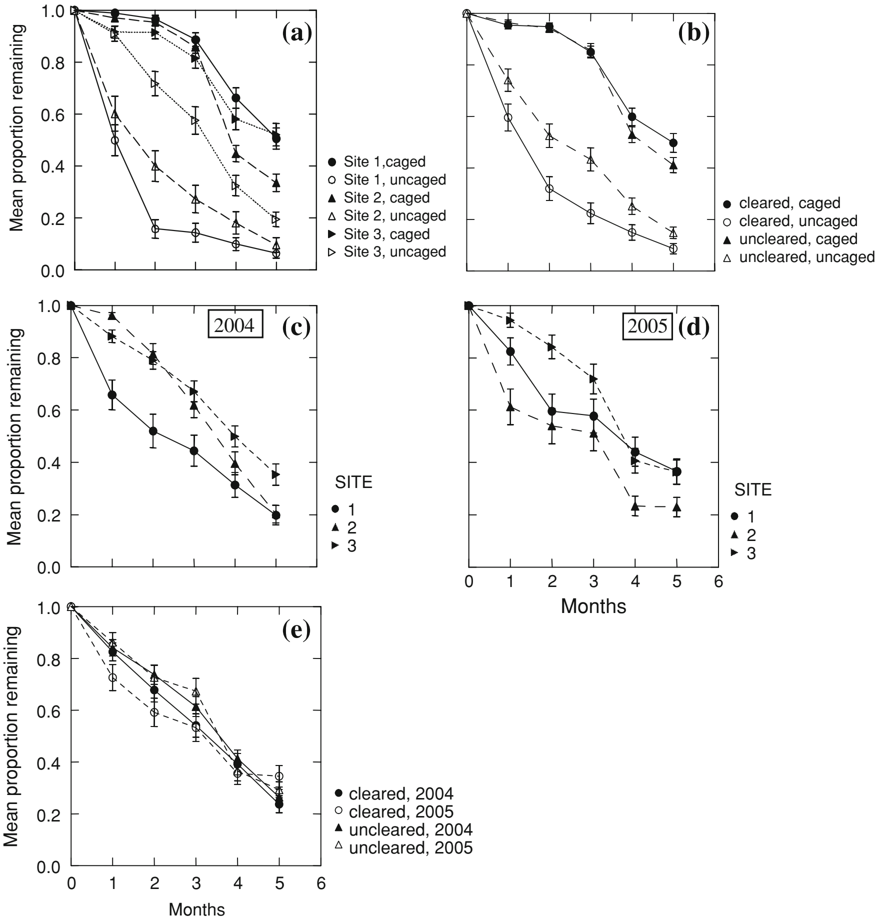

Fig. 1 Survival of seeds or seedlings over the first 5 months of the experiment, showing the mean proportion surviving (±1 standard error). The following interactions of *between subjects* factors were significant in the repeated measures ANOVA; (**a**) site × cage, (**b**) clearing × cage and (**c** and **d**) site × year. In addition, these interactions were significant *within subjects* as well as (**e**) clearing × year. *Between subjects* factors affect the overall degree of mortality, while *within subjects* factors affect the rate of seed loss

Table 2 Results of repeated measures ANOVA for the proportion of seeds or seedlings surviving up to 5 months after planting. Only main factors and significant interactions at $\alpha = 0.01$ are shown

Source of variation	SS[a]	df	MS[b]	*F* ratio	*P*	G–G[c]	H–F[d]
Between subjects							
Site	6.72	2	3.36	19.40	<0.001		
Microhabitat class	0.33	2	0.16	0.94	0.39		
Clearing treatment	1.13	1	1.13	6.51	0.01		
Cage treatment	60.45	1	60.45	348.80	<0.001		
Year	0.003	1	0.003	0.02	0.90		
Site × Cage	9.91	2	4.95	28.58	<0.001		
Site × Year	5.64	2	2.82	16.26	<0.001		
Clearing treatment × Cage	2.61	1	2.61	15.07	<0.001		
Error	41.42	239	0.17				
Within subjects							
Time	54.20	4	13.55	480.57	<0.001	<0.001	<0.001
Time × Site	1.61	8	0.201	7.12	<0.001	<0.001	<0.001
Time × Microhabitat class	0.27	8	0.03	1.21	0.29	0.30	0.30
Time × Clearing	0.78	4	0.20	6.94	<0.001	<0.001	<0.001
Time × Cage	3.39	4	0.85	30.05	<0.001	<0.001	<0.001
Time × Year	0.79	4	0.20	7.00	<0.001	<0.001	<0.001
Time × Site × Cage	2.87	8	0.36	12.71	<0.001	<0.001	<0.001
Time × Site × Year	1.82	8	0.23	8.09	<0.001	<0.001	<0.001
Time × Clearing × Year	0.46	4	0.12	4.12	0.003	0.008	0.005
Error	26.95	956	0.03				

[a] SS, sum of squares; [b]MS, mean square; [c]G–G, Greenhouse–Geisser; [d]H–F, Huynh–Feldt

to become seedlings (Table 3). More seeds escaped predation under high-density cover than under low-density cover (Fig. 2a) and more seeds escaped predation under vertebrate exclusion (Fig. 2b). Post hoc tests were not able to detect differences in the site × year interaction at $\alpha = 0.01$, although it is apparent that the main driver of this interaction is the difference between years at the Sites 2 and 3 (Fig. 2c).

At the conclusion of the experiment, only the level of caging ($F_{1,217} = 13.96$, $P < 0.001$) and a clearing × year interaction had a significant influence on the proportion of genets remaining alive. Seeds and seedlings in caged microsites had survival of approximately 6%, more than three times that of uncaged microsites (Fig. 3a). More seeds and seedlings survived in uncleared microsites than in cleared microsites in 2004 or than in either clearing treatment in 2005 (Fig. 3b). The clearing treatment did not significantly affect seed or seedling survival in 2005. A small number of apparently viable seeds remained after several months of exposure (9 from 2004 and 1 from 2005). These readily germinated in laboratory conditions.

The final fate of seeds as estimated by their remains at the end of the experiment indicated that invertebrates were responsible for, on average, 21.7 ± 2.1% of seed predation where there was no exclusion of vertebrates. Where vertebrate predators were excluded, this increased to 56.9 ± 2.0%. Site, year, clearing and a number of interactions significantly affected the final fate of seeds (Table 4). Clearing the vegetation and litter cover reduced the proportion of seeds eaten by invertebrates from 44.8 ± 2.5% to 33.9 ± 2.5%. A strong site × cage interaction indicated spatial variation in the relative importance of vertebrate predators. The proportion of seeds found eaten in uncaged microsites at Site 3 was much greater than at Sites 1 or 2, suggesting that the levels of invertebrate to vertebrate predation were more equal at Site 3 than at the other two sites (Fig. 4a). Nevertheless, even at Site 3, a

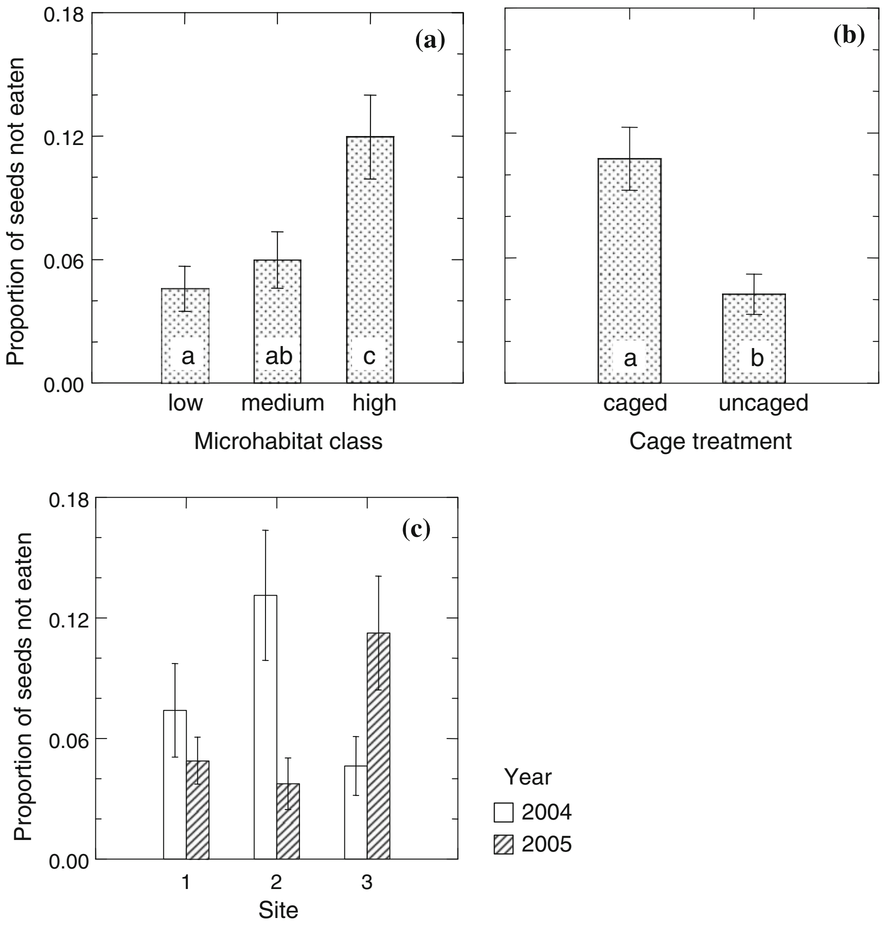

Fig. 2 The proportion of seeds (±1 standard error) that ever had the opportunity to become established as seedlings as estimated at the end of the experiment (i.e. not eaten by predators), approximately 7 months after planting. (**a**) Microhabitat effects, (**b**) cage effects and (**c**) site × year interaction. Different letters indicate significantly different means at $\alpha = 0.01$

Table 3 Results of ANOVA for the proportion of seeds that ever had the opportunity to become established as seedlings. Only main factors and significant interactions at $\alpha = 0.01$ are shown

Source of variation	Sum-of-Squares	df	Mean-Square	*F*-ratio	*P*
Site	0.020	2	0.01	0.51	0.60
Microhabitat class	0.26	2	0.13	6.44	0.002
Clearing treatment	0.15	1	0.15	7.48	0.007
Cage treatment	0.33	1	0.33	16.66	<0.001
Year	0.02	1	0.02	0.74	0.39
Site × Year	0.28	2	0.14	6.97	0.001
Error	4.30	217	0.020		

significantly smaller proportion of eaten seeds were retrieved from uncaged microsites than from caged microsites. A year × cage interaction was the result of very few seed remains being retrieved from uncaged microsites in 2005 (Fig. 4b). The proportion of eaten seeds retrieved from caged microsites was similar in both years and was significantly greater than in uncaged microsites in either year. A site × year interaction reflects variation in both space and time, with Site 1 showing a similar response in both years, while at the other two sites invertebrates were responsible for greater seed predation in 2004 than in 2005 (Fig. 4c).

Discussion

Loss of seeds of *T. speciosissima* to predators was rapid and greatly reduced the potential for post-fire recruitment. Although there was considerable variation among sites and years, vertebrate predators consumed a large proportion of seeds in the first 2 months. Loss to invertebrates was slower, with most losses occurring between 3 and 4 months after

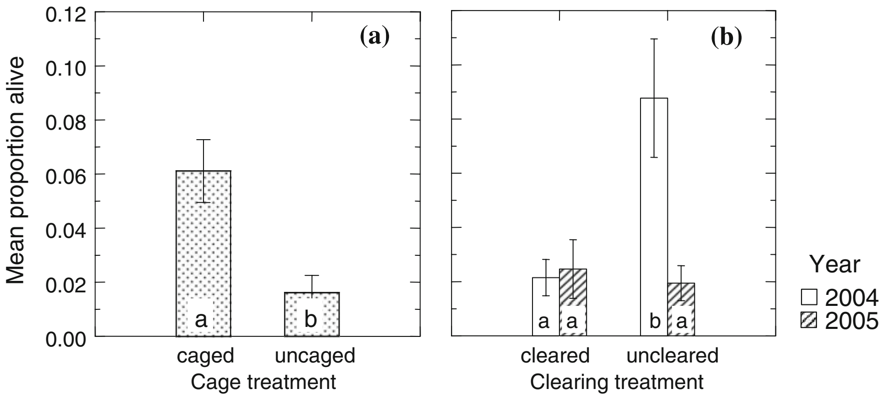

Fig. 3 The proportion of seeds or seedlings (±1 standard error) that remained alive at the end of the experiment under different treatments. (**a**) Cage effects, (**b**) Clearing treatment × year interaction. Different letters indicate significantly different means at $\alpha = 0.01$

Table 4 Results of ANOVA for the proportion of seeds that had been eaten by invertebrates at the end of the experiment. Only main factors and significant interactions at $\alpha = 0.01$ are shown

Source of variation	Sum-of-Squares	df	Mean-Square	*F*-ratio	*P*
Site	1.10	2	0.55	11.79	<0.001
Microhabitat class	0.04	2	0.02	0.44	0.65
Clearing treatment	0.86	1	0.86	18.39	<0.001
Cage treatment	8.97	1	8.97	191.62	<0.001
Year	0.58	1	0.58	12.32	0.001
Site × Cage	1.01	2	0.50	10.74	<0.001
Site × Year	0.87	2	0.43	9.27	<0.001
Cage × Year	0.33	1	0.33	6.95	0.009
Error	11.18	239	0.05		

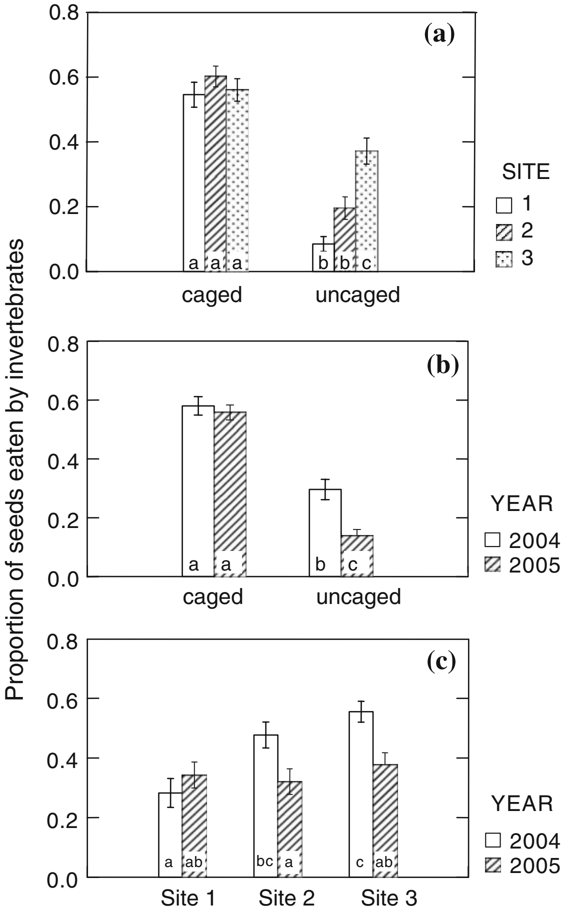

Fig. 4 The mean proportion of seeds that were eaten by invertebrates (±1 standard error) as identified by seed remains. (**a**) Cage × site interaction, (**b**) Cage × year interaction, (**c**) Sites × year interaction. Different letters indicate significantly different means at $\alpha = 0.01$

seed placement. These rates of loss are comparable to those found for species lacking an elaiosome on their seeds, both soon after fire and in long unburnt habitats (Auld and Denham 1999, 2001). The relatively high density of seeds introduced into the sites (approximately 0.5 seeds/m^2 compared with 0–0.31 seeds/m^2 of natural seed fall) may have influenced the foraging behaviour of vertebrate predators. However, densities of this magnitude may occur naturally, as observed previously at two of these sites (Denham and Auld 2002), and are unlikely to influence invertebrate predators since they operate on a much smaller spatial scale.

Microsite modifications had a small effect on the rate of loss of seeds relative to the effect of caging, with cleared locations losing seeds slightly more rapidly than uncleared locations. However, microsites with high levels of cover were twice as likely as those with low cover to be associated with recruitment, regardless of caging. Ultimately, few seedlings or viable seeds persisted for 7 months, and caged microsites had three times as many genets remaining alive than uncaged microsites.

Based on the collection of seed remains, it is apparent that removing litter and vegetation increased the probability that seeds would be found by vertebrate predators. This is consistent with other reports of the ability of rodents to find seeds in litter (Clark et al. 1991; Myster and Pickett 1993; Russell and Schupp 1998; Reed et al. 2006). Although vertebrate seed predators are also reported to avoid areas of low cover (Manson and Stiles 1998; Spencer et al. 2005), this behavioural response is likely to be at a larger spatial scale than the cover reductions created by manipulations of litter and vegetation in this experiment. Variation at the site level may reflect such habitat preferences or other factors not examined in this study. In contrast, invertebrate seed predators in this study and elsewhere (Reed et al. 2006) are apparently unimpeded by vegetation and litter cover, and were able to locate and eat seeds in situ.

The identity of vertebrate predators was not determined. However, rodents (such as *Rattus fuscipes*) and swamp wallabies (*Wallabia bicolor*) are likely to be major contributors (Auld and Denham 1999; Denham and Auld 2002). A number of ant species were observed eating seeds. Some of these may not be the primary cause of death of seeds, but merely scavengers on damaged seeds. I could not eliminate the possibility that other invertebrates, particularly nocturnal species, ate seeds. Nevertheless, it seems likely that ants are the major invertebrate predators of *T. speciosissima* seeds, a view consistent with reports on other species in similar habitats (Wellington and Noble 1985; Andersen 1987; Yates et al. 1995).

Due to the rapid rate of seed loss, conditions suitable for germination need to occur within weeks of seed fall if many seeds are to escape predation by becoming seedlings. These conditions did not occur in either of the 2 years of substantial seed production after the 2001 fire. Such escape through germination has been observed elsewhere (Curran and Webb 2000). High levels of vertebrate seed predation suggest that predators have built up sufficient populations to fully exploit this limited food resource. Satiation of predators is unlikely, because the mass release of seeds from species with canopy seed banks had finished 2 years before *T. speciosissima* released seeds, and few other plant species release seeds in this late post-fire recruitment period. Invertebrate predation was also severe. High levels of invertebrate activity soon after fire, especially by ants, have been observed in other studies (Whelan et al. 1980; O'Dowd and Gill 1984; Andersen and Yen 1985), although satiation of ants as predators, by mass seed release, has also been demonstrated (O'Dowd and Gill 1984; Andersen 1987, 1988). Andersen (1988) observed that high rates of seed removal by ants continued until at least 2 years after fire.

Recruitment of *T. speciosissima* at these sites after this (2001) fire is likely to be substantially lower than after the previous one (1994), due to higher overall levels of seed predation (Denham and Auld 2002). High spatial and temporal variability in seed predation may reflect changes in the local densities of seed predators, which in turn may be due to differences in severity and extent of the fires and the relatively short time between them (Whelan et al. 2002). However, the amount and timing of seed production, with the first seed release a year later after the 2001 fire than after the 1994 fire, may also have influenced seed predation rates. This further delay in seed release reduces the probability that the few seedlings established will achieve fire-resistance when the habitat next burns (Bradstock 1995). Nevertheless, even seedling establishment rates as low as observed in this study may be sufficient to maintain populations, depending on the rate of later mortality of seedlings and the background mortality of established individuals. With these mortality rates unknown, there is a risk that resprouting plants, such as *T. speciosissima*, may undergo substantial population declines before land managers observe and attempt to redress them.

In contrast to many species in fire-prone habitats, seeds of *T. speciosissima* have no secondary dispersal mechanisms, such as an elaiosome, nor are its predators known or expected to move or cache seeds in other locations. Its seeds are non-dormant and must either germinate on the soil surface or ultimately face loss of viability or predation by vertebrates or invertebrates. In habitats where most seedling establishment occurs within months of fire (Moles and Westoby 2004; Ooi et al. 2004), it is surprising that up to 4 years after fire, microhabitat suitable for seedling establishment was still present. Myerscough et al. (1996) also reported that the seed bank did not saturate the available space for establishment in similar coastal heath sites, suggesting that suitable microhabitat would persist for some time after fire.

In this study I demonstrated that recruitment of *T. speciosissima* was limited by seed availability rather than by microsite availability (*sensu* Munzbergova and Herben 2005), and that post-dispersal seed predators had a significant impact on seedling establishment. The impact of this predation is in addition to losses due to pre-dispersal seed predation, which varied from 0 to 19% of fruits in the years of this experiment (Table 1). For species which flower more or less annually after fire and form persistent seed banks, temporal variation in both pre- and post-dispersal seed predation may preclude additions to the seed bank in some years (e.g., Auld and O'Connell 1989; Campbell and Clarke 2006). In contrast, for species such as *T. speciosissima* that do not form a seed bank, the impacts of predation observed in the few post-fire seasons when fruiting occurs will influence recruitment for the entire fire cycle. Recruitment in *T. speciosissima*, and probably in other pyrogenic flowering species, depends upon the release of seeds into locations where the probability of vertebrate predation is reduced (that is, in microsites with dense litter and vegetation cover) at times when climatic conditions are suitable for rapid germination. Only rapid germination and seedling establishment appears to allow the seeds of *T. speciosissima* to escape from invertebrate predators.

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