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seed predation

Andrew J. Denham
University of Wollongong

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**Seedling establishment in a pyrogenic flowering
species: the role of time-since-fire, litter and post-
dispersal seed predation**

A thesis submitted in partial fulfilment of the requirements for the
award of the degree

MASTER OF SCIENCE (RESEARCH)

from

UNIVERSITY OF WOLLONGONG

by

Andrew J. Denham BSc University of Sydney

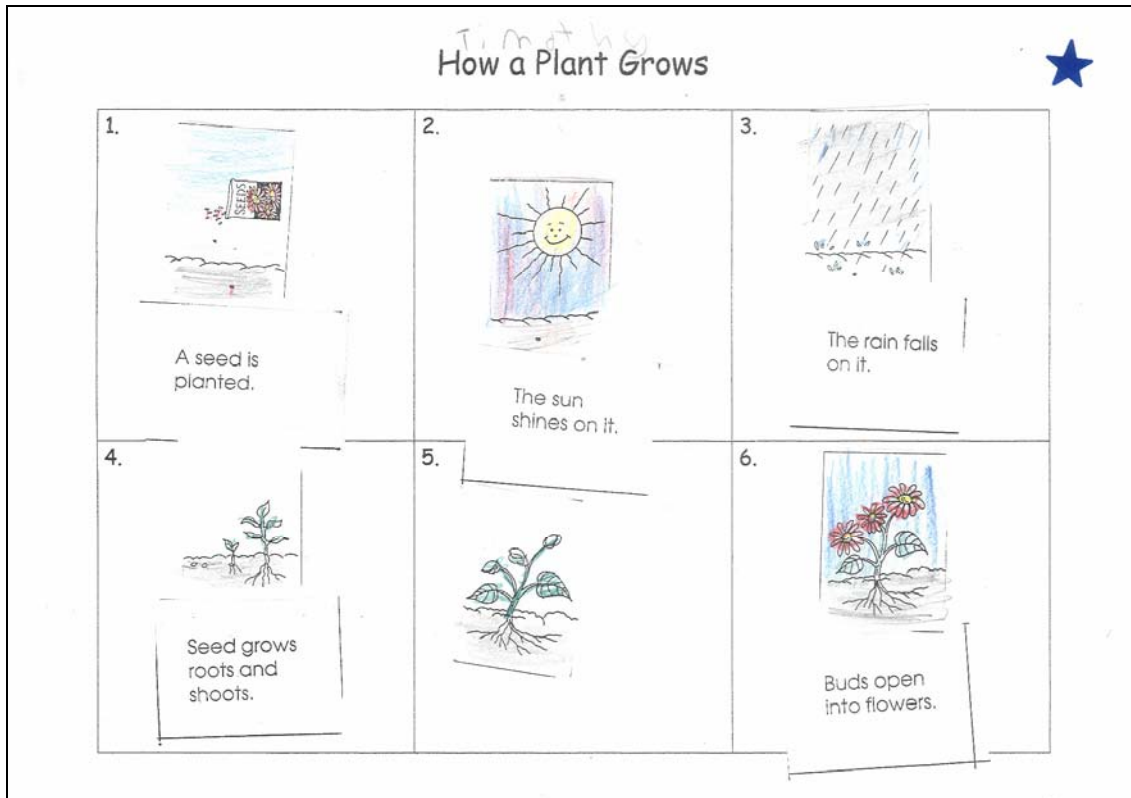
SCHOOL OF BIOLOGICAL SCIENCES

2007

Certification

I, Andrew John Denham, declare that this thesis, submitted in partial fulfilment of the requirements of the award of Master of Science (Research), in the School of Biological Sciences, University of Wollongong, is entirely my own work except where otherwise acknowledged, and has not been submitted for qualifications to any other university or institution.

Andrew Denham



Part of the life-cycle of a plant, as illustrated by Timothy, age 6.

If only it were that simple....

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Abstract

In fire prone environments, the period immediately following fire events is perceived to provide the only opportunity for recruitment for many plant species. Resprouting shrubs do not need to recruit after every fire, because many individuals survive each fire and therefore may contribute to the population. However, without periodic recruitment, the accumulated mortality of adults both during and between fires would lead to local extinction even of these species. Most plant species establish seedlings within a year of fire from either canopy or soil seed banks. In contrast, species with pyrogenic flowering have no seeds available immediately after fire and thus have their recruitment delayed. The work of this thesis aims broadly to investigate the mechanisms by which species with delayed recruitment persist. For one of these species, *Telopea speciosissima*, I asked the following questions –

- Do seedlings establish under shade and litter and tolerate competition from existing plants, or must they establish in open spaces?
- Does post-dispersal seed predation strongly influence seedling recruitment or are its seeds less susceptible to predation than those of early post-fire recruiters? and
- Does *T. speciosissima* have particular characteristics that tie seedling establishment to the late post-fire environment or is it only its life history (constrained by its phylogeny) that prevents earlier seed release?

Telopea speciosissima is a pyrogenic flowering species – it has no seed bank, but it resprouts, flowers and sets fruit in the post-fire environment. I examined recruitment in *T. speciosissima* using two seed-addition experiments, in which I manipulated predator access, microhabitat characteristics, and time of seed arrival in relation to fire. For contrast, I included *Banksia serrata*, a resprouting canopy seed bank species with seed mass similar to in *T. speciosissima*, in one of these experiments.

In the first experiment (in sites that were 3 and 4 years post-fire), seed predation was measured by placing caches of seeds within experimental microsites. These microsites were left open or covered with 12mm mesh to exclude vertebrates. The habitat within the experimental microsites was classified according to litter and vegetation cover. It was then either left intact or the litter and vegetation were removed. Seed predation was high overall (47-80%), regardless of access to vertebrates. Predation varied among sites. Few seeds or seedlings survived to 9 months after planting. Survival

of seeds or seedlings was improved in microsites with dense vegetation and litter cover. Removing the litter and vegetation cover increased the probability of seed predation by vertebrates in the first year of the experiment, but it did not influence predation by invertebrates.

In the second experiment (in sites that were 0.5 and 2-3 years post-fire), vertebrate predators were excluded from all experimental microsites. Vegetation within experimental microsites was not modified, but the litter was modified such that half the microsites had the mean mass of the early post-fire sites, the other half the mean mass of the later post-fire sites. Here I compared seedling establishment of *T. speciosissima* with that of the canopy seed bank species, *B. serrata*. I hypothesised that seedling establishment would be linked to the timing of seed release determined by the natural history of the species, with the prediction that *B. serrata* would establish more seedlings soon after fire, while *T. speciosissima* would establish more seedlings later after fire. The litter treatment tested the hypothesis that litter mass made a significant contribution to differences between the habitats with different times since fire. Seedling establishment overall was poor (< 36% of seeds), peaking within 3 months of planting. Both species established more seedlings in late post-fire sites, but litter treatments did not influence seed survival or seedling establishment. Seeds of *T. speciosissima* suffered greater predation in early post-fire sites (69.5%) than in late post-fire sites (51.2%). Predation of *B. serrata* was lower and did not vary significantly among sites (47.3%).

Since the canopy seed bank species (*B. serrata*) may establish seedlings in early or late post-fire habitats, its recruitment opportunities are determined by the timing of seed release after fire. In contrast, the greater susceptibility of *T. speciosissima* to seed predation in early post-fire sites suggests that this may be a factor favouring delayed seed release. This provides support for the hypothesis that *T. speciosissima*, as a pyrogenic flowering species, has characteristics that favour late post-fire recruitment. The seeds and seedlings of both these species tolerate relatively high levels of vegetation and litter cover. However, for pyrogenic flowering species, effective post-fire recruitment may require the coincidence of favourable environmental conditions and low levels of seed predation.

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Chapter 1 - General Introduction

How important is early post-fire recruitment for plants in fire prone environments? Variation among species and the ecological significance of delayed post-fire recruitment

1.1 Introduction

Plant species in fire prone environments are commonly classified according to their survival and regeneration strategies. If adults survive fire, they are generally classified as ‘fire tolerant’ or ‘resprouters’ (Gill 1981). If adults are killed by fire, they are classified as ‘fire sensitive’ or ‘seeders’ because they rely on new seedlings for perpetuation of populations (Gill 1981). New recruits (genets) come from seeds, and a number of seed bank properties are recognised – serotinous or canopy seed banks (bradysporous, Lamont 1991), soil seed bank or transient / no seed bank (Gill 1975; Parker & Kelly 1989; Lamont *et al.* 1991; Keith 1996).

The magnitude of mortality of adult plants after each fire determines the importance of the regeneration strategy. For species that resprout, populations can be sustained without recruitment after each fire (Auld 1986a; Bradstock & Myerscough 1988; Bond & van Wilgen 1996; Keith 1996). For fire sensitive species, recruitment after each fire may be necessary for population persistence. However, in some species with soil seed banks, not all seeds germinate after any one fire, thus providing a buffer to a lack of regeneration after a particular fire prior to any new input of seeds to the seed bank (Auld & O'Connell 1991; Tozer 1998; Smith *et al.* 1999; Auld & Denham 2006; Auld *et al.* 2007; McKenna 2007).

Variation in resprouting or fire survival ability also alters the reliance of species on recruitment from seedlings (Keeley & Zedler 1978; Clark 1988; Morrison 1995; Rice & Westoby 1999; Morrison & Renwick 2000; Bond & Midgley 2001). Some fire-response classifications emphasise the timing of post-fire recruitment. For example, Keeley (1986, 1991) referred to species as ‘fire-recruiters’ or ‘fire-resisters’. This distinction represents a special case indicating the degree of coupling of recruitment to disturbance events as outlined by Grubb (1988). Fire-resisters are able to resprout, but

their recruitment is not cued to fire events and occurs either continuously or in the prolonged absence of fire (e.g., *Eriogonum* Horton & Kraebel 1955, *Quercus* spp. Keeley 1992). Bond & van Wilgen (1996) offered a modification of the schemes proposed by Keeley (1992) and Gill (1981) to provide a two-way table relating fire to the processes of recruitment and survival in species (Table 1.1).

I begin this review by describing the changes in the environment that typically occur after fire and considering the significance of these changes to populations of plants. Then, focussing on fire-recruiting species in forests and heaths of temperate ecosystems, I explore the precise nature of the perceived post-fire flush of germination, to assess how many species display late or recurrent recruitment. Finally, after describing some late fire-recruiting life histories in detail, I consider the costs and possible benefits of late post-fire recruitment in these ecosystems.

Table 1.1. Fire life histories based on vegetative survival and the effect of fire on seedling recruitment (from Bond & van Wilgen 1996).

Recruitment	Vegetative response	
	Survive fire by sprouting	Killed by fire, non-sprouters
Stimulated by fire	Fire-recruiting sprouters	Fire-recruiting non-sprouters
Not stimulated by fire	Non-fire-recruiting sprouters	Non-fire-recruiting non-sprouters

1.2 What is special about the immediate post-fire environment?

Generalisations are often made about the changes in the post-fire environment. Primarily they refer to properties that may improve seedling recruitment and survival. However, these changes are variable in space and time both within and among fires and locations. Changes in the environment after fire will be influenced not only by the characteristics of the fire just past, but also by the prior fire history of the site (aspects of the fire regime - Whelan 1995). Here I review observations of the less subtle changes.

1.2.1 Soils

Although much work has been done on how fire changes soil properties, few generalisations are possible. The below-ground effects of fire have been reviewed by

Humphries & Craig (1981), Neary *et al.* (1999) and Certini (2005), and some of their findings are summarised below. Recent work has begun to examine the consequences of soil / fire interactions and their effect on vegetation. For example, LaJeunesse *et al.* (2006) found that ground layer (understorey) vegetation in mixed pine forests in the southeastern United States was influenced by the interaction between soil texture and time-since-fire.

Physical effects

A number of physical changes can be expected in soils as a result of fire, including changes in colour and structure (Certini 2005). Changes that have a more immediate impact on plants are discussed here. Daily soil temperature regimes are altered by fire, leading to greater flux in temperatures, to a greater depth (Christensen & Muller 1975a; Raison *et al.* 1986a; Auld & Bradstock 1996). A combination of factors is responsible for this: removal of litter reduces insulation and alters albedo, removal of vegetative cover increases exposure to sunlight and increases surface wind speeds. Severe soil heating experienced in some surface fires causes significant changes in soil physical properties (Neary *et al.* 1999; Massman & Frank 2004). An example of these changes is the occurrence of soil water repellency (DeBano 2000) or hydrophobicity and associated increased soil erosion (Rubio *et al.* 1997; Neary *et al.* 1999; Howell *et al.* 2006). The occurrence of soil water repellency depends on the soil temperatures experienced during the fire. The temperature depth profile and its maximum will determine at which depth, if any, soil water repellency occurs. Depending on its longevity, hydrophobicity must affect the timing and magnitude of post-fire recruitment of seedlings. Although this has not been specifically investigated, Tozer (1998) suggested that anomalies between the distribution of depths from which seedlings emerged after experimental soil heating and that of the seeds in the soil seed bank of *Acacia saligna* may be due to this factor. Furthermore, spatial variation in hydrophobicity will influence the spatial structure of the regenerating vegetation (Howell *et al.* 2006).

Nutrient effects

Fire has a significant impact on soil nutrients (Certini 2005), but the effects of these changes on existing plants and seedlings are complex. Simple (inorganic) nutrient levels are generally increased after low to moderate severity fires (Pryor 1963; Christensen &

Muller 1975a,b; Raison 1980, Wilbur & Christensen 1983; Thanos & Rundle 1995; Schmidt & Stewart 1997; Neary *et al.* 1999), but not always (e.g., Anderson & Menges 1997; Carrington & Keeley 1999). Adams *et al.* (1994) found that long unburnt soils had higher levels of nitrogen and carbon, while frequently burnt soils had more available phosphorous. Where it is apparent at all, the soil nutrient flush is usually short-lived (Grove *et al.* 1986; Anderson & Menges 1997; Carter & Foster 2004; Certini 2005) and superficial, and erosion may lead to overall nutrient loss. Severe fires cause significant losses of nutrients due to vaporisation (Neary *et al.* 1999; but see Grove *et al.* 1986). The increase in nutrients near the surface *may* favour seedling growth over regrowth by plants that survive the fire, especially if surface roots of resprouters are killed by the fire. However, unless seed germination and seedling growth are very rapid, resprouting plants are likely to receive a greater benefit from this nutrient flush (Grove *et al.* 1986). Measurable increases in nutrient levels do not guarantee increased nutrient availability to plants (Christensen 1977; Schmidt & Stewart 1997), although O'Dowd & Gill (1984) found that growth rates of *Eucalyptus* seedlings growing in soil from burnt sites were greater than in unburnt sites. Anderson & Menges (1997) found increased nutrient status in resprouting plants shortly after fire. They proposed that this was due to the rapid uptake of available nutrients. The subsequent dilution of these nutrients by the growth of the plants explained the relative decline in nutrient status over time.

The post-fire nutrient status of soils may vary over spatial scales that will influence the patterns of re-vegetation (Rice 1993), affecting the relative magnitude of seedling establishment and the recovery of resprouts. Other chemical changes can also affect species differentially, for example, ash beds under *Pinus halepensis* were unsuitable for germination of most species in Mediterranean pine forests, while seedlings of *P. halepensis* tolerated this substrate (Izhaki *et al.* 2000; Ne'eman *et al.* 2004).

Mycorrhizae

Soil organisms are affected by fire, with immobile forms more likely to be reduced through mortality (Certini 2005). Mycorrhizal associations are often important in fire prone environments, as their soils are usually low in nutrients (Bellgard 1991). The impacts of fire and fire regimes on mycorrhizal associations are not yet well understood (Neary *et al.* 1999; Torpy *et al.* 1999). It appears that fires generally cause an immediate reduction in root colonisation and propagule levels (Torpy *et al.* 1999; Chen & Cairney

2002, but see Bellgard *et al.* 1994) and although this change may be short-lived (Knorr *et al.* 2003; Anderson & Menges 1997), frequent long term prescribed burning may alter below ground fungal communities (Bastias *et al.* 2006). Since fires have a direct impact on mycorrhizae and soil nutrients, their interaction in relation to fire is likely to be complex, and will influence the relationship of mycorrhizae to host plants (Torpy *et al.* 1999; Wilson *et al.* 2001).

1.2.2 Space and light

By consuming litter and above ground vegetation, fire increases the amount of space available to plants for recruitment and the amount of light that reaches the soil surface (Christensen & Muller 1975a; Hulbert 1988). These two factors are generally linked - few terrestrial habitats are strictly space-limited, unlike some marine environments (e.g., Dayton 1971; Paine 1984). Fire increased the space available for recruitment of obligate seeding herbs in Florida sand scrub (Hawkes & Menges 1995, 1996; Quintana-Ascencio & Menges 2000), but whether it was space or light that had limited recruitment was not examined. Competition for light influences the relative density of some species (McPherson & Muller 1967; Jutila & Grace 2002), but not of others (McPherson & Muller 1967), with fire postulated to enable release from this constraint (but see Vila & Sardans 1999 for a review of competitive processes in Mediterranean-type vegetation). Light and light quality can both influence seed germination, with some species in fire prone environments more likely to germinate when overstorey and litter is removed (Roy & Sonie 1992; Bell *et al.* 1999; Smith *et al.* 1999). Increases in light levels at the soil surface also increase soil heating and the soil moisture flux (Christensen & Muller 1975a; Auld & Bradstock 1996). For some plant species, these changes after fire, in conjunction with the removal of the tempering influence of litter, may reduce seedling survival compared with unburnt sites (O'Connell *et al.* 1979; O'Dowd & Gill 1984; Tozer & Bradstock 1997).

1.2.3 Litter

Litter has a variety of influences on plants and plant recruitment (Fowler 1988; Facelli & Pickett 1991a, b). Fire clearly changes the influence of litter, by consuming it, but these changes are complex and often conflicting in their positive and negative effects. Germination and growth of seedlings is often associated with the removal of humus and

leaf litter by fire, due to a greater connection between seeds and the soil surface (Hille & den Ouden 2004). Facelli *et al.* (1999) found that although litter addition improved soil-water relations and reduced the summer temperature maxima, it also increased herbivory and consequently seedling growth was reduced at high litter levels. By increasing the humidity of the soil/air interface, litter can also foster fungal growth. Fungal pathogens have been identified as a major cause of seedling mortality in tropical ecosystems (Augsburger 1983), but have not been considered in fire prone habitats. Variation in individual fires will alter the quality and amount of litter remaining after fire, and the rate of post-fire litter deposition (O'Dowd & Gill 1984; Lamont *et al.* 1993).

1.2.4 Other consequences of the consumption of litter and above ground biomass

There are other associated impacts of reduced litter and vegetation after fire including increased wind dispersal (Hammill *et al.* 1998), removal of phytotoxins (McPherson & Muller 1969; Hunter & Menges 2002, but see Reigosa *et al.* 1999; Inderjit & Callaway 2003 and Halsey 2004 for reviews of allelopathy) and release from competition (Tyler 1995, 1996; Tyler & D'Antonio 1995). Complex interactions of fire and phytotoxins are probably common, but as yet poorly understood. One such interaction involves the creation of charcoal by the combustion of plant material. Charcoal in soils from young forests (<100 years after fire) was shown to have a greater ability to adsorb phytotoxic compounds than charcoal from soils in older forests (Zackrisson *et al.* 1996). Similar processes may be important over the shorter fire intervals experienced by many fire prone environments. Another complex interaction involves the effects of fire and litter on seed dormancy. Leachates of unburnt litter suppress germination of the post-fire annual, *Nicotiana attenuata*, while leachates of burnt litter trigger germination of dormant seeds (Preston & Baldwin 1999). Thus, this species uses these chemical signals to locate its post-fire successional niche. Mallik (2003) reviewed the interaction between fire and the two potentially dominant species in conifer-Ericaceae forests of the northern hemisphere. Fires of low to moderate severity do not foster conifer regeneration as ash-beds are not formed, but allow rapid resprouting and seedling recruitment of ericaceous shrubs. These shrubs perpetuate themselves by producing phytotoxins that further inhibit conifer regeneration and growth. Fires of high severity destroy these phytotoxins and provide ideal conditions for conifer seed

germination, allowing conifer regeneration as long as seed is available. In chaparral, the removal of overstorey shrubs was one factor that improved the survival of herbs, although germination was triggered by soil heating during fire, while for shrubs reduced herbivory was more important (Tyler 1995, 1996). Changes to the litter layer and the amount and structure of the standing vegetation will strongly influence the abundance and behaviour of herbivores and seed predators (discussed further below).

1.3 Other effects of fire

1.3.1 Herbivores and seed predators

Fires are expected to reduce vertebrate seed predator and herbivore abundance (Leigh & Holgate 1979; Whelan & Main 1979; Fox & MacKay 1981; Fox 1982; D'Antonio *et al.* 1993; Tyler 1996, but see Fisher & Wilkinson 2005). This clearly varies among species or guilds of herbivores (Fox 1982), and also depends on the characteristics of the habitat (e.g. the presence of areas of refuge from direct fire mortality) and on the size, patchiness and intensity of each fire (Whelan 1995; Auld & Denham 1999; Whelan *et al.* 2002). Whelan *et al.* (1996) found that the small mammal *Antechinus stuartii* not only survived the impact of the fire by avoiding lethal temperatures in rock outcrops, but also appeared to maintain populations in the post-fire environment. While this species is insectivorous, similar sized herbivores and granivores such as *Rattus fuscipes*, utilise the same habitat and also maintained populations after fire.

Fires also affect populations of invertebrates, but their response is even more variable than vertebrates. High levels of invertebrate activity soon after fire, especially by ants, have been reported (Whelan *et al.* 1980; O'Dowd & Gill 1984; Andersen & Yen 1985), with some species increasing in abundance or foraging activity, resulting in variable levels of seed predation depending on the characteristics of the habitat and the fire regime. However, predator satiation through the synchronous release of seeds from canopy seed banks soon after fire may nullify the impact of any increase in seed predation (O'Dowd & Gill 1984; Wellington & Noble 1985a; Bell *et al.* 1987; Andersen 1987, 1988).

Thus the dynamics of herbivory and seed predation are highly variable among species, habitats and fires. Consequently generalisations about their impact on plant recruitment may be inappropriate (Fox 1982; Whelan 1995; Whelan *et al.* 2002).

1.3.2 Effects of fire on plant seeds

Fires directly affect plants by the heating or consumption of plant tissues. Depending on the patchiness, severity and intensity of the fire, this leads to the death of fire-sensitive plants and the loss of some or all above-ground parts of resprouting species. Scorching of canopy seed storage organs (cones and woody infructescences) or the death of their supporting limbs causes the release of seeds in serotinous species. Consumption of the litter and heating of the soil by fire causes the death of seeds near the surface and may also stimulate germination of other seeds in the soil seed bank (Auld 1986b; Keeley 1987; Auld & O'Connell 1991). The degree of soil heating determines the depth to which seeds are killed or have their dormancy broken, while the ability of seeds to emerge from depth also affects the timing and magnitude of post-fire emergence (Auld & O'Connell 1991; Bond *et al.* 1999; Hanley *et al.* 2003; Auld & Denham 2006). Chemicals produced from the consumption of plant materials also break dormancy and stimulate germination in some plant species (Keeley *et al.* 1985; Keeley 1987; Dixon *et al.* 1995; Kenny 2000; Thomas *et al.* 2003). These chemicals are found in charred wood (charcoal), smoke and ash. The combined effect of seed mortality due to soil heating and the effective depth of fire-caused germination cues in conjunction with post-fire climatic conditions will determine the timing and magnitude of seedling emergence of species with soil seed banks after fire. Similarly, for canopy seed bank species, the rate of seed release and subsequent seedling emergence depends upon the degree of cone scorch and the post fire climatic conditions. These and other influences on the rate of seedling emergence after fire are discussed below.

1.4 Variation in the timing of post-fire seedling emergence

Numerous studies have examined the recovery of vegetative cover after fire, including seedling recruitment (e.g. Horton & Kraebel 1955; Purdie 1977a,b; Keeley *et al.* 2006), but few studies have been designed to estimate changes in abundance of individual species over short time periods. A survey of studies of post-fire regeneration in temperate forests and heaths provides some indication of the variation in recruitment times (Table 1.2). Many of the estimates in this table are imprecise because they have had to be based on statements made in the text of the primary publications rather than on published empirical data. However, it is clear that the great majority of species with recruitment related to fire establish seedlings less than 18 months after fire.

1.4.1 Soil seed bank species

In some habitats, soil seed bank species may emerge after the fire as soon as there is sufficient soil moisture to allow germination to occur. Legumes are generally the first to appear, with recruitment occurring within 3 months in suitable conditions (Auld 1986b; Auld & Tozer 1995; Valbuena & Trabaud 2001). Although a few species may not be observed until 3 years after fire, this may be because early post-fire seedlings died or were eaten before they were observed (Henkin *et al.* 1999). Many herbaceous species also appear very quickly after fire. In Florida sand pine scrub, *Eriogonum* (Polygonaceae) and *Palafoxia* (Asteraceae) emerge as soon as 3 weeks after fire (Carrington 1999). There is a large range of emergence times among other soil seed bank species, with the majority of species recruiting seedlings within a year of the fire (Table 1.2, e.g., Horton & Kraebel 1955; Keeley & Keeley 1981; Auld & Tozer 1995). In these species, most germination is confined to the first favourable season for germination, usually winter or spring (Purdie 1977a; Keeley 1991; Odion & Davis 2000; Odion & Tyler 2002; Quintana *et al.* 2004). For Western Australian species in a mediterranean-climate region, Bellairs & Bell (1990) suggested that post-fire soil temperatures may inhibit germination until the cooler winter months. In the Sydney region, without a strong seasonal rainfall influence, seedlings may emerge more or less continuously after fire breaks seed dormancy and therefore allows germination. In some species, emergence is rapid, such as for *Acacia suaveolens* and *Grevillea* spp. (Auld & Tozer 1995, Fig. 1.1). In other species, such as *Persoonia lanceolata*, there may be a more staggered pattern of emergence (Fig. 1.1, Auld *et al.* 2007). Nevertheless, very few new seedlings of this species emerged later than two years after the fire.

A few species show delays of several months and / or continual seedling emergence after fire. These include many members of the Ericaceae, including *Epacris* (Keith 2002) and *Leucopogon* (Ooi *et al.* 2004a), as well as Cistaceae (Roy & Sonie 1992; Luis-Calabuig *et al.* 1996), and chaparral species such as *Artemisia californica* (Horton & Kraebel 1955). For *Leucopogon* species, Ooi *et al.* (2004a) found a seasonal pattern of emergence, with emergence occurring in winter, regardless of the season of fire. This led to delays of 2 to 10 months, with additional pulses of emergence observed in the subsequent year (Fig. 1.1). Further work has shown that the seeds of these species have complex morphophysiological dormancy (Ooi *et al.* 2006). After primary

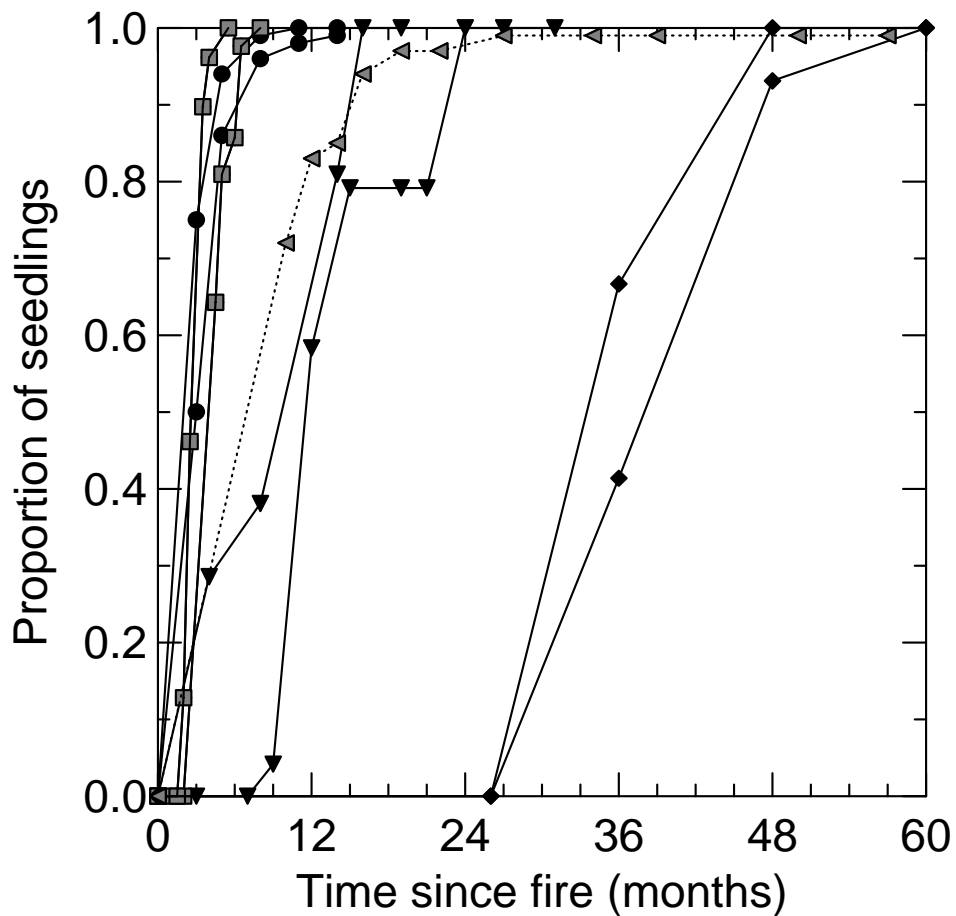


Figure 1.1. Emergence times of plants after fire. Species can be classified into different groups according to their timing of emergence and type of recruitment strategy. Canopy seed bank species such as *Banksia ericifolia* (■) generally emerge rapidly after fire (data for an autumn and a summer fire), some soil seed bank species such as *Acacia suaveolens* and *Grevillea* spp., also emerge rapidly (●), while others such as *Persoonia lanceolata*, emerge more gradually (▲) or like *Leucopogon exolasius*, have a seasonal restriction on emergence (▼: data for a winter and an autumn fire). Finally, shrubby pyrogenic flowering species such as *Telopea speciosissima* (◆) have their emergence delayed by at least a year (data for two sites after a summer fire). Data from Bradstock & Myerscough (1981), Auld & Tozer (1995), Denham & Auld (2002), Ooi et al. (2004a) and Auld et al. (2007).

dormancy is overcome by exposure in the soil to several months of warm temperatures (warm stratification), germination may occur, but even then it is restricted to the cooler months. Emergence of seedlings in unburnt habitat provides evidence that fire is not a necessary trigger for germination in these species, although it appears to enhance it (Ooi *et al.* 2004a). A seasonal influence on the pattern of seedling emergence has also been observed in Western Australian species from a variety of families (Roche *et al.* 1998). Here the season of application of a germination stimulant (smoke) determined the abundance and success of post-fire germination over two growing seasons.

Thus, for soil seed bank species, the vast majority recruit new seedlings within a year of fire (Table 1.2). Although there are some species that may recruit new seedlings beyond 18 months post-fire, this is in conjunction with earlier (and usually larger) cohorts of emergence in the same species.

1.4.2 Canopy seed bank species

The seeds of canopy seed bank species generally have no dormancy mechanisms (Lamont *et al.* 1991, but see Whelan & Brown 1998), although heat may enhance post-fire germination in some species (Hanley & Lamont 2000). Consequently, seeds germinate when they are exposed to suitable conditions, usually adequate moisture. In some circumstances, high temperatures after release may impose secondary dormancy (Bradstock 1985; Cowling & Lamont 1987). Variation in post-fire seedling emergence therefore, is related primarily to the rate of seed release from the canopy. This in turn is generally influenced by the intensity of the fire, and the post-fire climatic conditions. Hotter fires and arid post-fire conditions lead to more rapid release (Gill 1976; Bradstock & Myerscough 1981; Cowling & Lamont 1987; Enright & Lamont 1989a; Lamont *et al.* 1991). In these situations, recruitment will usually be concentrated in the first post-fire winter or spring when rainfall is adequate. Where release is delayed or occurs gradually, germination occurs in the first two years after fire (Table 1.2). For *Banksia ericifolia*, a delay in seedling emergence was found after a summer fire, where post-fire conditions were too dry to permit germination, while after a winter fire, emergence followed soon after seed release (Fig. 1.1, Bradstock & Myerscough 1981). Thus canopy seed bank species may be delayed by times similar to those observed by Ooi *et al.* (2004a) for soil seed bank species with morphophysiological dormancy. However, delayed germination in canopy seed bank species increases the exposure of

their seeds to desiccation and predation on the soil surface. Thus few seeds of canopy seed bank species are expected to remain viable after the first summer following a summer/autumn fire or the second summer following a spring/summer fire (but see Whelan & York 1998). This may explain the low level of recruitment observed in *B. ericifolia* by Bradstock & Myerscough (1981) after a summer fire.

The length and rate of seed release from canopy seed banks are characters that appear to be labile and therefore vary greatly among species (Dunlop 1996). The selective advantages of variation in these two characteristics of seed release for post-fire recruitment were explored by Dunlop (1996). He concluded that the variations he detected among species are likely to have been induced by selection, but that the strength of this selective force varies with post-fire conditions. In terms of seed release strategies, when conditions shortly after fire are consistently ideal for recruitment, an early and rapid release of seeds is beneficial. In contrast, if immediate post-fire conditions are often harsh (arid), then risk spreading by slow or delayed seed release increases recruitment opportunities, while minimising exposure to desiccation and predation. However, Dunlop (1996) did not list any species that released seeds beyond the first two years after fire, providing further evidence of strong selection against such late post-fire seedling establishment.

1.4.3 Species with transient seed banks or no seed bank

In most fire prone habitats, there are a number of species with no apparent seed bank at the time of the fire ('transient seed banks' *sensu* Parker & Kelly 1989). These species are either completely eradicated from the burnt area and must recolonise from unburnt habitats, or persist only through vegetative resprouting. There are few examples in the literature of the former response type. Quintana-Ascencio & Menges (2000) report that *Polygonella basiramia* is a fire sensitive species with an achene that appears to be adapted for wind dispersal. Its seedlings are rare in the first post-fire year, but it recolonises from unburnt patches within a few years of fire.

Table 1.2. Summary of literature giving time to recruitment of seedlings after fire for species of different seed bank types from fire prone environments in temperate forests and heathlands (modified from Denham & Auld 2002). Empty cells indicate that no examples were found.

Seed bank type	Location of study species	Time from fire to seedling recruitment	Source
Soil	Australia	<1 year	Purdie (1977b), Whelan (1985), Auld (1987), Hughes & Westoby (1992), Meney <i>et al.</i> (1994), Auld & Tozer (1995), Benwell (1998), Vaughton (1998), Ooi <i>et al.</i> (2004a), Auld & Denham (2005, 2006), Auld <i>et al.</i> (2007)
		1-2 years	Purdie (1977b), Whelan (1985), Ooi <i>et al.</i> (2004a), Keith (2002), Auld <i>et al.</i> (2007)
		> 2 years	Keith (2002), Auld <i>et al.</i> (2007)
	Mediterranean	<1 year	Ne'eman <i>et al.</i> (1992), Ferrandis <i>et al.</i> (1996), Henkin <i>et al.</i> (1999), Eshel <i>et al.</i> (2000), Valbuena & Trabaud (2001), Quintana <i>et al.</i> (2004)
		1-2 years	Izhaki <i>et al.</i> (1992), Roy & Sonie (1992), Henkin <i>et al.</i> (1999), Valbuena & Trabaud (2001), Quintana <i>et al.</i> (2004), Tavsanoğlu & Gurkan (2005)
		> 2 years	Roy & Sonie (1992), Tavsanoğlu & Gurkan (2005)
	South Africa	<1 year	Bond & Slingsby (1984), Kruger and Bigalke (1984), Musil & de Witt (1990), Musil (1991)
		1-2 years	
		> 2 years	
	North America	<1 year	Horton & Kraebel (1955), Keeley & Keeley (1981), Whelan (1985), Borchert (1989), Keeley (1991), Carrington (1999), Odion & Davis (2000), Odion & Tyler (2002)
		1-2 years	Horton & Kraebel (1955), Keeley & Keeley (1981), Keeley <i>et al.</i> (1981), Keeley (1991), Quintana-Ascencio & Morales-Hernandez (1997), Carrington (1999), Odion & Tyler (2002)
		> 2 years	Horton & Kraebel (1955)

Table 1.2 (continued)

Canopy	Australia	<1 year	Bradstock & Myerscough (1981), Whelan (1985), Gill & McMahon (1986), Bradstock & O'Connell (1988), Lamont & Barker (1988), Lamont <i>et al.</i> (1991), Benwell (1998), Whelan & York (1998), Enright & Goldblum (1999), Facelli <i>et al.</i> (1999), Wooller <i>et al.</i> (2002)
		1-2 years	
		> 2 years	
	Mediterranean	<1 year	Ne'eman <i>et al.</i> (1992), Daskalakou & Thanos (1996, 2004), Eshel <i>et al.</i> (2000)
		1-2 years	Herranz <i>et al.</i> (1997), Daskalakou & Thanos (2004)
		> 2 years	
	South Africa	<1 year	Bond <i>et al.</i> (1984), Wright <i>et al.</i> (1990), Le Maitre (1992), Keeley <i>et al.</i> (1999)
		1-2 years	Bond <i>et al.</i> (1984)
		> 2 years	
	North America	<1 year	Ne'eman <i>et al.</i> (1999), Turner <i>et al.</i> (1999), Borchert <i>et al.</i> (2003)
		1-2 years	Ne'eman <i>et al.</i> (1999)
		> 2 years	
Post-fire flowering (transient seed bank)	Australia	< 1 year	
		1-2 years	Auld (1986a), Benwell (1998), Curtis (1998), Taylor <i>et al.</i> (1998), Denham & Whelan (2000)
		> 2 years	Denham & Auld (2002)
	South Africa	<1 year	Le Maitre & Brown (1992)
		1-2 years	Le Maitre (1984), Le Maitre & Brown (1992)
		> 2 years	
	North America	<1 year	Whelan (1985), Carrington (1999)
		1-2 years	Horton & Kraebel (1955), Malanson & O'Leary (1982), Keeley & Keeley (1984), Whelan (1985), Keeley (1991), Brewer & Platt (1994), Carrington (1999), Tyler & Borchert (2002), Borchert (2004, 2006)
		> 2 years	Tyler & Borchert (2002)

Resprouting species that have no persistent seed bank include plants with a variety of different growth forms and recruitment strategies. Some, termed 'obligate resprouters' or 'fire resisters' (*sensu* Keeley 1991), are tall shrubs that recruit in long unburnt sites, often with animal dispersed seeds. These species are dependent on canopy openings for recruitment or are able to recruit into established vegetation (Malanson &

O’Leary 1982; Keeley & Keeley 1984; Keeley 1991; Lloret & Zedler 1991). Others are sub-shrubs that recruit soon after fire, but flower and release seeds in the absence of fire. These species are also capable of exploiting recruitment opportunities presented by other disturbances in the absence of fire (Keeley *et al.* 2006).

In contrast to other resprouters, pyrogenic flowering species rarely flower in the absence of fire. However, they respond to fire by vigorous resprouting and flowering in one or more subsequent seasons, utilising resources that are made available by the fire or from storage organs (Verboom *et al.* 2002). Many flower very soon after fire (some even within a week of fire, Le Maitre & Brown 1992; Bond & van Wilgen 1996), presumably to take advantage of a nutrient flush and / or to improve pollination success (Brewer 1995). These species generally release non-dormant seeds several months to several years after fire (Table 1.2, e.g., Gill & Ingwersen 1976; Parker & Kelly 1989 and references therein; Keeley 1991; Le Maitre & Brown 1992; Bell *et al.* 1993; Abrahamson 1999; Denham & Whelan 2000; Denham & Auld 2002; Tyler & Borchert 2003; Borchert 2004), although some produce seeds with innate dormancy (Bell *et al.* 1993; Lamont & Runciman 1993). Monocotyledons dominate this group of species, although dicotyledons are represented. Geophytes are common (Le Maitre & Brown 1992; Parsons & Hopper 2003; Proches *et al.* 2006), but non-geophytic pyrogenic flowering species appear to be rare in most fire prone habitats. Australia is the only continent where they have been reported in the literature (Keeley 1995). Some *Yucca* species in the USA may be analogous, although Keeley (1991) considered that *Y. whipplei* only survived fire by avoiding scorching due to its occurrence in sparsely vegetated habitat. Although data are scarce, I estimate that for non-geophytic pyrogenic flowering plants there are at least seven dicotyledonous species, 29 monocotyledonous species and one gymnosperm species in temperate forests and heathlands in Australia's fire prone environments (Table 1.3). Of these species, all but a four occur primarily in habitats where fire is the predominant cause of disturbance.

As a consequence of their relative obscurity, the evolutionary significance and conservation implications for species with this form of post-fire recruitment have rarely been considered. The eastern Australian shrubby dicotyledon, *Telopea speciosissima*, provides a good example of this post-fire response. Mature plants resprout vigorously after fire (Bradstock 1995) and flowering is generally restricted to the first three post-fire years (Pyke 1983; Denham & Auld 2002; but see Goldingay 2000). Seeds are not released until at least 15 months after the fire, depending on the season of the fire

(Denham & Auld 2002). Additional seeds may be released in subsequent years, but the seedlings derived from them may not survive subsequent fires depending on the length of the inter-fire interval, (Bradstock 1995; Denham & Auld 2002). In comparison to species with persistent seed banks, recruitment of *T. speciosissima* seedlings occurs in the tail of the post-fire recruitment phase (Fig. 1.1). Since the probability of subsequent fires increases with time since fire, this species may be at increased risk from repeated fires at short intervals or if conditions for successful recruitment of seedlings fail to be met over a number of fire cycles.

Table 1.3. Occurrence of non-geophytic pyrogenic flowering species in temperate forests and heathlands in Australia.

Family	Genus	Species with Reference pyrogenic flowering
Proteaceae	<i>Lomatia</i>	2 Denham & Whelan (2000), Harden (2002)
	<i>Telopea</i>	2 Denham & Auld (2002), pers. obs.
Myrtaceae	<i>Angophora</i>	3 Auld (1986a), Tierney (2004), pers. obs.
Xanthorrhoeaceae	<i>Xanthorrhoea</i>	27 Gill & Ingwersen (1976),
	<i>Kingia</i>	1 Benwell (1998), McFarland (1990), Curtis (1998), Taylor <i>et al.</i> (1998), Lamont <i>et al.</i> (2004)
Doryanthaceae	<i>Doryanthes</i>	1 Denham & Auld (2002)
Podocarpaceae	<i>Podocarpus</i>	1 Chalwell & Ladd (2005)

1.5 When do post-fire environments become less favourable for recruitment?

If the post-fire environment is beneficial to seedling recruitment, but the inter-fire period is less so or is antagonistic, then it is important to understand the transition between these two phases (Fig. 1.2). For some of the changes that occur during a fire, such as litter density and vegetative cover, a gradual return to the inter-fire environment

is expected, but for others such as soil nutrient status, there may be a rapid change. For fire-recruiting species, the benefits of the fire for recruitment may diminish gradually, leading to poorer recruitment probabilities, or there may be thresholds beyond which no recruitment is possible. Few studies have examined when these post-fire changes occur (but see Purdy *et al.* 2002). However, categorisation of plant species as fire-recruiters or inter-fire recruiters tacitly implies a definition of the end of the fire influence. Many studies have followed the incremental recruitment of new species into habitats after fire (e.g. Horton & Kraebel 1955; Purdie 1977a,b), but species whose recruitment is fire-related but delayed by several years (e.g., *T. speciosissima* – Denham & Auld 2002, *Xanthorrhoea* – Lamont *et al.* 2004) defy the general notion of a short post-fire influence. Indirect changes after fire such as in the abundance of seed predators or pollinators are highly significant for recruitment of plants. Experiments introducing seeds into environments at various post-fire times (e.g., Zammit & Westoby 1988; Tozer & Bradstock 1997; Quintana-Ascencio & Menges 2000; Purdy *et al.* 2002) provide some insights into this vexing question, although no studies have employed species with naturally delayed recruitment. Comparative studies examining related species with recruitment that is not coupled to fire and those that is coupled to fire (e.g., *Rhus* spp. Keeley 1991; Lloret & Zedler 1991; Izhaki *et al.* 1992) would also assist in explaining the importance of time-since-fire to recruitment in fire-prone areas.

1.6 What are the costs and benefits of delayed post-fire recruitment?

For late post-fire recruiting species to persist there must be some net benefits or no net cost in delaying recruitment, after at least some fires. The benefits of delaying recruitment may relate to the loss of factors that make the immediate post-fire environment hostile. Prominent among these are reduced soil surface temperatures and reduced soil temperature and moisture flux due to the re-establishment of vegetation and the litter layer (Fig. 1.2). Thus, delayed recruitment may favour species adapted to recruiting in closed forest or undisturbed vegetation. However, for most species in fire prone areas, it is difficult to identify any benefits of delaying recruitment after fire. Not only do seedlings of species that delay recruitment potentially miss out on the pulse of increased nutrients and light, they must compete with resprouting vegetation and established seedlings. There is a general acceptance that within a species, later emerging seedlings will suffer increased mortality and reduced growth as a result of competition



Figure 1.2. Photographs of habitats at different times since fire that emphasise the changes to the environment that occur over time. (a) Three months after fire. There is little evidence of vegetative resprouting or seedling emergence. On the ground there is a mosaic of newly fallen litter from scorched canopy leaves, charcoal from consumed vegetation and bare patches of soil. (b) Approximately three years after fire. The vegetation has recovered (largely by resprouting) and there is an established and relatively continuous litter layer. However, the pyrogenic flowering species, *Telopea speciosissima* (left foreground) has yet to release seeds after this fire.

(e.g., Whelan 1995; Jones *et al.* 1997), although this is not always true (Verdu & Traveset 2005). There are also likely to be similar interspecific impacts of delayed recruitment (initial or size advantage), although obtaining evidence for this would require disentangling the influence of the timing of recruitment and the relative competitive ability of each species (Wilson 1988; Gerry & Wilson 1995; Howard & Goldberg 2001; Hely & Roxburgh 2005). Thus it is important to consider whether there are particular characteristics that enable species with delayed recruitment to persist in fire prone environments.

For resprouting species that produce non-dormant seeds, there may be a trade-off between making use of the immediate post-fire resource flush to improve the quality or increase the quantity of seeds (Verboom *et al.* 2002), and the cost of delaying their dispersal and germination. This post-fire resource flush is not limited to space, light and nutrient availability that are directly influenced by fire event. Fires may indirectly improve the visibility of flowers to pollinators. Furthermore, Pyke and Paton (1983) found at 'typical' inflorescence densities, taller inflorescences of *T. speciosissima* had greater visitation rates from pollinators. Thus devoting resources to rapid growth *after* fire rather than seed production *prior* to a fire may lead to improved pollination success. However, delaying seed release until after fire means plants must also contend with a different seed predation regime. Since few plant species release seeds at this time, it is unlikely that seed predators would be satiated (Janzen 1971), but seeds could be more difficult for predators to find because the habitat is a more complex mix of established vegetation and litter (Clark *et al.* 1991; Auld & Denham 2001). Nevertheless, there is likely to be some overlap in seed release between pyrogenic flowering species and fire sensitive species with short primary juvenile periods or resprouters with short secondary juvenile periods.

For rapidly reproducing species, the impact of predispersal seed predation may be reduced in the first fruiting event after fire (Le Maitre 1984; Auld & O'Connell 1989). However, the relative benefits of this reduction in seed loss compared with the costs of delayed seedling recruitment after fire have yet to be explored.

Some fire-sensitive species with soil seed banks may show delayed recruitment, due to physiological dormancy. Like pyrogenic flowering species, these species obtain few of the general post-fire environmental benefits (depending on how long emergence is delayed), and must find suitable microsites in which to establish. The persistence of species with delayed recruitment suggests that post-fire resource use, particularly of

space/light is patchy (i.e., recruitment microsites are not saturated, Myerscough *et al.* 1996), or that species in these groups are superior competitors, able to out-compete earlier establishing species.

For all plants in fire prone areas, in order to maximise the probability that new individuals can contribute to the population either through pollen or seed, recruits must either attain fire-resistance (resprouting species) or flower and disperse seeds (fire-sensitive species) prior to the next fire. Depending on the frequency of fire events, the increased risk of fire occurring before one of these conditions is met is a major cost of delayed post-fire recruitment. This may explain why many obligate seeding species recruit rapidly after fire and have relatively short primary juvenile periods (e.g., Keith 1996; Enright & Goldblum 1999; Schwilk & Ackerly 2005). Resprouting species are resilient to short fire intervals in that most fire-resistant individuals will survive successive fires. However, if short fire intervals are regular (a regime of high fire frequency), then population declines would be expected, since seedlings will be eliminated in successive fires and there would be some loss of juveniles or adults either during fire events or between them. Species with no persistent seed bank clearly rely on seed production after each fire for recruitment; consequently the degree of buffering of populations to frequent fire is reduced. Thus, although it may take decades, persistent, frequent fire is likely to cause local extinctions of pyrogenic flowering species. Due to their resilience, these species may be overlooked by land management agencies in their consideration of appropriate fire regimes.

The reproductive behaviour of pyrogenic flowering species and the mechanisms behind pyrogenic flowering have been the subject of a number of studies (e.g., Gill & Ingwersen 1976; Lamont & Runciman 1993; Verboom *et al.* 2002). However, since the seedlings of shrubby pyrogenic flowering species occur in late post-fire habitats, they are often neglected in studies of plant recruitment after fire. Experimental studies are needed to explore the mechanisms that enable these species to persist, both in terms of the fire regime itself and in relation to competitive interactions with other plant species. In particular, key aspects of plant demography such as seed predation and seedling establishment need to be investigated. Such studies may involve experiments where seeds are placed in the habitat at various times after fire and in conjunction with better known species from other functional groups. Other critical aspects requiring investigation include the length of the young juvenile stage (the time taken for seedlings

to reach fire-resistance, Bradstock 1995); and the length of the primary juvenile stage (the time taken for seedlings to produce flowers).

1.7 Overview of thesis

The work described in this thesis aims broadly to investigate the mechanisms by which shrubby pyrogenic flowering species might persist within a plant community exposed to recurring fires. The focus is on the establishment of seedlings since the behaviour of these species in other respects is similar to other, better known, early post-fire recruiters. For the eastern Australian species, *Telopea speciosissima*, I asked:

- Do seedlings establish under shade and litter and tolerate competition from existing plants, or must they establish in open spaces?
- Does post-dispersal seed predation in *T. speciosissima* strongly influence seedling recruitment or are its seeds less susceptible to predation than those of early post-fire recruiters? and
- Does *T. speciosissima* have particular characteristics that tie seedling establishment to the late post-fire environment or is it only its life history (constrained by its phylogeny) that prevents earlier seed release?

To address these questions I carried out two seed-addition experiments, manipulating predator exclusion, habitat and time of seed arrival in relation to fire. In the first experiment I added seeds of *T. speciosissima* in habitats when existing plants were also releasing seeds after fire. In the other experiment I introduced seeds of *T. speciosissima* into habitats before seed release would normally occur after fire as well as into habitats where it normally would have occurred. In this latter experiment, to provide contrast, I also added seeds of *Banksia serrata*, a resprouting canopy seed bank species with seed mass similar to in *T. speciosissima*.

In the following chapters, I completed the following:

- Characterised the litter layer in early (six month old) and later (2-3 years old) post-fire habitats (Chapter 2),

- Tested the importance of invertebrate and vertebrate predation, litter and vegetative cover on seed survival and seedling recruitment after fire in the pyrogenic flowering species *Telopea speciosissima* (Chapter 3)
- Contrasted seed survival and seedling recruitment between *T. speciosissima* and a canopy seed bank species, *Banksia serrata*, in early and late post-fire habitats (Chapter 4).

In Chapter 5, I summarise and discuss how the findings of studies described in Chapters 2 to 4 improve our understanding of post-fire seedling recruitment. I also highlight how these findings help to identify remaining gaps in our knowledge and suggest further work that may answer some of the remaining questions.

The main chapters in this thesis are written as manuscripts to be submitted for publication. Each chapter therefore has its own Abstract and in the introduction sections of each there is some inevitable repetition of material already presented in Chapter 1.

Chapter 2 - Characterising the litter in post-fire environments: implications for plant recruitment

2.1 Abstract

Litter is an important component of fire prone habitats, and the amount of litter varies greatly with time since fire. Although it strongly affects seed predation and plant recruitment, few studies of litter dynamics in fire prone habitats have focussed on this influence. I examined early post-fire litter dynamics to help understand the relationship between litter and seed predation and plant recruitment after fire. I sampled litter from two recently burnt sites (approximately 6 months after fire) and from two sites that were burnt 2-3 years previously. I characterised the litter in terms of the contributions of the two major components: charcoal (the remaining pre-fire litter) and sticks and leaves (the post-fire litter). I assessed variability within sites and compared the amounts of litter among time-since-fire categories. Using published data on the seed mass of various species from fire-prone habitats, I examined seed mass variation in relation to the timing of seed arrival in post-fire habitats. Early post-fire sites had almost twice as much charcoal as later post-fire sites, but only two thirds as much litter overall. Within site variation was high, suggesting spatial patchiness in litter cover. Seeds of canopy and soil seed bank species are present before the fire and are likely to encounter a habitat of spatially variable litter mass, with some areas covered by little or no litter. Seeds of these species showed great variation in mass. In contrast, the seeds of shrubby pyrogenic flowering species arrive some 1-3 years after fire and will encounter a habitat with more litter overall and thus fewer patches with little or no litter. Seeds of these species were relatively large and consistent in mass. This provides some evidence that over evolutionary time scales, changes in the litter layer after fire may have had an influence on seed size. This influence may have come directly through its affect on germination and seedling survival or indirectly through its affect on seed predators.

2.2 Introduction

Recruitment of seedlings can be greatly affected by the amount and composition of the litter in which they occur (e.g., Fowler 1988; Facelli & Pickett 1991; Lamont *et al.* 1993; Jensen & Gutekunst 2003; Eckstein & Donath 2005). Litter appears to facilitate recruitment in some species, but not others, depending on the size of seeds, their position in the litter and their tolerance of shading and desiccation.

Litter can also influence the foraging activity and ability of seed predators to locate seeds. Reduced amounts of litter after fire, for example, can improve the ability of vertebrate seed predators to locate seeds, thus increasing seed predation rates (Bond 1984; Clark *et al.* 1991; Myster & Pickett 1993; Auld & Denham 1999, 2001; Reed *et al.* 2006), despite possible reductions in the population sizes of predators after fire (Fox 1982; Botha & Le Maitre 1992; Sutherland & Dickman 1999). Fire-induced modifications to the litter layer may influence the abundance, composition and behaviour of invertebrate seed predators, particularly ants (Andersen 1988; Andrew *et al.* 2000; York 2000; Reed *et al.* 2004), with some species increasing in abundance or foraging activity, resulting in variable levels of seed predation depending on the characteristics of the habitat and the fire regime. However, predator satiation through the synchronous release of seeds from canopy seed banks after fire may nullify the impact of any increase in seed predation (O'Dowd & Gill 1984; Wellington & Noble 1985a; Bell *et al.* 1987; Andersen 1988; Lamont *et al.* 1991).

In fire prone environments, considerable variations in the litter occur over time since fire. In the first few days after fire, litter amounts are expected to be low and composed mainly of remnants of litter present before the fire that is partially consumed or unconsumed. The amount of litter consumed will depend on the moisture content of the litter and other fuel components, as well as the weather conditions at the time of the fire (McCaw *et al.* 1997). In the following weeks, many scorched, but unconsumed, leaves would be expected to drop from the canopy of shrubs and trees, resulting in a rapid increase in the amount of litter (O'Connell *et al.* 1979, Andersen 1988; Birk & Bridges 1989; Burrows & Burrows 1992; Facelli & Kerrigan 1996). Subsequently, incremental or seasonal inputs are expected (Maggs & Pearson 1977) as the leaves of resprouting plants or seedlings senesce. Litter is also re-sorted over the landscape by wind and water; accumulating in some areas and leaving other patches bare (Lamont *et al.* 1993; Howell *et al.* 2006). The proportion of charcoal in the litter decreases as these components are incorporated into the humus (Raison *et al.* 1983) and as the overall

amount of litter increases with new contributions through leaf-fall. Equilibrium in the total amount of litter may occur when decomposition matches new contributions (Olson 1963; Hutson & Veitch 1985), although in many fire-prone ecosystems this is unlikely to happen prior to the next fire (Birk & Simpson 1980; Mitchell *et al.* 1986, but see Lamb 1985).

The immediate changes in litter structure and amount after fire have not been thoroughly studied. This is surprising given that many characteristics of the post-fire environment are strongly linked to the consumption of litter by fire. Surface insolation, soil moisture and heat flux, wind and water erosion are greatly modified after fire (Whelan 1995; Auld & Bradstock 1996) and are all influenced by the amount of litter cover. Most studies of litter dynamics relate to fire susceptibility, primary productivity and ecosystem health for forest management (e.g., Conroy 1993, Duchesne & Wetzel 1999). These studies often use traps suspended above the ground to estimate litter fall rates or combine litter with other components of fuel such as live plant tissues. They often do not sample the unconsumed litter after fire (but see McCaw *et al.* 1997; O'Connell & McCaw 1997), or account for the lateral movement of litter across the landscape. Similarly, although there has been much study of invertebrate populations after fire, few carefully characterise the litter, the primary habitat of their target biota. A few studies sample in a manner that allows the assessment of the amount and composition of standing litter in relation to time since fire (Fox *et al.* 1979; O'Connell *et al.* 1979, Raison *et al.* 1983; Lamb 1985; Raison *et al.* 1986b; Birk & Bridges 1989; Conroy 1993, York 1999), although spatial variation and early post-fire measurements are not well sampled.

For plants that recruit after fire, the amount of litter that their germinating seeds encounter depends on when these seeds arrive in the environment. For soil seed bank species, this encounter depends only on how fire-related factors or post-fire environmental conditions affect dormancy mechanisms, as the seeds are present in the soil prior to the fire. Most species that have soil seed banks recruit within a year of fire (e.g., Horton & Kraebel 1955; Purdie 1977; Keeley & Keeley 1981; Auld & Tozer 1995; Odion & Tyler 2002), although there are exceptions (e.g., Roy & Sonie 1992; Ooi *et al.* 2004a). Species that have canopy seed banks vary in the timing of seed release, but this is generally within a year of the fire (Gill 1976; Bradstock & Myerscough 1981; Lamont & Barker 1988; Enright & Lamont 1989a; Lamont *et al.* 1991), with recruitment occurring shortly after suitable rainfall events (Bradstock & O'Connell

1988; Benwell 1998). Hence, species with soil seed banks and also those with canopy seed banks would usually encounter litter levels characteristic of recently burnt sites. Although they generally have no persistent seed bank, many geophytic species also recruit soon after fire, with seedlings often seen 12-18 months after fire (Le Maitre & Brown 1992; Tyler & Borchert 2002; Borchert 2004). These pyrogenic flowering species resprout, grow rapidly and flower soon after fire, often becoming inconspicuous after only one or two years (Stone 1951; Keeley *et al.* 1981; Tyler & Borchert 2002). The seeds of some shrubby pyrogenic flowering species are released into the habitat later still, that is, 12 – 24 months after fire (Malanson & O’Leary 1982; Keeley & Keeley 1984; Auld 1986a; Bradstock 1995; Benwell 1998; Curtis 1998; Taylor *et al.* 1998; Denham & Whelan 2000; Denham & Auld 2002; Bowen & Pate 2004), with germination dependent on rainfall events. Differences in the litter between early and late post-fire habitats may influence the recruitment probabilities for species in these groups directly by affecting their germination and survival or indirectly by influencing their probability of being consumed by seed predators or herbivores.

The aim of this study was to characterise the litter in the post-fire environment, comparing the amount and composition of litter in early post-fire and late post-fire sites. The results of this assessment are then discussed in the context of the timing of seed arrival and germination, with different implications for plants that recruit soon after fire (soil and canopy seed bank species) to those that recruit later (pyrogenic flowering species).

2.3 Methods

I located two sites that were early post-fire (<1 year since fire – Sites 1 and 2) and two that were late post-fire (≥2 years since fire – Sites 3 and 4). Sites were located within 11 km between Colo Vale and Bargo in the southern tablelands of NSW (Approx. 150°30'E; 34°23'). The vegetation at sites varied from dry sclerophyll forest to woodland, but had many plant species in common including *Banksia serrata*, *B. spinulosa*, *Bossiaea obcordata*, *Corymbia gummifera*, *Cyathochaeta diandra*, *Entolasia stricta*, *Lomandra filiformis*, *L. obliqua*, *Lomatia silaifolia*, *Patersonia glabrata*, *Persoonia levis*, *Pimelea linifolia*, *Platysace linearifolia* and *Telopea speciosissima*. At each site, I set up a 30 x 30 m (900 m²) plot and marked 20 locations using randomly

generated grid references. At each of these locations, I placed a plastic cylinder (0.06 m^2 , 5cm tall) and harvested all litter from within it, cutting through leaves and sticks that were partially outside it. Harvesting took place over 3 days approximately 3 months after the fires at Sites 1 and 2, and 2 years (Site 3) or 3 years (Site 4) after fires at Sites 3 and 4.

I separated litter into two components - post-fire litter, which was predominantly sticks and leaves, and pre-fire litter, which was mostly charcoal particles, both fine and coarse, but included small pieces of unburnt leaves. This latter component of the litter is hereafter referred to as 'charcoal'. The litter was weighed after oven-drying at 80°C for 5 days.

Litter mass in kg/m^2 was plotted using frequency distributions to assess normality. Skewness (a measure of the symmetry of the distribution about its mean) and kurtosis (a measure of the length of the tail of the distribution) were estimated and considered significant where the ratio of the measure to its standard error was greater than two (Wilkinson & Engelman 2005). Cochran's test was used to assess heteroscedasticity. Coefficient of variation (CV) was calculated for each site to allow among-site comparisons of the degree of within-site variation. I tested the effects of site and time since fire on the amount of charcoal and post-fire litter using 2-factor ANOVAs with sites nested in time-since-fire category (early vs. late), following square root transformation.

2.4 Results

2.4.1 Charcoal

The mass of charcoal in the litter layer was highly variable, with individual samples ranging from a minimum of 0.028 kg/m^2 at Site 2 to 0.783 kg/m^2 at Site 1. There was more charcoal at the early post-fire sites than at the late post-fire sites. Variation was high within sites with CV ranging from 0.52 at Site 2 to 0.83 at Site 3 (Table 2.1). Most sites showed significant positive skewing (a long right tail to distributions) and kurtosis was significantly positive (longer tails than a normal distribution) at Sites 1 and 3 (Fig. 2.1). Square root transformation generally improved skewing and kurtosis, and although skewing remained significant at Site 4, variances were relatively homogeneous (Cochran's Test not significant at $\alpha = 0.05$). Analysis of Variance on the transformed

data was significant (Table 2.2) with late post-fire sites (0.17 kg/m^2 , SE 0.02) having significantly less charcoal than the early post-fire sites (0.30 kg/m^2 , SE 0.03, Fig. 2.2).

Table 2.1. Coefficient of variation (CV) for the amount of litter at each site, expressed as individual components and as the total litter.

Site	Charcoal	Post-fire litter	Total
Site 1	0.70	0.68	0.48
Site 2	0.52	1.1	0.65
Site 3	0.83	0.37	0.45
Site 4	0.72	0.41	0.37

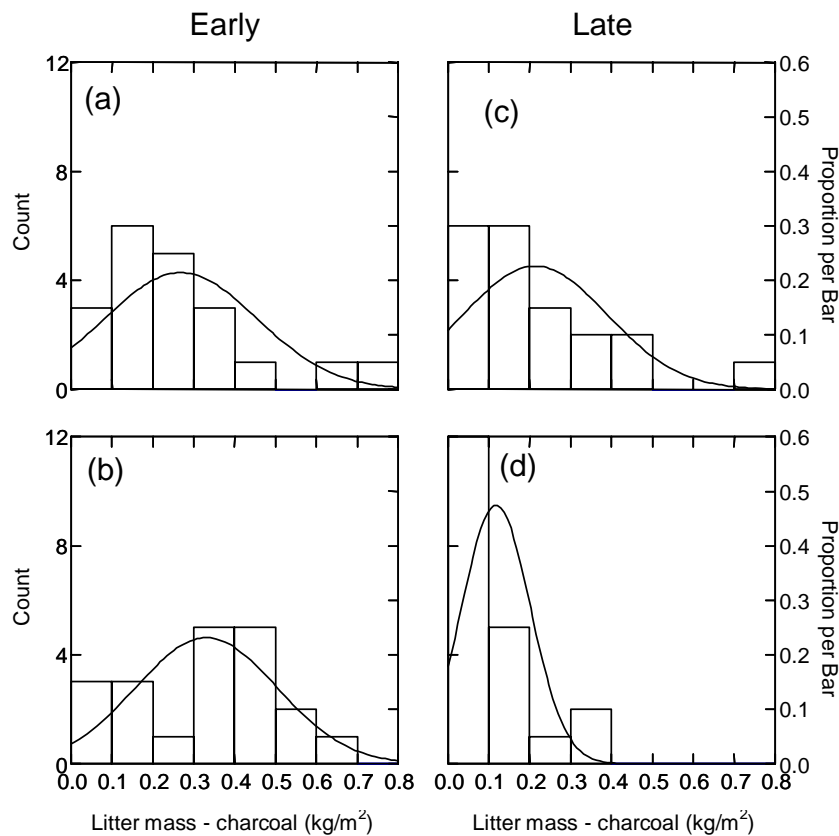


Figure 2.1. Frequency histograms for the charcoal component of the litter: early post fire sites - (a) Site 1, (b) Site 2; late post-fire sites - (c) Site 3, (d) Site 4. The line shows a normal curve with identical mean and variance to the data.

Table 2.2. Results of the two ANOVAs for the charcoal and post-fire (sticks and leaves) components of the litter.

Source ¹	Sum-of-Squares		df	Mean-Square		F-ratio	P		
	Char-coal	Post-fire		Char-coal	Post-fire		Char-coal	Post-fire	
TSF	0.410	2.323	1	0.410	2.323	16.41	81.74	<0.001	<0.001
Site(TSF)	0.140	0.144	2	0.070	0.072	2.811	2.526	0.066	0.087
Error	1.898	2.160	76	0.025	0.028				

¹ TSF = Time-Since-Fire

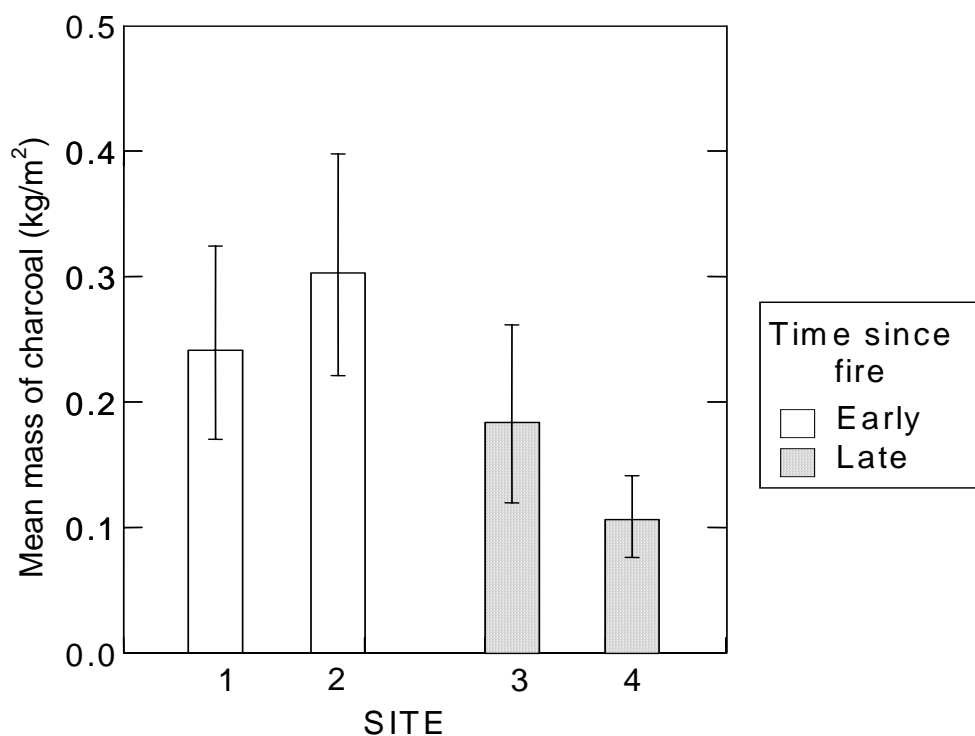


Figure 2.2. Back transformed means (kg/m^2) and 95% confidence intervals for the mass of the charcoal component of the litter at each site. Time-since-fire categories were significantly different ($P < 0.001$).

2.4.2 Post-fire litter

The post-fire litter was also highly variable, with individual samples ranging from 0.005 kg/m^2 at Site 2 to 1.38 kg/m^2 at Site 4. There was considerably more post-fire litter at

late post-fire sites than at early ones. Early post-fire sites were more variable with CV of 0.68 and 1.1 compared with 0.37 and 0.41 at the late post-fire sites (Table 2.1). All sites except Site 3 showed significantly positive skewing and kurtosis indicating departures from normality (Fig. 2.3). Square root transformation provided a partial solution, although after this transformation the data remained heteroscedastic, so I was conservative in using ANOVA with significance reduced to 0.01. Nevertheless the difference between time-since-fire categories was highly significant (Table 2.2) with early post-fire sites having much less post-fire litter (0.22 kg/m^2 , SE 0.03) than late post-fire sites (0.61 kg/m^2 , SE 0.04, Fig. 2.4). Excluding one sample with an exceptionally large value at Site 2, allowed this site to be distinguished from all others as having the least post-fire litter.

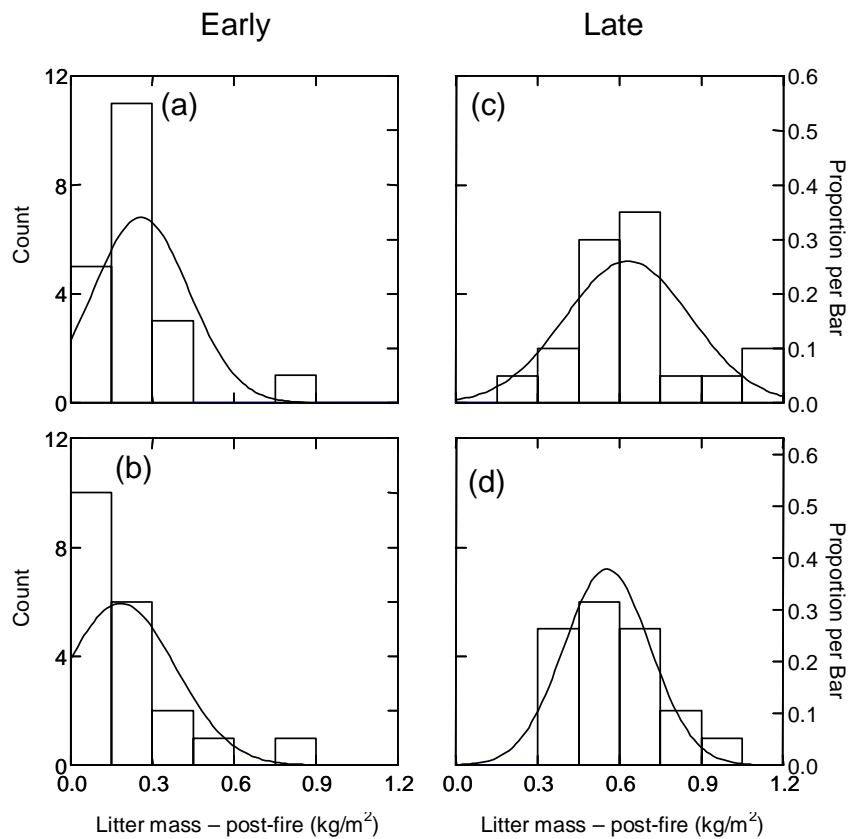


Figure 2.3. Frequency histograms of the post-fire (stick and leaves) component of the litter: early post-fire sites - (a) Site 1, (b) Site 2; late post-fire sites - (c) Site 3, (d) Site 4. The line shows a normal curve with identical mean and variance to the data.

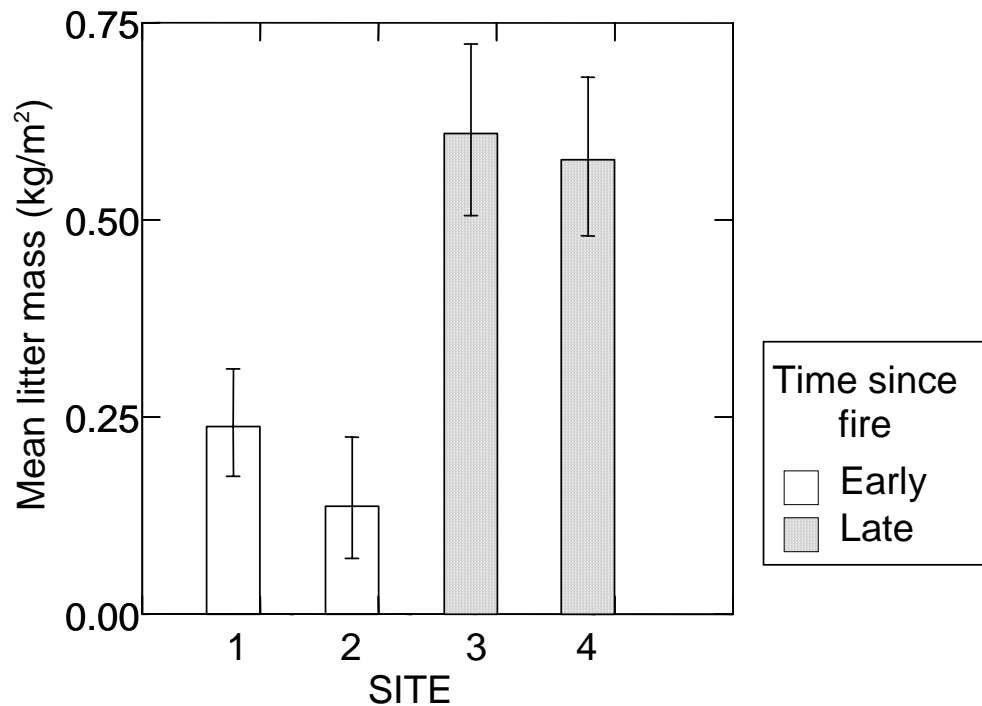


Figure 2.4. Mean mass of the post-fire (sticks and leaves) component of the litter at each site (back transformed data with 95% confidence intervals). Time-since-fire categories were significantly different ($P < 0.001$).

2.5 Discussion

As expected, the quantity and quality of litter varied between time-since-fire categories but it also varies substantially among sites within a particular time since fire. The high degree of variability of the new post-fire litter at early post-fire sites probably results from movement of litter into patches by wind and water (Fig. 2.5a) as observed by Lamont *et al.* (1993) and Howell *et al.* (2006). In later post-fire sites, more obstructions in the form of new or resprouting plants would, after further contributions of litter, reduce this patchiness (Fig. 2.5b). Nevertheless, the range in CV across all sites for both litter components pooled (0.37-0.65) was already less than that recorded for sites 10 years post-fire (0.47-0.68), although those measurements included attached plant tissues (Whelan & York 1998). The charcoal (pre-fire) litter component may be less mobile than the post-fire litter, resulting in values of CV that reflect patchiness in fire intensity or pre-fire fuel availability rather than post-fire movement of particles.

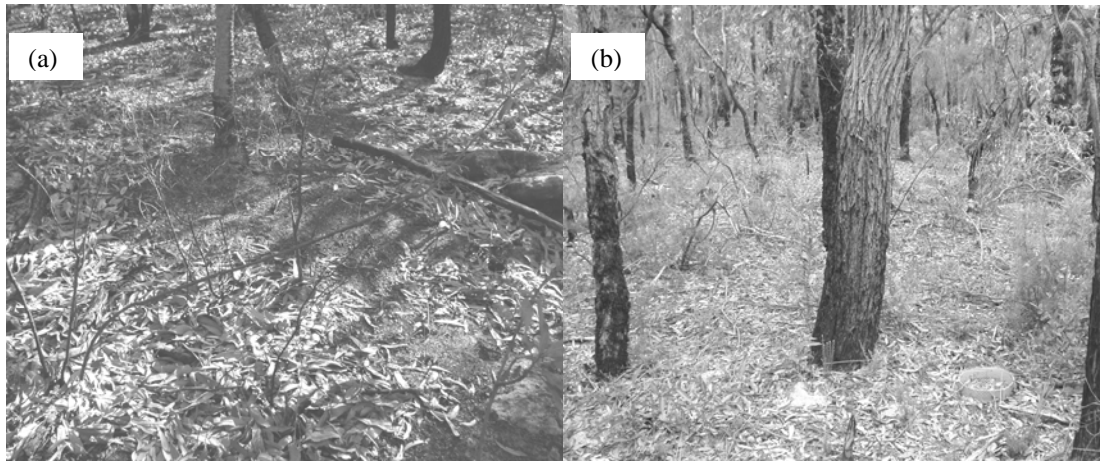


Figure 2.5. (a) Site 2, approximately three months after fire, showing the accumulation of recently fallen scorched leaves into dense litter patches interspersed with areas of relatively bare ground. (b) Site 3, approximately 2.5 years after fire, showing a large amount of relatively evenly distributed litter.

The primary difference between the two time-since-fire categories is that early post-fire sites had less litter overall, but a greater *amount and* proportion of charcoal (Fig. 2.6) than late post-fire sites. This could be explained by consumption and scorching of existing litter during the fire and the fall of scorched leaves from the canopy soon after. Over time, decomposition occurs and incorporation of charcoal components into the humus layer of the soil reduces the contribution of this component (Raison *et al.* 1983). Following the initial fall of scorched leaves from the canopy, more or less continuous leaf fall occurs. Variation among sites is likely to be due to a number of factors, including vegetation differences, microtopographic effects (such as the predominance of rock outcrops or variation in slope), differences in the most recent fire, or differences in fire history. My observations suggest that the fire at Site 2 was relatively intense, causing considerable canopy leaf scorch, while no canopy leaf scorch was apparent at Site 1. It is more difficult to infer fire intensities from the late post-fire sites, but survival of the stems of some individuals of lignotuberous species (*Petrophile pedunculata*) and fire sensitive species (*Hakea sericea*) at Site 3 suggest this fire was of low intensity. This was not the case at Site 4 where all stems of lignotuberous species and all fire sensitive species were killed by the fire.

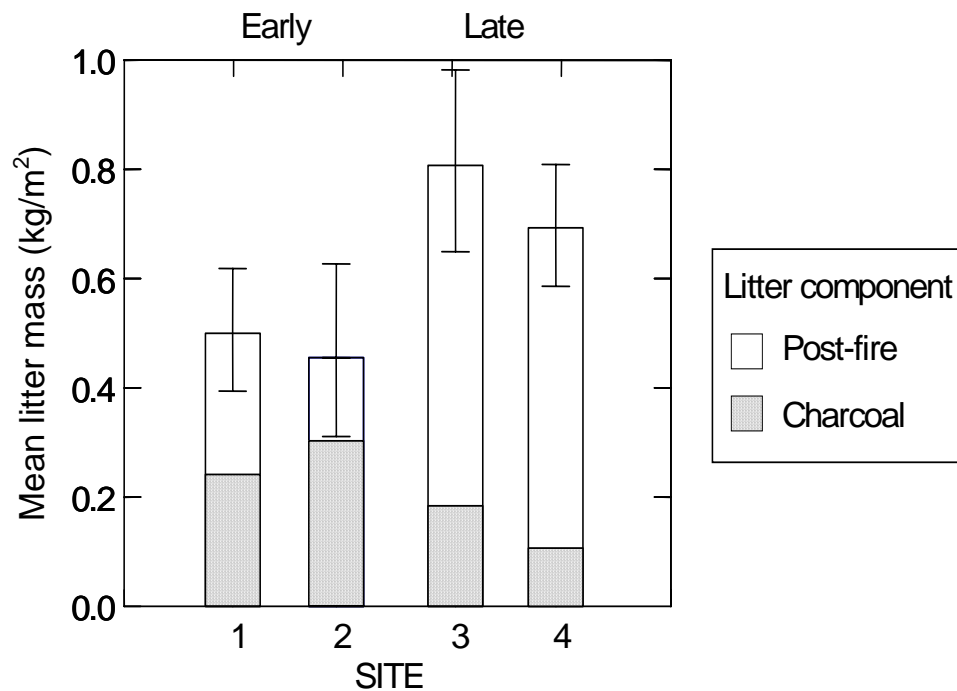


Figure 2.6. Mass of total litter at different sites. Data are back-transformed means with 95% confidence intervals. Hatching illustrates the charcoal component of the litter; the open section illustrates the post-fire component (sticks and leaves).

In comparison with other studies in similar vegetation, the amount of litter at early post-fire sites (0.52 kg/m^2) was close to that observed by Conroy (1993) (0.57 kg/m^2) but somewhat less than that observed by Hamilton *et al.* (1991). Birk & Bridges (1989) observed an increase in early post-fire litter from 0.05 kg/m^2 to 0.34 kg/m^2 in the first month, due to the fall of scorched leaves with a subsequent decline to 0.17 kg/m^2 after 12 months. Early post-fire results reported here include the contribution of scorched leaves, but a subsequent decline in litter mass does not appear to have occurred (pers obs.). The amount of litter found here for late post-fire sites (0.78 kg/m^2) fits well with values from Fox *et al.* (1979), but is slightly higher than that reported by Conroy (1993). However, the time-since-fire categories employed by Conroy (1993) overlap at three years, with a rapid increase in litter mass between 1-3 years (0.64 kg/m^2) and 3-6 years (1.14 kg/m^2) since fire, suggesting that data presented here are likely to fit between these two categories.

Seeds of canopy seed bank species are likely to arrive into a habitat that has a relatively small amount of litter overall and some areas with little or no litter. If the release of seeds occurs before or soon after the fall of scorched leaves from the canopy, these seeds are likely to be moved along the surface by wind and water (Hamill *et al.* 1998), possibly into dense litter drifts or litter dams (Lamont *et al.* 1993; Howell *et al.* 2006). If release occurs some time after the fall of scorched leaves, the seeds may remain where they fall, resulting in a random fall of seeds into a patchy litter environment. In these scenarios, seeds are exposed to a variety of conditions and conflicting selective pressures may prevent the development of specialisation in seed characteristics. Similarly, seeds from soil seed bank species will encounter varying litter upon emergence in the first post-fire year. In contrast, seeds of shrubby pyrogenic flowering species arrive into an environment that has a generally higher litter mass than the early post-fire environment with consequently fewer areas with little or no litter. The seeds of these species may thus be subject to relatively different levels of seed predation and greater levels of shading and moisture.

These selective pressures may have led to more specialised seed characteristics. For example, it is generally accepted that greater light tolerance and ability to emerge from under litter is found in species with large seed mass (e.g., Seiwa & Kikuzawa 1996; Moles & Westoby 2004). A selection of woody species in fire-prone areas in the Sydney Basin from Westoby *et al.* (1990) shows a high degree of variation in seed mass for soil and canopy seed bank species encompassing very small to very large seeds (Fig. 2.7). In contrast, the pyrogenic flowering species show limited variation, with minimum seed mass much greater than for the other groups (Fig. 2.7). If *Macrozamia communis* (a species with seed mass at least one order of magnitude greater than all other species in the figure) is excluded, these species exhibit relatively little variation in seed mass, providing support for the notion that selective pressures may have led to this seed size characteristic. Further exploration of potential seed characteristics or selective forces should be made through experimental manipulations of predator access, litter amount and timing of seed release with time-since-fire among species with different modes of post-fire regeneration.

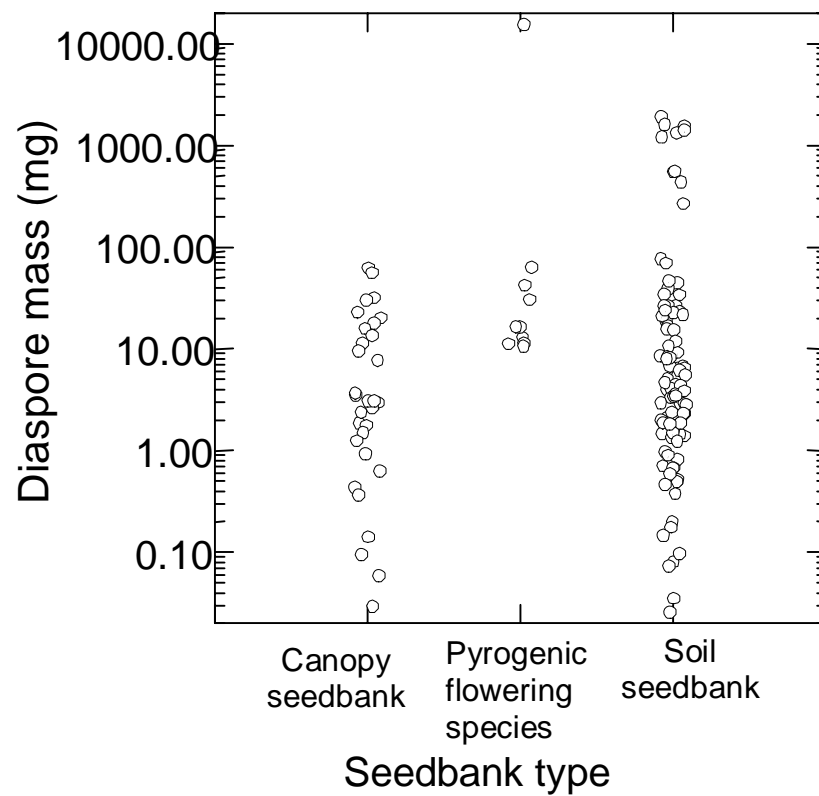


Figure 2.7. Variation in diaspore mass among a selection of woody species from fire-prone areas in relation to seed bank type. Data are jittered for clarity; y-axis is on a log scale. Numbers of species are canopy seed bank, 31 spp; pyrogenic flowering species, 10 spp; soil seed bank, 95 spp. Data are from Westoby et al. (1990).

Chapter 3 - The importance of escape from seed predation to post-fire recruitment in the waratah (*Telopea speciosissima* R. Br.)



Ants eating a seed of *Telopea speciosissima*.

3.1 Abstract

Recruitment after fire may be delayed if species lack a soil- or canopy-stored seed bank and must resprout, flower and mature fruit before seeds are available for germination. In pyrogenic flowering species, non-dormant seeds may be released more than one year after fire, with an additional release in one or more subsequent years. The fate of these seeds depends on whether or not they are discovered by predators prior to germination. In this relatively late post-fire environment, seed predation and habitat characteristics may differ from those experienced by the majority of early post-fire recruiting species. To assess the role of these factors in limiting seedling establishment after fire in *T. speciosissima*, I used a seed-planting experiment, manipulating vertebrate access to

seeds and the combined cover of litter and vegetation within microsites. I replicated the experiment in the two years of natural seed fall after a fire in southeastern Australia. Losses to vertebrate and invertebrate seed predators were rapid and substantial. No seedlings were observed until after two months, by which time 50% of seeds in exposed locations had been consumed. When vertebrates were excluded, 50% of seeds were consumed after five months. After seven months, only 6% of genets (seeds or seedlings) remained alive, even where vertebrates were excluded. Removing litter and vegetation increased the probability that seeds would be eaten by vertebrate predators in the first year of the experiment, but not in the following year, and had little influence on losses due to invertebrates in either year. Seven months after seed placement, microsites with dense vegetation and litter cover were twice as likely to have surviving seeds or seedlings as those with less dense cover. Levels of seed predation observed in this experiment were similar to those found in long unburnt vegetation. In conclusion, *T. speciosissima* appears to rely on the coincidence of favourable climatic conditions and reduced predation soon after seed release to allow recruitment of seedlings. The ability of some juvenile and most adult plants to resprout following fire buffers populations against rapid declines in the absence of these conditions after any one fire.

3.2 Introduction

For most plant species in fire-prone environments, most recruitment of seedlings occurs within the first one to two years after the passage of a fire (Horton & Kraebel 1955; Keeley & Keeley 1981; Lamont *et al.* 1991; Auld & Tozer 1995; Keeley *et al.* 2006). Several direct benefits to plants in early germination after fire have been identified, largely to do with the availability of light, space and nutrients as a result of the consumption of live plant tissues and litter (Christensen & Muller 1975a; Wellington & Noble 1985b; Zammit & Westoby 1988; Keith 1996; Purdy *et al.* 2002). However, the ultimate benefits relate to the ability of new seedlings to reach a stage by which they can contribute to the population after a subsequent fire. For fire-sensitive species, this means that new seedlings must survive, mature and form a seed bank, while seedlings of resprouting species must reach a fire-resistant size. Early germination will increase

the probability that recruits will meet these requirements, even in the absence of other benefits for seedling growth in the immediate post-fire environment.

There may be costs associated with early germination and recruitment. Such costs include a harsher physical environment with increased insolation (Certini 2005; Urretavizcaya *et al.* 2006), soil moisture flux (Neary *et al.* 1999) and exposure to grazing or predation (Andersen 1988; Reed *et al.* 2004, 2005). Many of these characteristics of the post-fire environment are ameliorated by the formation of a litter layer, which may be established within months of the fire, and is generally substantial after the second year (O'Connell *et al.* 1979; Raison *et al.* 1986b; Chapter 2).

For a few species with fire-related recruitment, this recruitment is delayed for up to three years after fire. Some of these species have soil seed banks with complex dormancy that cause delays in germination depending on the season of the fire (Ooi *et al.* 2004a), although such delays should not exceed one year. Others 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 & Ingwersen 1976; Auld 1986a; Denham & Whelan 2000; Denham & Auld 2002), *Brodiaea*, *Marah*, *Sabal*, *Serenoa* and *Zigadenus* in the USA (Stone 1951; Parker & Kelly 1989; Keeley 1991; Abrahamson 1999; Tyler & Borchert 2002; Borchert 2004), and *Cyrtanthus*, *Watsonia* and other geophytes in South Africa (Le Maitre & Brown 1992; Keeley 1993; Bond & van Wilgen 1996). Due to the absence of a persistent seed bank, recruitment in these species is likely to be greatly affected by post-dispersal seed predation.

Determining how pyrogenic flowering species differ from the majority of earlier recruiting species is an area that deserves attention because so few studies have examined their population dynamics (Auld 1986a; Bradstock 1995; Denham & Auld 2002; Borchert 2004, 2006). Given that there appear to be strong selective pressures for early recruitment, it is pertinent to ask what features of the environment, or of the species themselves, allows their persistence? In this study, I followed the fate of seeds of *Telopea speciosissima* (Sm.) R. Br., an eastern Australian pyrogenic flowering species, over two years in a manipulative seed planting experiment. Using exclosures to

manipulate the access of vertebrate predators to seeds, I assessed the relative impact of vertebrate and invertebrate predators on the size of the potential pool of post-fire recruits. I also examined the importance of litter and vegetation cover to seedling establishment by modifying its combined density within experimental microsites. Studies in other habitats have demonstrated that the ability of seed predators to locate seeds is affected by the level 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 me to assess how cover influences the abilities of predators to find seeds in Australian fire-prone habitats.

3.3 Methods

3.3.1 Species

The NSW waratah, *Telopea 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 (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 & Auld 2002). Fruits mature and dehisce in autumn, with seed release occurring through late autumn and winter. 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, most seeds were released 3 and 4 years after fire. These were the only years in which substantial fruiting occurred at these sites (author's unpubl. data).

3.3.2 Sites

Three sites were selected within a 10 km radius in Royal National Park, approximately 35 km south of Sydney (34°03' 151°03'). All sites were on soils derived from the Triassic Hawkesbury Sandstone Formation, although Sites 1 and 2 (with an ironstone

influence) had soils that were slightly more fertile than those at Site 3. Site 1 was in Ironstone Woodland vegetation (Keith & Tozer unpubl.) with an overstorey of *Eucalyptus sieberi*, *Corymbia gummifera*, *Banksia serrata*, *Xylomelum pyriforme* and *Ceratopetalum gummiferum*. The shrubby understorey included *Grevillea diffusa*, *Banksia spinulosa*, *Lissanthe strigosa*, *Prostanthera* sp., *Isopogon anemonifolius*, *Acacia myrtifolia*, *Xanthorrhoea media*, *Lomandra* spp. and *Dianella* sp. Site 2, also in Ironstone Woodland vegetation, was located approximately 0.5 km S of Site 1, and was floristically similar, with an overstorey of *Eucalyptus sieberi*, *E. sclerophylla*, *Corymbia gummifera* and *Banksia serrata*. The shrubby understorey included *Telopea speciosissima*, *Banksia spinulosa*, *Hakea gibbosa*, *H. laevipes*, *H. propinqua*, *H. sericea*, *Grevillea oleoides*, *G. sphacelata*, *Lissanthe strigosa*, *Monotoca scoparia*, *Leptospermum juniperinum*, *L. trinervium*, *Isopogon anemonifolius*, *Acacia myrtifolia*, *Xylomelum pyriforme*, *Persoonia levis*, *Gompholobium grandiflorum*, *Phyllota phyllicoides*, *Pultenaea elliptica*, *Daviesia corymbosa*, *Pimelea linifolia*, *Platysace linearifolia*. Herbaceous species included *Xanthorrhoea media*, *Lomandra* spp., *Patersonia glabrata*, *P. sericea*, *Micrantheum ericoides*, *Phyllanthus hirtellus*, *Dampiera stricta*, *Stylidium lineare*, *Entolasia stricta*, *Stipa pubescens*, *Schoenus ericetorum*, *Lepyrodia scariosa*, *Leptocarpus tenax*, and *Cyathochaeta diandra*. Site 3, approximately 9 km S of Site 1, was in Sandstone Heath vegetation (Keith & Tozer unpubl.) with a short overstorey of *Corymbia gummifera*, *Eucalyptus obstans*, *E. sclerophylla* and *Banksia serrata* and a shrubby understorey that included *Lambertia formosa*, *Lissanthe strigosa* and sedges such as *Xanthorrhoea media*, *Restio dimorpha* and *Cyathochaeta diandra*. Plant nomenclature follows Harden (1990-1993, 2002). Sites were located where seed-bearing individuals of *Telopea speciosissima* occurred and all sites had identical recent fire histories (all burnt in 1994 and 2001).

3.3.3 Methods

A 30 by 30 m plot (900 m²) was marked out within each site. Seeds were collected in the years of the experiment (2004 and 2005) from plants fruiting within 200 m of the plot, but not from inside the plot. Seeds from each fruit were visually assessed for 'plumpness'. I assumed that 'unfilled' seeds were inviable and these were discarded,

while the remainder were pooled within sites. Random grid locations within plots (with x and y coordinates ranging from 1 to 29 m), were found and subjectively classified according to the characteristics of litter and vegetation cover within the microsite (microhabitat classification, Table 3.1). These locations 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 locations that corresponded to these classes were passed over until all microhabitat classes had 16 locations per site. Each microsite was randomly assigned to one of two vertebrate exclusion (caged, no cage) and clipping treatments (clipped, not clipped), resulting in a total of 48 microsites per site, each in one of 12 treatment combinations (Fig. 3.1). At each location, a short plastic cylinder, approximately 35 cm in diameter and 7 cm in height was bedded into the soil to 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 clipping 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 (Fig. 3.2). Collected litter was weighed after being oven-dried at 80° C for 24 hours. For the exclusion treatment, wire mesh with a 1 cm grid was fastened onto the top of the plastic cylinder to exclude vertebrate seed predators from the experimental microsite. It was considered impractical to attempt to exclude invertebrate predators. Once treatments had been applied, ten seeds (five in the exclusion treatment in 2004) were scattered into the experimental microsite. Loss of most seeds in some experimental microsites in 2004 prompted further seed additions to some plots up to a maximum of 20 per microsite. Seeds were placed in July and August of 2004 (1290 in total) and in July of 2005 (1450 in total), within the time span of natural seed fall.

The survival of seeds and seedlings was monitored until April 2005 for 2004 planting, and until June 2006 for 2005 planting. Initial monitoring was twice weekly, tapering to every three weeks after five months. I observed the timing of germination (emergence of a radical) and seedling emergence (indicated by a raised hypocotyl and green cotyledons), and collected the remains of eaten seeds or shed seed coats when they were visible. At the termination of the experiment, I sieved the litter to locate any surviving ungerminated seeds or remaining seed coats. Remaining intact seeds were

placed on moist filter paper in petri dishes, with germination used as an indication of viability.

Table 3.1. Classification of microhabitat based on visual assessment of the cover of litter and vegetation.

Microhabitat class	Relative litter cover	Relative vegetation cover
low	low	low
low	low	medium
low	medium	low
medium	low	high
medium	medium	medium
medium	high	low
high	medium	high
high	high	medium
high	high	high

3.3.4 Analysis

To quantify the litter component of the microhabitat classification, I used ANOVA to compare the oven dry mass of collected litter across microhabitat classes and sites from 2004 data. These data were square root transformed to improve heteroscedasticity. I analysed the survival of seeds across levels in the experiment for the first five months in each year of planting using repeated measures ANOVA. Factors included are those listed in Fig. 3.1, with major factors, two-way and three-way interactions included. In this analysis I was examining 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. This analysis allows comparison of the rate of loss of seeds over the test period. Using data from approximately seven months after the start of the experiment, I used ANOVAs to examine the proportion of seeds that had recruited and died or were still alive (as either

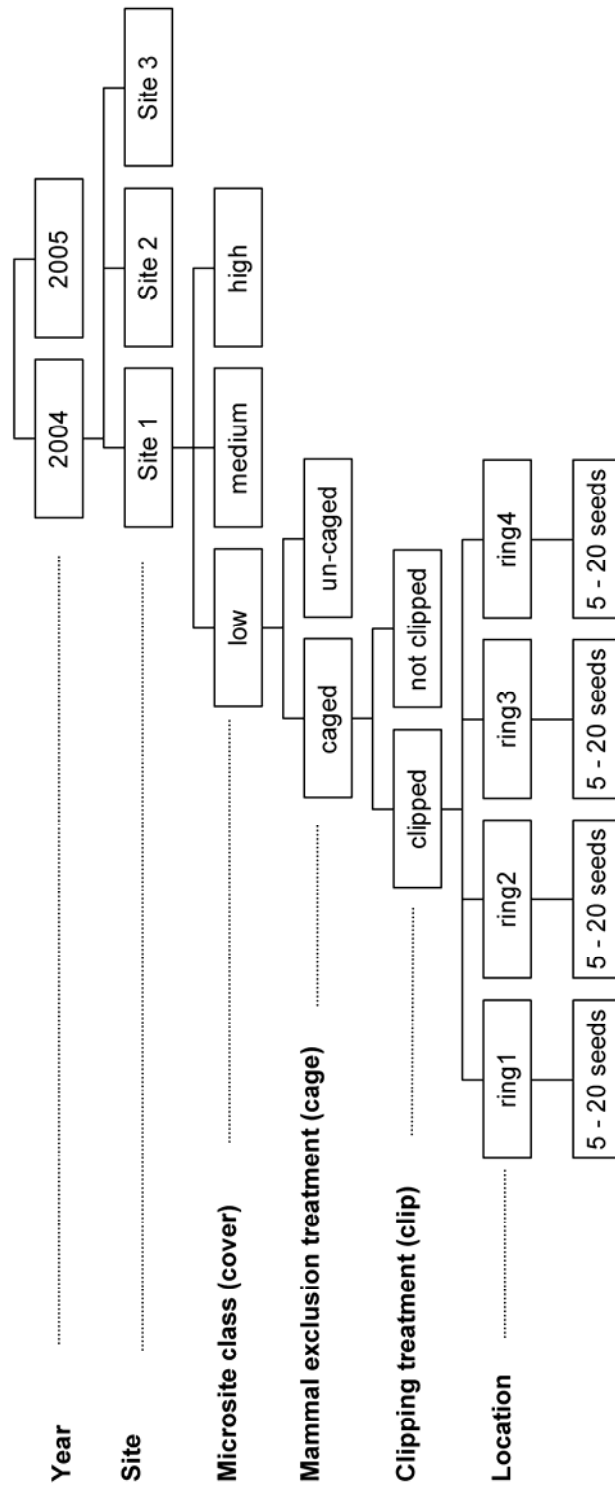


Figure 3.1. Schematic representation of experimental design. The diagram shows only one branch of the design for illustration.

seeds or seedlings), and the proportion of seeds or seedlings that were still alive. After sieving the litter at the end of the experiment I used ANOVA with the same design to analyse the proportion of seed remains found in each experimental microsite. This estimates the relative importance of vertebrate to invertebrate predation. In all cases, the data was non-normal and heteroscedastic, and was not greatly improved by transformation. As a result, I used conservative levels of probability ($\alpha=0.01$) to determine the significance of factors.

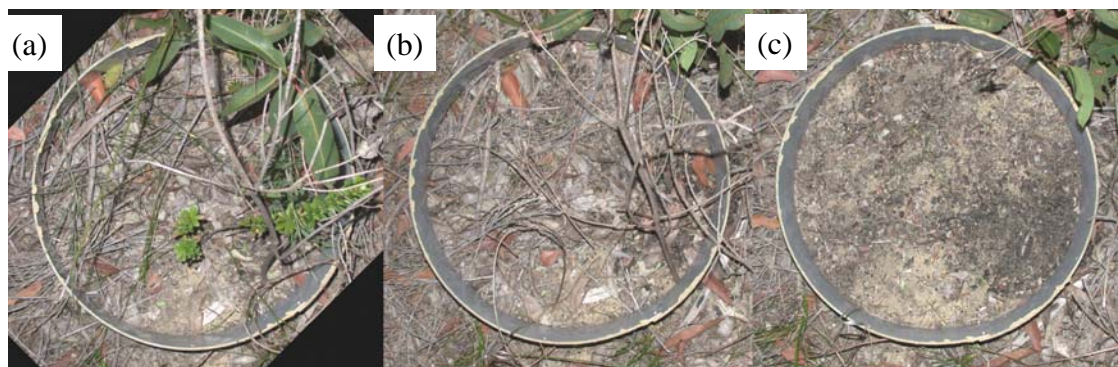


Figure 3.2. An example of a location with a microhabitat classification of medium. (a) Prior to clipping treatment, (b) after clipping, but prior to litter removal, (c) after litter removal.

3.4 Results

3.4.1 Litter and the classification of microhabitats

The mass of litter in each experimental microsite and its subjective microhabitat classification matched reasonably well. Microhabitat and site were significant factors, while the interaction term was not significant (Table 3.2). Post hoc tests indicated that the litter content of each microhabitat classification was distinct. However, there was significantly less litter overall at Site 3 than at Site 1, while Site 2 was intermediate and not significantly different from the other sites (Fig. 3.3).

Table 3.2. Analysis of Variance table for litter content in sites and microhabitat classes.

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Microhabitat class	1290.16	2	645.08	16.89	<0.001
Site	987.85	2	493.92	12.93	<0.001
Microhabitat class x Site	144.97	4	36.24	0.95	0.438
Error	4429.79	116	38.19		

3.4.2 Seed survival

Seed loss was substantial and rapid with most seeds removed from some experimental microsites within two weeks of placement. Many seeds disappeared from within uncaged microsites or were observed being eaten *in situ* by ants. Germination was first observed after four weeks, while seedlings were not established until after 8 weeks. By this time, approximately half of the seeds in uncaged microsites had been removed or eaten (Fig. 3.4).

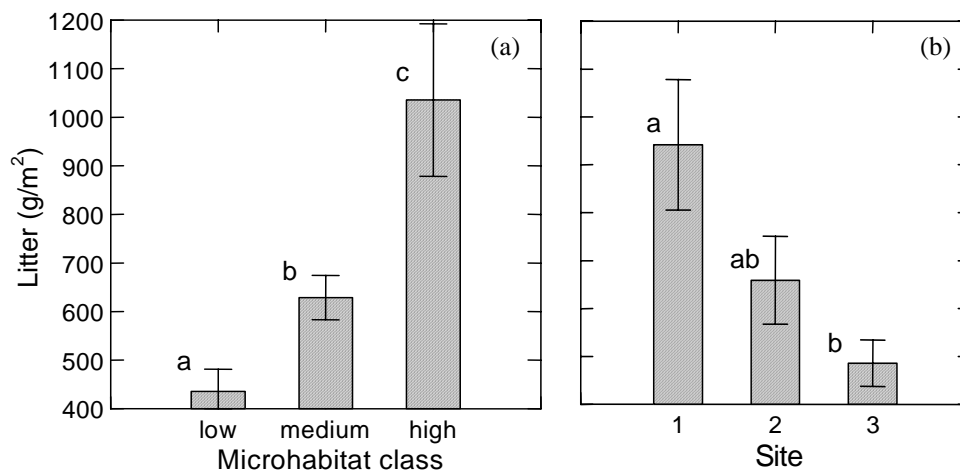


Figure 3.3. The mean amount of litter (± 1 standard error) harvested from experimental microsites in (a) different microhabitat classes and (b) at different sites (data in g/m²). Different letters represent significantly different means at $\alpha=0.01$.

For the proportion of genets (seeds or seedlings) remaining, the repeated measures ANOVA revealed strong site x cage, site x year and clip x cage interactions for between subject comparisons (Appendix 3.1). The site x 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. 3.4a). The clip x 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. 3.4b). The site x 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. 3.4c, d). These same factors were significant in within-subject comparisons, indicating that their effect on the *rate* of seed loss varied over time. In addition there was a significant clip x year interaction (Appendix 3.1). This indicates that the *rate* of seed loss in the different clipping treatments depended on the year of the experiment. This effect is most apparent between months 3 and 4 where losses from unclipped plots in 2005 exceeded losses from all other combinations (Fig. 3.4e).

Approximately seven 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%). Interestingly, a small number of seeds remained viable after several months of exposure (9 from 2004 and 1 from 2005). These readily germinated in laboratory conditions. The microhabitat classification, the level of caging and a site x year interaction (Fig. 3.5) significantly affected the proportion of seeds that had ever had the opportunity to become seedlings (Appendix 3.2). More seeds survived under high density cover than under low density cover (Fig. 3.5a) and more seeds survived under vertebrate exclusion (Fig. 3.5b). *Post hoc* tests were not able to detect individual mean differences in the site x year interaction at $\alpha=0.01$, although it is clear that the main driver of this interaction is the difference between years at the Sites 2 and 3 (Fig. 3.5c).

For the proportion of genets remaining alive at the conclusion of the experiment, only the level of caging and a clip x year interaction had a significant influence. Seeds in caged microsites had survival of approximately 6%, more than three times that of

uncaged microsites (Fig. 3.6a), while unclipped microsites in 2004 had more genets alive than clipped in 2004 or either treatment in 2005 (Fig. 3.6b, Appendix 3.3).

The final fate of seeds as estimated by their remains at the end of the experiment indicated that invertebrates were probably responsible for, on average, 21.7% of seed predation where there was no exclusion. Where vertebrate predators were excluded, this increased to 56.9%. Site, year, clipping and a number of interactions were significant in the ANOVA (Appendix 3.4). Clipping reduced the average proportion of seed remains collected from 44.8% to 33.9%. A strong site x 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 balanced at Site 3 than at the other two sites (Fig. 3.7a). Nevertheless, a greater proportion of eaten seeds was retrieved from caged rings. A year x cage interaction is the result of very few eaten seeds being retrieved from uncaged microsites in 2005 (Fig. 3.7b).

Again, the proportion of eaten seeds retrieved from caged microsites in both years was significantly greater than in uncaged microsites in either year. A site x year interaction reflects variation in both space and time, with Site 1 showing a similar response in both years while the other sites differed substantially (Fig. 3.7c).

3.5 Discussion

Loss of seeds of *Telopea 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 large numbers of seeds in the first two months. Some of the seeds removed from un-caged rings may have been moved by vertebrates, but not consumed. However, I consider this outcome to be unlikely since no previous studies have observed movement or caching of seeds by native vertebrate predators in Australia (e.g., Denham & Auld 2002, Auld & Denham 1999, 2001). Loss to invertebrates was slower, with most losses occurring between 3 and 4 months after seed placement. These rates of loss are comparable to those found both soon after fire and in long unburnt habitats, for species lacking an elaiosome on their seeds (Auld & Denham 1999, 2001).

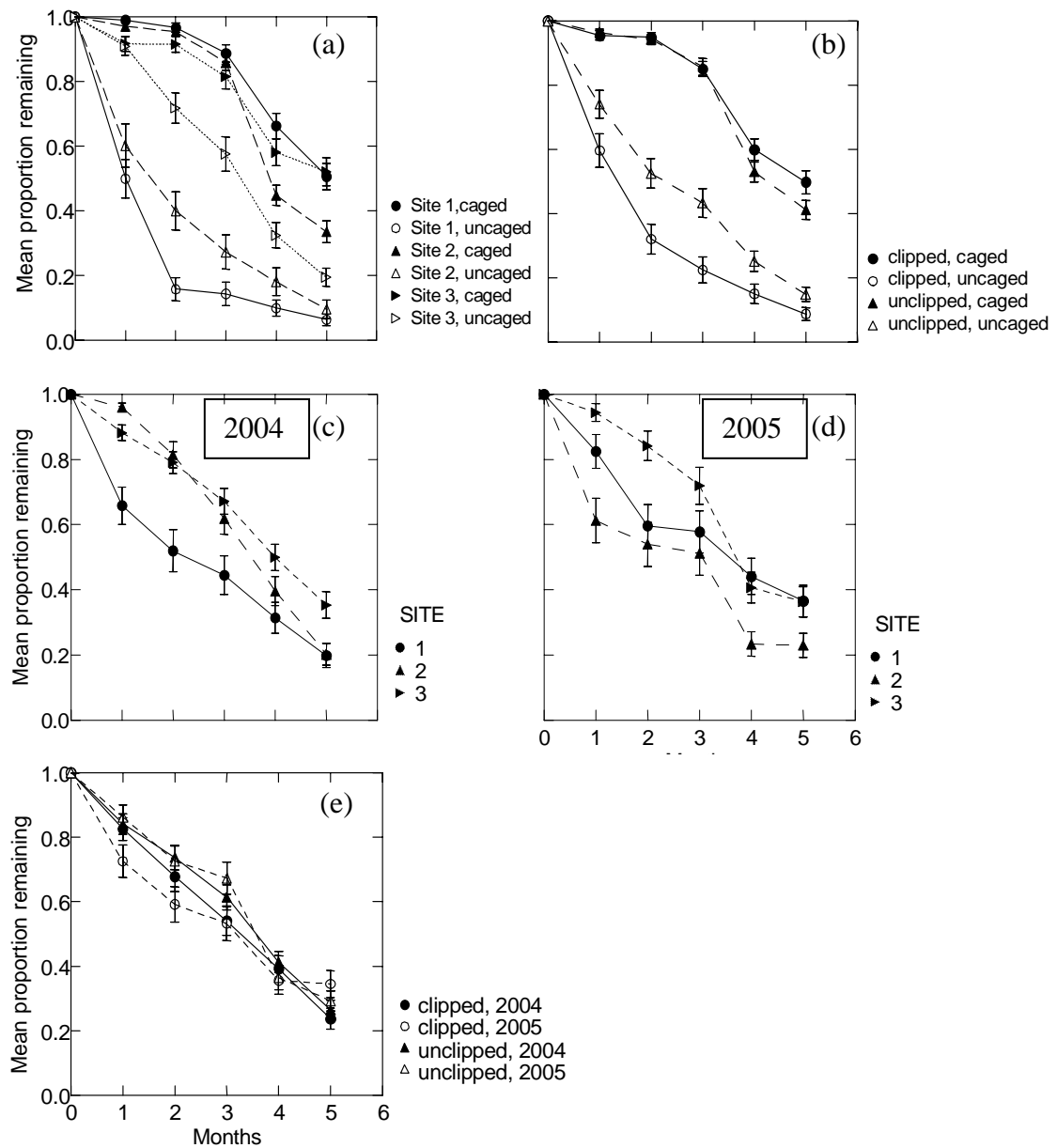


Figure 3.4. Survival of genets over the first five months of the experiment, showing the mean proportion of seeds surviving (± 1 standard error). The following *between subjects* factors were significant in the repeated measures ANOVA; site x cage (a), clip x cage (b) and site x year (c and d). These factors were also significant *within subjects* and the clip x year (e) factor was also significant. *Between subjects* factors affect the overall degree of seed loss, while *within subjects* factors affect the rate of seed loss.

Microsite modifications had a relatively small effect on the rate of loss of seeds compared to caging, with clipped locations losing seeds slightly more rapidly than unclipped locations. However, microsites in microhabitats with high levels of cover were approximately twice as likely to provide opportunities for recruitment as those with low cover. Ultimately, few seedlings or viable seeds persisted for seven months, with caged locations having three times as many genets remaining alive than uncaged locations.

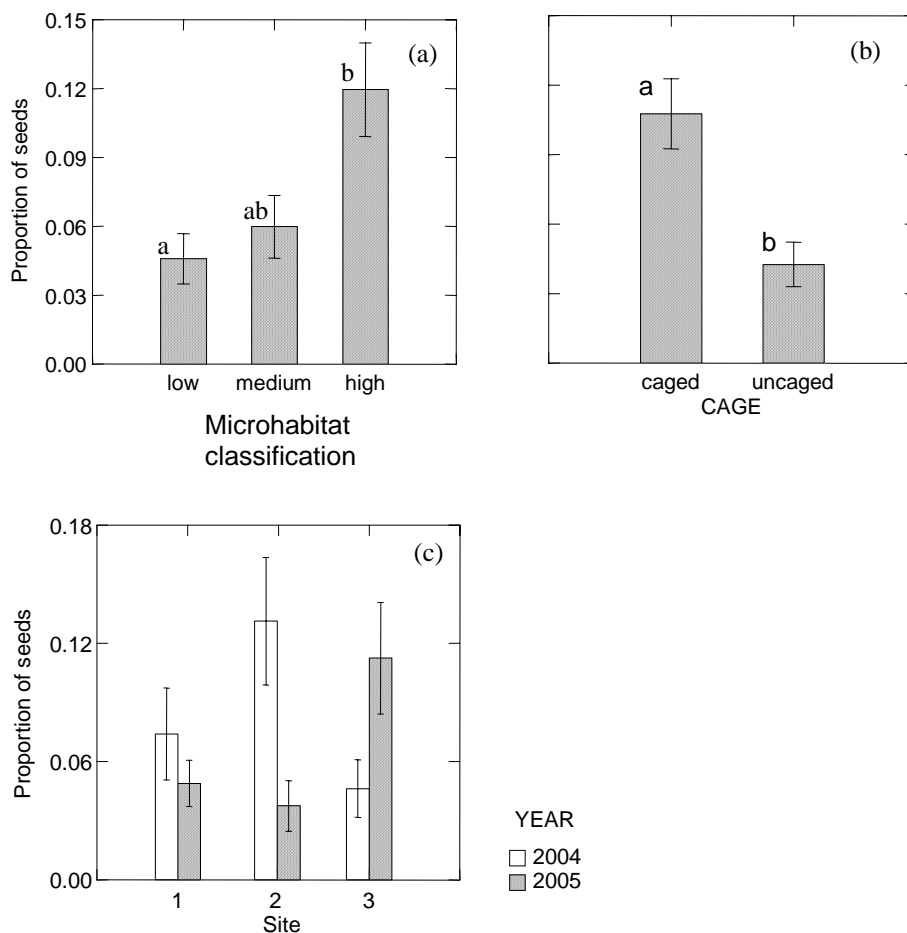


Figure 3.5. The proportion of seeds (± 1 standard error) that ever had the opportunity to become recruits as estimated at the end of the experiment (approximately 7 months after planting). (a) Microhabitat effects, (b) cage effects, and (c) site and year effects. Different letters indicate significantly different means at $\alpha=0.01$.

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 & Denham 1999; Denham & 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 seeds that germinated and died before becoming established as seedlings. I could not eliminate the possibility that other invertebrates, particularly nocturnal species, ate seeds. However, 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 & Noble 1985a; Andersen 1987; Yates *et al.* 1995).

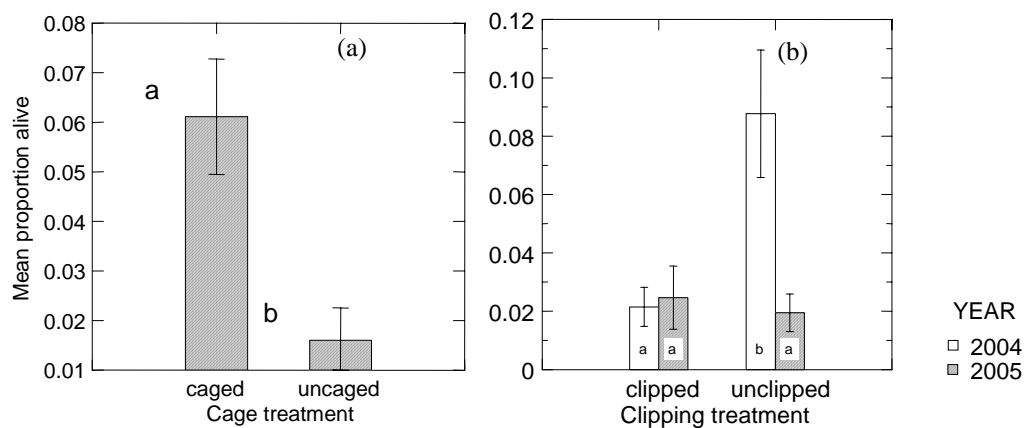


Figure 3.6. The proportion of genets (± 1 standard error) that remained alive at the end of the experiment under different treatments. Different letters indicate significantly different means at $\alpha=0.01$. (a) Effect of caging, (b) Effect of clipping and year. Note that graphs have different scales on their y-axis.

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 & Pickett 1993; Russell & Schupp 1998; Reed *et al.* 2006). Although vertebrate seed predators are also reported to avoid areas of low cover (Manson & 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. However, while most seeds that appeared to have been eaten by invertebrates would have been directly killed by them, some may have germinated and then died, with invertebrates scavenging on their remains.

Given 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 two years of substantial seed production after the 2001 fire (author's unpubl. data). Such escape through germination has been observed elsewhere (Curran & 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 the many species with canopy seed banks had finished two years before waratah seed release, and few other plant species release seeds in this late post-fire 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 & Gill 1984; Andersen & Yen 1985), although satiation of ants as predators, by mass seed release, has also been demonstrated (O'Dowd & Gill 1984; Andersen 1987, 1988). Andersen (1988) observed that high rates of seed removal by ants continued until at least two years after fire.

In comparison to an earlier study in this area (Denham & Auld 2002), recruitment after this (2001) fire is likely to be substantially lower than after the previous one (1994), due to greater overall levels of seed predation. Since Sites 1 and 3 in this study are identical to those of Denham & Auld (2002), a more detailed comparison is possible. In the current study, two months after placement, less than 20% of seeds that had vertebrate access survived at Site 1 compared to more than 60% at Site 3 (Fig. 3.4). At a similar time after placement, Denham & Auld (2002) found that about 80% survived at Site 1 compared to less than 40% at Site 3. This reversal in the

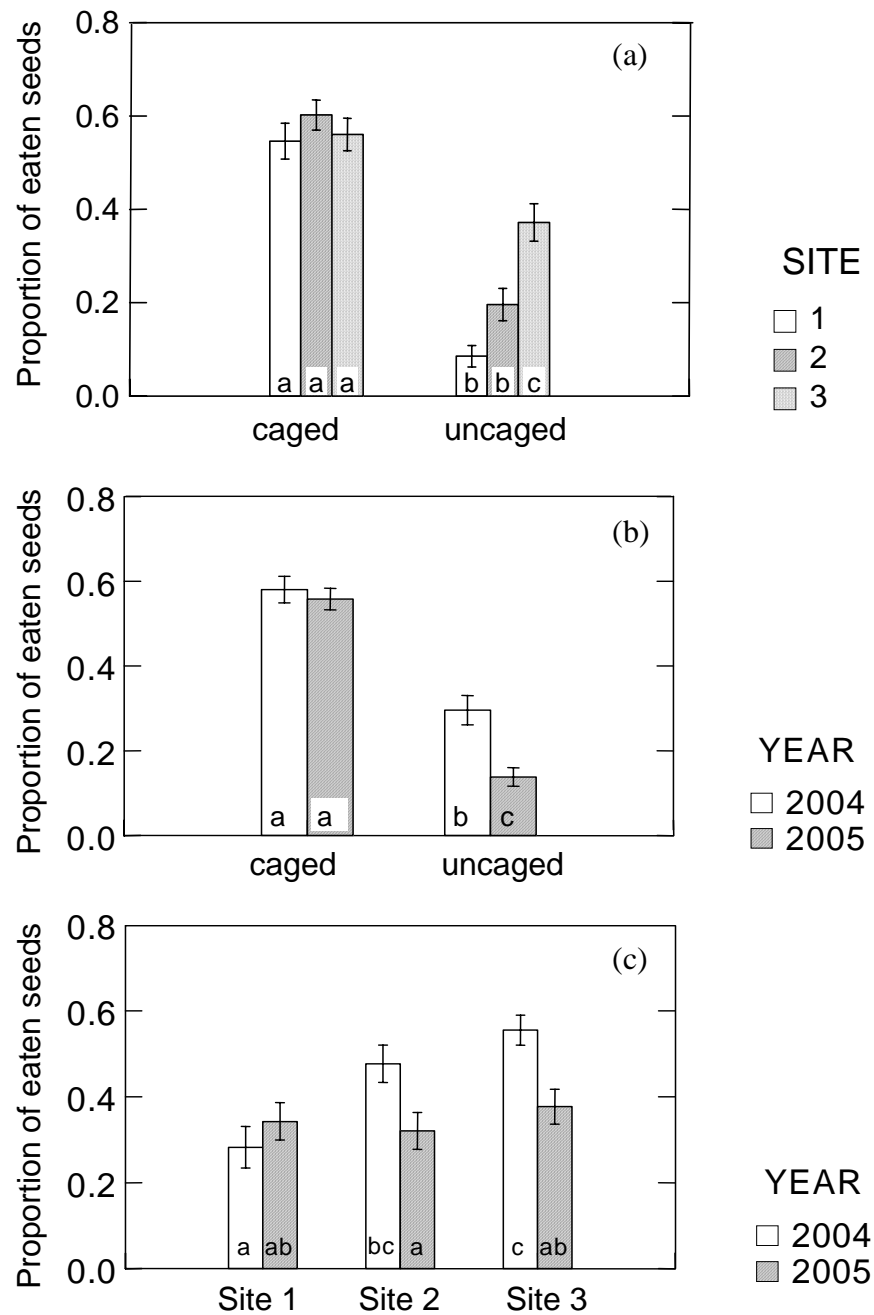


Figure 3.7. The mean proportion of seeds that were eaten by invertebrates (± 1 standard error) identified by seed remains. (a) Cage treatments at each site. (b) Cage treatments in each year (c) Sites in each year. Different letters indicate significantly different means at $\alpha=0.01$.

differences in levels of 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 (approx. 7 years). However, the amount and timing of seed production, with the first seed release a year later in this study than in the previous one, may also have influenced seed predation rates.

In contrast to many species in fire-prone habitats, seeds of *Telopea speciosissima* have no secondary dispersal mechanisms, such as an elaiosome, nor are its predators known 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. Species in this functional group are therefore highly reliant on the coincidence of suitable conditions for establishment with low levels of predation. Thus, it is not surprising that significant recruitment is not observed after each fire. Since most individuals of *T. speciosissima* survive fire by resprouting, recruitment of new seedlings after each fire is not necessary to maintain populations. Determining the primary juvenile period and levels of adult mortality from fire and in its absence are necessary to predict the levels of recruitment necessary to prevent population declines (Bradstock 1995). Periodic high recruitment after certain fires is likely to buffer populations for several decades from lack of recruitment. Nevertheless, it is surprising that up to four years after fire, suitable microsites remain in these habitats to enable recruitment at all. In this experiment, *T. speciosissima* was seed rather than microsite limited (Eriksson & Ehrlén 1992; Myerscough *et al.* 1996), thus seed predators had a significant impact on seedling establishment (cf. Andersen 1989). Ultimately, the persistence of this species may depend upon this lack of microsite limitation to enable recruitment when and where predation is reduced (Orrock *et al.* 2006) or where the impact of predation is minimised by rapid germination.

Chapter 4 - The importance of time-since-fire on seed predation and seedling establishment in two resprouting shrub species



A seedling of *Telopea speciosissima* (left) and *Banksia serrata* (right) emerging through litter 42 days after placement.

4.1 Abstract

In fire prone habitats, resprouting shrubs do not need to recruit after every fire, because many adult plants survive each fire and therefore continue to contribute to the population. However, without periodic recruitment, accumulated mortality of adults both during and between fires would lead to local extinction. Canopy seed bank species release their seeds shortly after fire and usually establish seedlings within a year of fire. In contrast, species with pyrogenic flowering have no seeds available immediately after

fire and release seeds following post-fire flowering. Unlike species that form soil seed banks, most species in this group have seeds with no innate dormancy. The delay in seedling establishment in pyrogenic flowering species, of up to two years, calls in to question the universal selective advantages of establishing seedlings as soon after fire as conditions permit. If this selective force is so strong, why do pyrogenic flowering species persist? The aim of this component of my study was to investigate the possibility that recruitment of pyrogenic flowering species is facilitated by the characteristics prevailing in late post-fire environments and the corollary, that canopy seed bank species are specialised to recruit in early post-fire environments.

Using a seed planting experiment, I was able to test the effects of time-since-fire and microsite condition on seedling establishment for two resprouter species in the Proteaceae with these contrasting recruitment strategies. I planted seeds in two early and two late post-fire sites (6 months and 2-3 years after fire respectively) in southeastern Australia. Litter cover is dynamic soon after fire and has an important influence on microsite condition and hence seedling establishment. To assess the impact of litter mass on seedling establishment, at each site I varied litter levels so that half of the seeds were placed in the mean of the early and half in the mean of the late post-fire litter mass. I excluded vertebrate seed predators to maximise the probability of detecting differences due to time-since-fire and litter amount in the experiment. Seed and seedling fates were followed for 9 months after planting.

Banksia serrata, the canopy seed bank species, established more seedlings at all sites than *Telopea speciosissima*, the pyrogenic flowering species. This was despite a lower level of seed viability in *B. serrata* and the more rapid establishment of *T. speciosissima* seedlings after suitable rainfall. Seedling establishment overall was poor, peaking within 3 months of planting at 35.6% (*B. serrata*) and 29.7% of seeds (*T. speciosissima*). High levels of mortality occurred during periods of hot dry weather and, as a result, few seedlings (<7% of seeds) were alive at the end of the experiment. Both species established more seedlings in late post-fire sites than in early post-fire sites independent of the amount of litter. There were very few seedlings in one early post-fire site, limiting the generality of time-since-fire comparisons. The fate of seeds inferred from examination of their remains indicated that invertebrate seed predators consumed

most of the seeds, although some germinated and then died, and some were inviable. Very few seeds (6.6%) remained intact and ungerminated 9 months after placement. Less than half of these were considered viable in cut-tests. Significantly more seeds of *T. speciosissima* were eaten in early post-fire sites (69.5%) than in late post-fire sites (51.2%), while seed predation levels for *B. serrata* were comparable across sites (average 47.3%) and consistently less than for *T. speciosissima*.

Seedling establishment in the pyrogenic flowering species (*T. speciosissima*) soon after fire was limited in part by its susceptibility to seed predation. This suggests that there may be some benefit in later seed release in this species. In contrast, the canopy seed bank species (*B. serrata*) appears to have greater flexibility in the timing of its recruitment after fire. Greater seedling establishment in late post-fire sites by both species and the lack of influence of the litter treatment suggests that the simple microsite modification applied in this experiment did not explain differences in establishment between early and late post-fire sites.

4.2 Introduction

The early post-fire environment is generally considered to provide conditions that are most conducive to recruitment for plants in fire-prone habitats (Christensen & Muller 1975b; Wellington & Noble 1985b; Zammit & Westoby 1988; Keith 1996; Purdy *et al.* 2002) and has provided the selective force behind the evolution of canopy seed storage in many species (Lamont *et al.* 1991). Fires result in the consumption of standing vegetation and litter, and the deposition of ash, increasing the amount of space, nutrients, water and light available to new seedlings (e.g., Christensen & Muller 1975a; Hawkes & Menges 1995; Tyler 1995, 1996). However, not all changes are likely to be beneficial to seedling establishment. The physical environment may be harsher, with increased insolation, and increased soil moisture and temperature flux (Christensen & Muller 1975a; Raison *et al.* 1986a; Auld & Bradstock 1996; Tozer & Bradstock 1997). There is also evidence of an interaction between fire and the impact of seed predators (e.g., Andersen 1987). While fire may reduce population sizes of seed predators through mortality and changes in the habitat (Fox 1982; Botha & Le Maitre 1992; Sutherland & Dickman 1999), it may also affect their foraging behaviour and efficiency of seed harvesting. One major influence on seed predator foraging ability is the consumption of litter by fire and the rate of subsequent re-establishment of a litter layer. Litter reduces the ability of rodents, in particular, to find seeds (Clark *et al.* 1991; Myster & Pickett 1993; Reed *et al.* 2004, 2005, 2006), while ants have been reported to forage further and remove more seeds in the absence of a litter layer (Andersen 1988; Parr *et al.* 2007). In addition, the release of seeds from canopy seed banks of many species simultaneously may satiate predators (Ashton 1979; O'Dowd & Gill 1984; Wellington & Noble 1985a; Bell *et al.* 1987; Andersen 1988), allowing more seeds to escape through to germination.

For fire-sensitive (obligate seedling) species, recruitment is necessary for populations to re-establish and to replenish seed banks. Obligate seeders with soil seed banks may retain some seeds in the soil after fire (Auld & Denham 2006; Auld *et al.* 2007), but unless fires are patchy, those with canopy seed banks depend on the recruitment of new seedlings to prevent extinction of local populations. In contrast, for

resprouting species (those with some fraction of the population that survives fire), recruitment is not necessary after every fire, although some established individuals will be killed by fire or die from other causes in the inter-fire period (Auld 1986a; Bradstock & Myerscough 1988; Keith 1996).

For successful recruitment, seedlings of resprouting species must reach fire-resistant size prior to the following fire. The allocation of resources to organs such as lignotubers, to achieve fire-resistance, results in long primary juvenile periods for many of these species (Carpenter & Recher 1979; Keith 1996; Enright & Goldblum 1999). Thus when fire intervals are approximately the same as this primary juvenile period (in the order of every 10-20 years), not only does the post-fire environment favour recruitment, but there is also a temporal advantage in early seedling establishment. In this context, there is a sharp contrast between species with a persistent seed bank and those with a transient (or no) seed bank. Many species that maintain a persistent seed bank are able to establish new seedlings almost as soon as conditions (such as suitable rainfall) occur after fire. This is because fire stimulates the release of non-dormant seeds from canopy seed banks (e.g., Gill 1976; Habrouk *et al.* 1999) while, for soil seed banks, dormancy may be broken by soil heating (e.g., Auld & O'Connell 1991) or by a combination of heat and the chemical components of combustion (e.g., Keeley *et al.* 1985; Dixon *et al.* 1995; Thomas *et al.* 2003). In contrast, pyrogenic flowering species must resprout, flower, fruit and release seeds before they can establish new seedlings. Thus these species may be up to two years behind soil or canopy seed bank species in establishing seedlings depending on the season in which the fire occurs (Auld 1986a; Denham & Auld 2002). This large time difference suggests that the later establishing species must have characteristics that allow them to establish well after many other species, and they also must reach fire-resistance sooner after germination than earlier establishing species.

Using a seed-planting experiment (seed augmentation *sensu* Turnbull *et al.* 2000), this study aims to investigate the means by which a pyrogenic flowering species (*Telopea speciosissima* (Smith) R. Br.) persists and to estimate the importance of selective pressures that may have acted to produce its recruitment strategy. To provide contrast, a similar, related species, *Banksia serrata* L. f. (Table 4.1), with a different

recruitment strategy was chosen. This species maintains a persistent canopy seed bank that is released soon after fire. By manipulating the timing of seed arrival in these two species after fire (by choosing sites of differing time-since-fire) and habitat quality (by modifying litter mass), the following hypotheses could be tested.

- *Banksia serrata* has greater seedling establishment sooner after fire than later, while *T. speciosissima* has poorer establishment sooner after fire than later (recruitment in the two species is closely tied to the time of seed release set by life history).
- *Banksia serrata* has better establishment in microsites with less litter, while *T. speciosissima* has better establishment with more litter, regardless of time since fire (litter cover is the explanation for any observed time-since-fire effect).

Previous studies have identified that vertebrate seed predation remains very high after fire for *T. speciosissima* (Denham & Auld 2002; Chapter 3), and while Bradstock (1991) found no loss to seeds of *B. serrata* after fire, other studies involving *Banksia* spp. (e.g., Cowling & Lamont 1987) have identified significant vertebrate predation. However, in order to maximise the probability of detecting differences in establishment among species resulting from microsite manipulations, I chose to exclude vertebrates from all treatments in this experiment.

Table 4.1. Comparative biology of the study species

Species	<i>Banksia serrata</i>	<i>Telopea speciosissima</i>
Phylogeny (family, subfamily, tribe)	Proteaceae, Grevilleoideae, Banksieae	Proteaceae, Grevilleoideae, Embothrieae
Seed mass (mg)	76.9-77.5	71.9-75
Seed bank type	Serotinous (bradysporous)	None (transient)
Fire survival	Resprouter	Resprouter
Distribution	Widespread in DSF and woodland on sandstone and consolidated sand dunes in eastern Australia	Widespread in DSF on sandstone soils in the NSW central and southern coast and tablelands botanical divisions

4.3 Methods

4.3.1 Study species

Telopea 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 (Harden 2002). Its striking red blooms, particularly when they emerge above the resprouting shrubby vegetation in the post-fire environment, have led to its use as a species in architectural and artistic design since the late 19th century and its adoption as the floral emblem of NSW in 1962 (Nixon 1987). Within the Proteaceae, *T. speciosissima* is one of 5 species (Crisp & Weston 1993; Weston & Crisp 1994; Harden *et al.* 2000) in the tribe Embothrieae within the subfamily Grevilleoideae (Johnson & Briggs 1975; Harden *et al.* 2000). The species survives fire by having dormant buds protected in an underground lignotuber (Bradstock 1995). Aerial stems are completely regrown after each fire. Flowering begins in spring some 9 months or more after fire with seeds released the following autumn (Pyke 1983; Denham & Auld 2002). Flowering may recur over the following 3 years and in some sites over more than 10 years (Goldingay 2000). However, there are no records of effective recruitment beyond the first few years after fire (Bradstock 1995; Denham & Auld 2002).

Banksia serrata L. f. (Proteaceae) is a shrub or tree to 16 m tall, common in dry sclerophyll forest and woodlands on the coast and adjacent tablelands of eastern Australia. It occurs on soils derived from sandstone and on consolidated sand dunes (Harden *et al.* 2000). Its main range extends over 2000km, from Cooloola, Queensland to Wilsons Promontory, Victoria. There is an outlying population a further 300 km south at Sisters Creek in northwest Tasmania (George 1996). Within the Proteaceae, *B. serrata* is one of 76 species in the tribe Banksieae within the subfamily Grevilleoideae (Johnson & Briggs 1975; Harden *et al.* 2000). *Banksia serrata* survives fire by resprouting from epicormic buds in arborescent individuals or from a lignotuber in shrubby or juvenile individuals (Bradstock & Myerscough 1988). Seeds are stored in woody fruits (cones) on the plant, forming a persistent seed bank. Cones open shortly

after fire, with establishment generally only occurring in the first year after fire (Bradstock & Myerscough 1988, but see Whelan *et al.* 1998).

These two species thus have contrasting seed bank and recruitment characteristics, but both are resprouters in the subfamily Grevilleoideae and have similar seed mass (Table 4.1; Westoby *et al.* 1990; Bradstock 1995; Hammill *et al.* 1998).

4.3.2 Sites

I located sites where both *Banksia serrata* and *Telopea speciosissima* were present. I chose two sites that were early post-fire (<1 year since fire – Sites 1 and 2) and two that were late post-fire (≥ 2 years since fire – Sites 3 and 4). These sites, located within 11km between Colo Vale and Bargo in the southern tablelands of NSW, about 100km SW of Sydney (approx. 150°30'E; 34°23'), were previously used to assess post-fire litter accumulation (Chapter 2). Sites occurred on dry sclerophyll forest vegetation, with the overstorey at Sites 1 and 3 dominated by *Eucalyptus piperita* var. *urceolaris*, while at Sites 2 and 4 it was dominated by *E. sieberi* and *Corymbia gummifera*. Plant species composition varied among sites, but there were many species in common including *B. spinulosa*, *Bossiaea obcordata*, *Corymbia gummifera*, *Cyathochaeta diandra*, *Entolasia stricta*, *Lomandra filiformis*, *L. obliqua*, *Lomatia silaifolia*, *Patersonia glabrata*, *Persoonia levis*, *Pimelea linifolia* and *Platysace linearifolia*. Climate information for Moss Vale, approx. 30km south of the study sites is presented in Figs 4.1 and 4.2.

4.3.3 Seed collection and viability

Seeds of *T. speciosissima* were collected in the year of the experiment (2006) from a number of populations in the Sydney Region. Seeds were visually assessed with filled ('plump' or 'firm') seeds retained and unfilled (or aborted) seeds discarded (see Bond 1984; Cowling *et al.* 1987; Enright & Lamont 1989b; Hoenig *et al.* 1992; Denham & Whelan 2000). The remaining ostensibly viable seeds were pooled prior to placement. *Banksia serrata* seeds were sourced from a commercial seed supplier and their provenance was unknown. These seeds were also visually assessed for viability and damaged or unfilled seeds were omitted. Seed viability was estimated using germination trials of a sample of seeds (85 for *T. speciosissima*, 100 for *B. serrata*). Seeds were

placed in petri dishes on two layers of filter paper and moistened with distilled water. Five seeds were placed in each dish, with species kept separate. Dishes were placed in random locations in an incubator with a 'summer' temperature regime (25°/15° C on a 12 hr cycle). Germination (defined by the emergence of a radicle) was monitored every 3 to 8 days for 5 weeks by which time any seeds that had not germinated showed signs of decay.

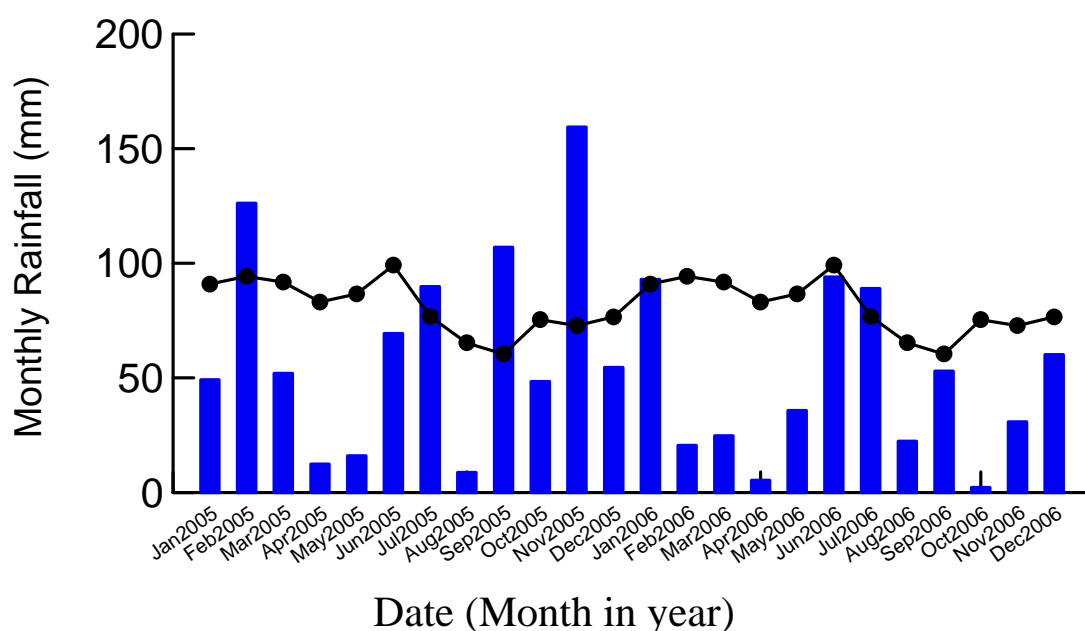


Figure 4.1. Monthly rainfall data for Moss Vale, approximately 30km south of the study sites. Solid line is the long-term mean monthly rainfall; bars are rainfall for actual period.

4.3.4 Seed planting experiment

At each site, to define experimental microsites, I placed 60 grey plastic cylinders, 30 cm in diameter and 5 cm high, at random locations (Fig. 4.3). The cylinders were bedded 1 cm into the soil and pegged into place. These cylinders prevented further dispersal of seeds by wind or water. Within each experimental microsite, I removed all surface litter. I then replaced the pre-fire litter (charcoal) and on top of this placed 10 seeds of each species, scattered to maximise separation between seeds (Fig. 4.4a). Finally, I replaced the post-fire litter (sticks and leaves - see Chapter 2) over the top of the seeds and

covered the cylinder with 1 cm grid size wire mesh to exclude vertebrate seed predators and herbivores (Fig. 4.4b). Litter was obtained from within the experimental microsite

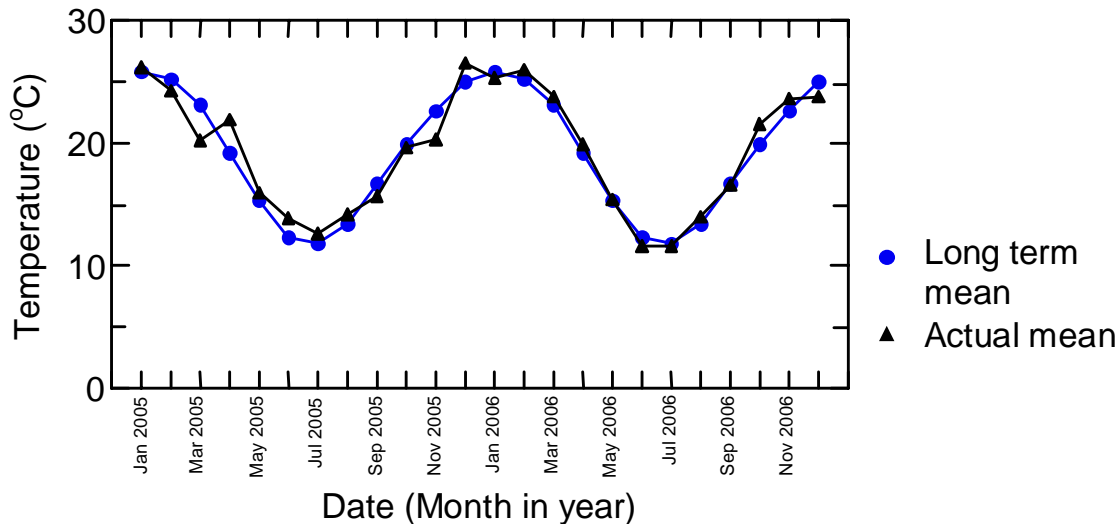


Figure 4.2 Mean monthly maximum temperatures for Moss Vale, approximately 30 km south of the study sites. Circles for the long term mean monthly maximum; triangles are mean maximum temperatures for the actual period.

or from elsewhere in the site. The total mass of litter in each experimental microsite was in one of two densities - high (the mean dry litter mass of the late post-fire sites 0.78 kg/m^2) or low (the mean dry litter mass of the early post-fire sites 0.52 kg/m^2). These estimates of litter mass were based on 20 samples at each site (see Chapter 2). It was considered impractical to exclude invertebrate predators because many (especially ants) are small and subterranean. A schematic representation of the experimental design is shown in Fig. 4.5.

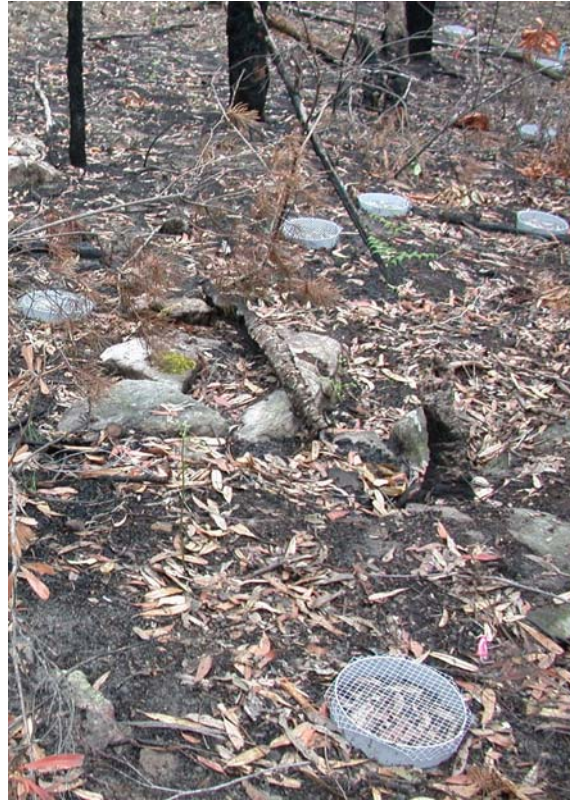


Figure 4.3. Site 1, an early post-fire site, six months after fire, showing randomly located experimental microsites used for the seed-planting experiment.

The survival of seeds and their germination and the survival of seedlings were monitored from placement in September 2005 until October 2006. Intervals between censuses varied from two to six weeks, depending in part on weather conditions. I recorded the timing of germination (emergence of a radicle) and seedling emergence (indicated by a raised hypocotyl and green cotyledons), and collected the remains of eaten seeds or shed seed coats (testae) when they were visible. At the termination of the experiment, I sieved the litter to locate any surviving ungerminated seeds or remaining testae. The testae of intact seeds were cut and examined to estimate viability (Clauss & Venable 2000; Ooi *et al.* 2004b).



Figure 4.4. Close-up photographs of an experimental microsite used for the seed-planting experiment showing (a) seeds placed on the surface after the addition of pre-fire litter (charcoal) and (b) after the addition of post-fire litter with wire mesh placed over the top. This experimental microsite has the high density litter treatment and is located at Site 4 (a late post-fire site).

4.3.5 Analysis

I compared the germination success of seeds of each species in the laboratory using a one-factor ANOVA of the proportion germinated. Replicates were individual petri dishes. I analysed the emergence of seedlings across experimental levels for the first nine months using repeated measures ANOVA. Factors included species, time-since-fire (TSF) category, litter treatment and site nested in TSF (Fig. 4.5), with up to three-way interactions included. The number of live seedlings and the cumulative number of seedlings (including those that had died) were analysed separately. In both cases I corrected the dependent variable for the viability of the seed lot, estimated using the laboratory germination trial. Since the dependent variables were proportions, they were arcsine transformed prior to analysis. After sieving the litter at the end of the experiment I allocated each seed to one of six fates depending on the condition of the remaining testa. With factors as above, I used separate ANOVAs to compare the proportion of seeds that had established as seedlings or that were eaten by invertebrates. All data sets were non-normal and heteroscedastic despite transformation. As a result, I used

conservative levels of probability ($\alpha=0.01$) to identify significant factors. For all pair-wise comparisons I used Bonferroni-adjusted tests (Wilkinson & Coward 2005).

4.4 Results

4.4.1 Seed viability and germination in the laboratory

Seed lots of both species had high viability. Significantly more apparently viable seeds of *Telopea speciosissima* (95.3%) germinated than of *Banksia serrata* (71.5%) ($F_{1,35}=19.6$, $P<0.001$). *Telopea speciosissima* seeds also germinated more rapidly under the temperature regime employed, with 60% of seeds germinating within ten days after the addition of water compared with 21 days for *B. serrata* (Fig. 4.6). Seeds that did not germinate either had unformed cotyledons, or had imbibed but failed to produce a radicle.

4.4.2 Seedling emergence and survival

Seedling emergence in the field was low, and few seedlings survived for more than three weeks (Fig. 4.7). Seedlings of both species had emerged by the second census (43 days after planting), with more seedlings of *T. speciosissima* present than *B. serrata*. Both the number of newly emerged seedlings and the number of live seedlings peaked at the third census with a substantial decline in both thereafter. This decline coincided with a period of hot dry weather in the summer of 2005-6 (Fig. 4.8). There was no influence of the litter treatment on the number of seedlings present at any one time, but species, TSF (time-since-fire) and site were all significant in the repeated measures ANOVA (Appendix 4.1). The species effect is due to the early emergence of *T. speciosissima* and the ultimately greater emergence of *B. serrata* seedlings. The site and TSF factors are significant primarily because of the very low number of seedlings emerging from Site 2 (Fig. 4.7b). The other early TSF site (Site 1, Fig. 4.7a) had only slightly fewer seedlings than the sites in the later TSF (Fig. 4.7c, d). Species, TSF and site also varied significantly over time, although after the second census, site and species were mostly consistent in rank. All the same factors were significant for the cumulative number of seedlings (Appendix 4.2). This indicates that the turnover of

seedlings, i.e., the number of new seedlings emerging versus the number of seedlings that had died, did not obscure other underlying patterns in the data (data not presented).

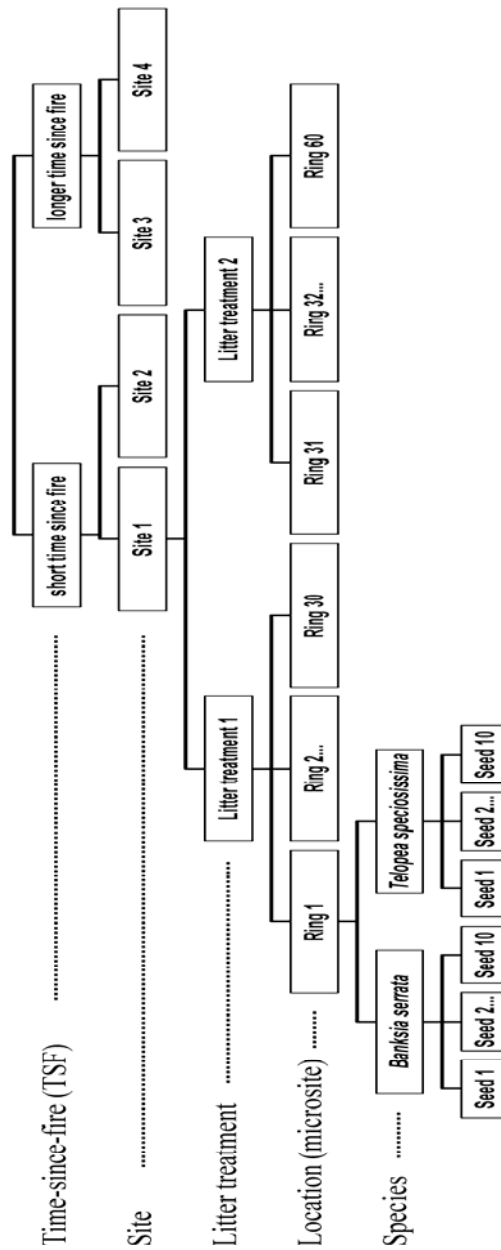


Figure 4.5. Schematic representation of design of the seed-planting experiment

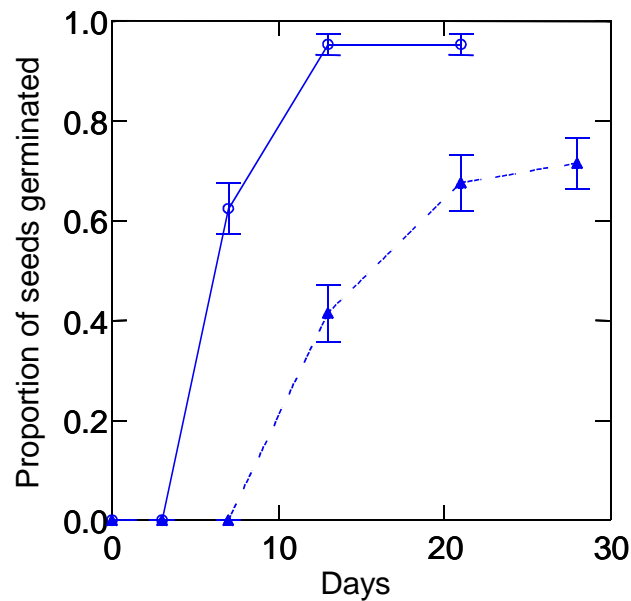


Figure 4.6. The proportion of seeds germinating over time under laboratory conditions. Open circles, solid line for *Telopea speciosissima*, closed triangles, dashed line for *Banksia serrata*. Data are means with standard errors.

4.4.3 Seed fate inferred from seed remains

The most likely fates of seeds of both species were to germinate, be eaten by invertebrates, or to go missing (Table 4.2). Since seeds recorded as missing are likely to have been eaten by invertebrates, it is apparent that almost half (47.3%) of *B. serrata* seeds were eaten, while more than half (60%) of *T. speciosissima* seeds were eaten. Overall, less than 6.7% of seeds were intact at the end of the experiment (9 months after the start) and only 2.6% (*B. serrata* 2.3%, *T. speciosissima* 0.3%) were considered to be viable after cut-tests.

Time-since-fire significantly affected the number of *T. speciosissima* seeds eaten, with a mean of 69.5% consumed in early post-fire sites compared with 51.2% in later post-fire sites. However, the number of *B. serrata* seeds eaten was not affected by time-since fire, with an overall mean of 47.3% consumed (Appendix 4.3, Fig. 4.9). In contrast, for seeds that were judged to have established as seedlings, TSF and site

(nested in TSF) were significant effects, but species was not (Appendix 4.4, Fig. 4.10). These data indicate that I failed to detect seedlings of *T. speciosissima* in monitoring - presumably they emerged and disappeared between censuses. Again the TSF pattern is strongly influenced by the paucity of seedlings that emerged from Site 2 of the two early TSF sites. However, pair-wise comparisons indicated that the other early TSF site (Site 1) had significantly fewer seedlings than one of the later TSF sites, while it ranked lower than both (Fig. 4.11). The litter treatment had no significant effect on either the number of seeds that became seedlings or on the level of invertebrate predation.

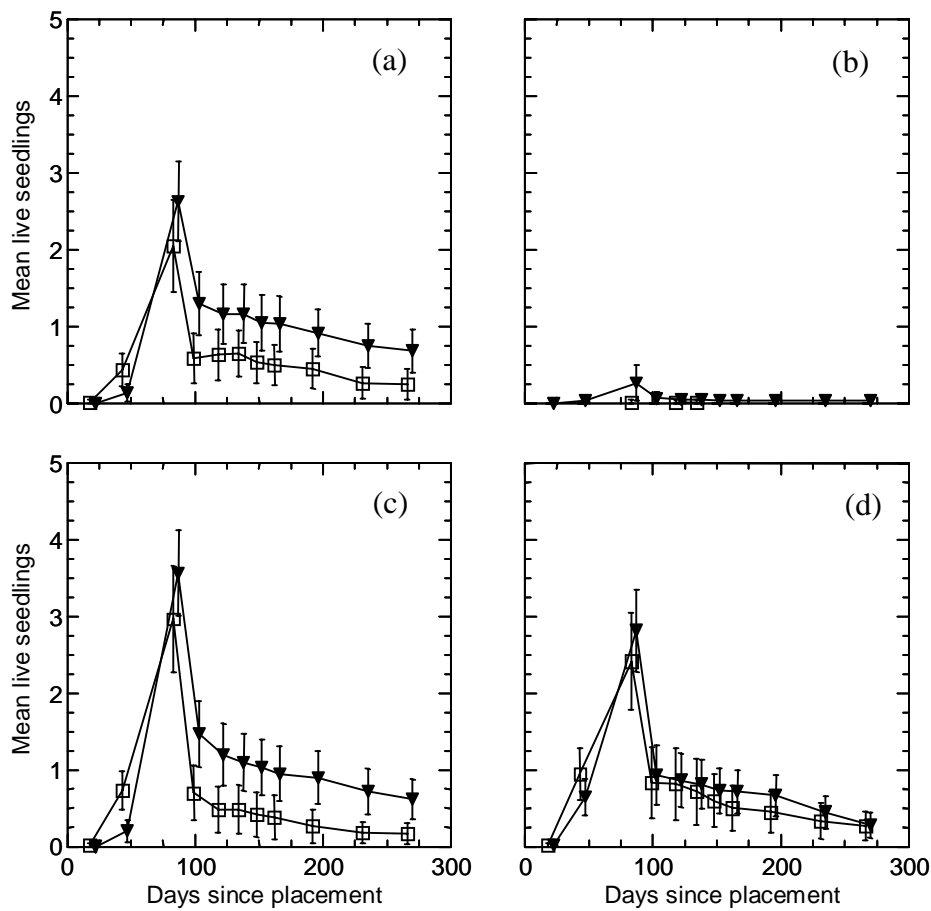


Figure 4.7. The mean number of seedlings alive at census times at each site. Top = early post-fire sites, (a) Site 1, (b) Site 2; bottom = late post-fire sites, (c) Site 3, (d) Site 4. Solid triangles for *B. serrata*, open squares for *T. speciosissima*. Data are slightly jittered on x-axis for clarity. Errors are 95% confidence intervals.

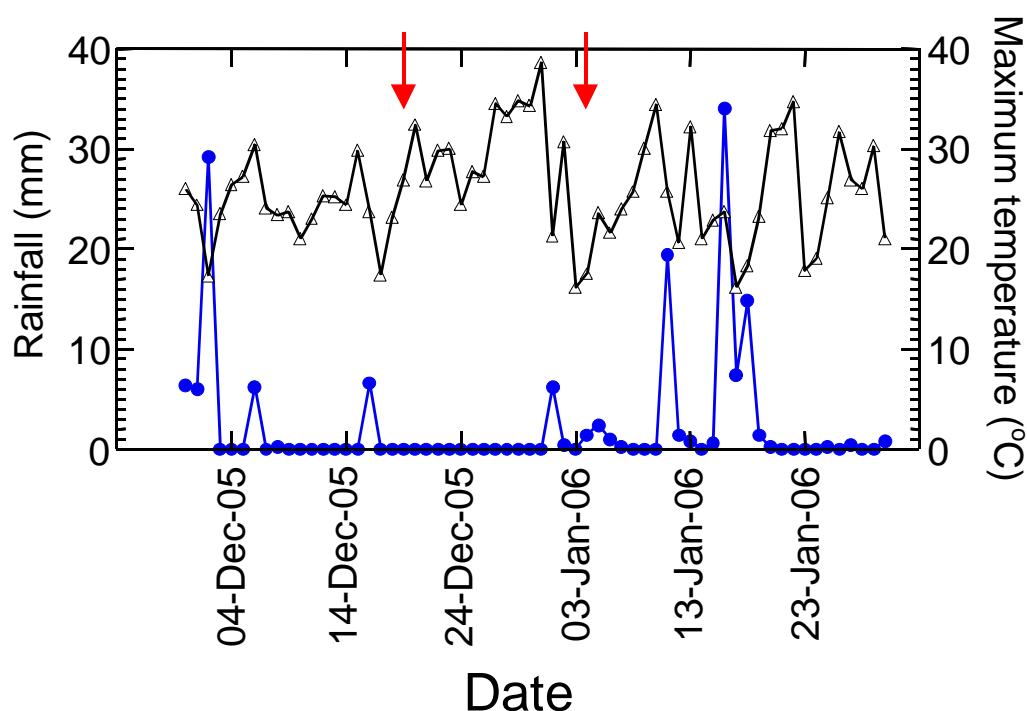


Figure 4.8. Daily rainfall (filled circles) and maximum temperatures (open triangles) at Moss Vale during December 2005 and January 2006. Census dates as marked by arrows are 19/12/2005 (3rd census) and 4/1/2006 (4th census).

4.5 Discussion

4.5.1 Seed viability and germination in the laboratory

The viability estimated by germination of *T. speciosissima* seeds was high (cf. Bradstock 1995 - 82%), while viability of *B. serrata* was considerably lower and was between the values observed by Bradstock (1990) for seeds five to 15 years old. Other studies of canopy seed bank and pyrogenic flowering species have also observed high levels of seed viability (e.g., Auld 1986a; Cowling & Lamont 1987; Curtis 1996). Rapid germination of *T. speciosissima* seeds as observed in the laboratory could result from selection in this species to avoid seed predation. While similar pressure is likely to act on *B. serrata*, its seeds generally fall among those of other canopy seed bank species possibly reducing the impact of seed predation through predator satiation.

Table 4.2. Summary statistics of the fate of seeds inferred from seed remains. The mean values represent the means of all 120 experimental microsites per time-since-fire (TSF) category, each with 10 seeds per species.

Fate ¹	Early TSF				Later TSF			
	<i>B. serrata</i>		<i>T. speciosissima</i>		<i>B. serrata</i>		<i>T. speciosissima</i>	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
complete	1.487	0.182	0.435	0.08	0.313	0.06	0.182	0.05
inviabile	0.47	0.08	0.41	0.08	0.13	0.04	0.26	0.07
x germ	1.554	0.131	0.525	0.07	0.98	0.111	0.434	0.07
eaten	1.94	0.15	4.13	0.20	2.86	0.18	3.19	0.17
missing	2.65	0.19	2.82	0.21	2.01	0.19	1.93	0.16
seedl	1.91	0.20	1.69	0.21	3.72	0.20	4.02	0.22

¹Key to fates: complete – intact apparently viable seed; inviable – intact, but apparently inviable seed (usually either empty or bloated); x germ – a seed that germinated, but did not survive to become a seedling; eaten – seed cases (testa) which have evidence of invertebrate chewing; missing- seeds that could not be accounted for by testa remains; seedl – identified either as a seedling at the time of census, or as an undamaged, but split and empty testa during sieving.

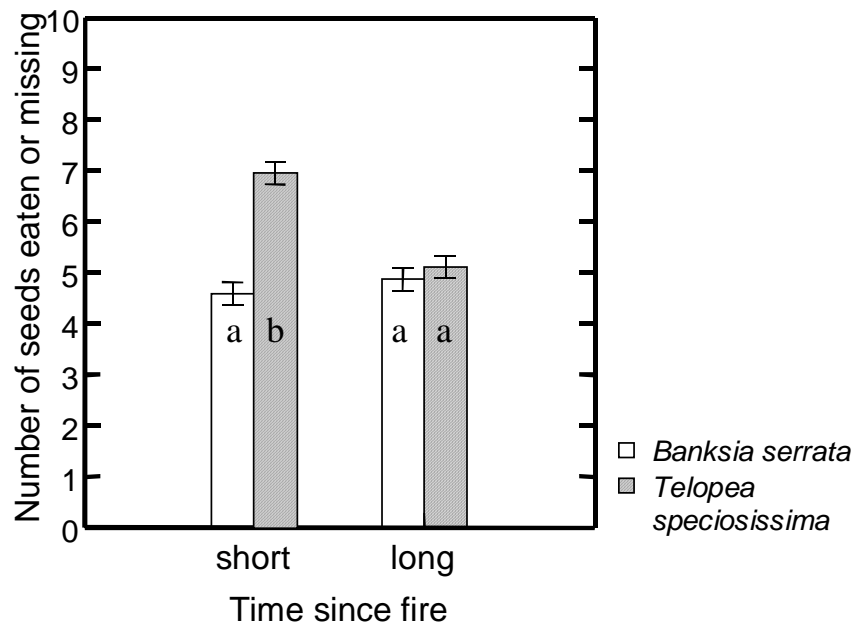


Figure 4.9. The mean number of seeds eaten or missing inferred from seed remains. Different letters represent significantly different means in pair-wise comparisons. Errors are 95% confidence intervals.

4.5.2 Seedling emergence and survival

Consistent with expectations, seeds germinated rapidly in the field after sufficient rain had fallen. Similar rapid germination has been observed in other canopy seed bank and pyrogenic flowering species (e.g., Auld 1986a; Cowling & Lamont 1987; Lamont *et al.* 1993; Curtis 1996). The earliest observed seedlings were dominated by *T. speciosissima* in line with the laboratory germination experiments. However, although there were more viable seeds of *T. speciosissima* than of *B. serrata* in each experimental microsite, the majority of seedlings established by the third census were of *B. serrata*. The maximum level of seedling establishment observed at the third census (*B. serrata*, 36%; *T. speciosissima*, 30%) is slightly greater than that found by Bradstock (1990) and greatly exceeds the estimates of Lamont & Groom (1998). However, in both of these studies, estimates included losses due to vertebrate seed predation. Witkowski & Lamont (1997) found equivalent or higher levels of emergence, regardless of level of predator exclusion, although they also incubated their seeds prior to placement, thus increasing the probability of successful emergence.

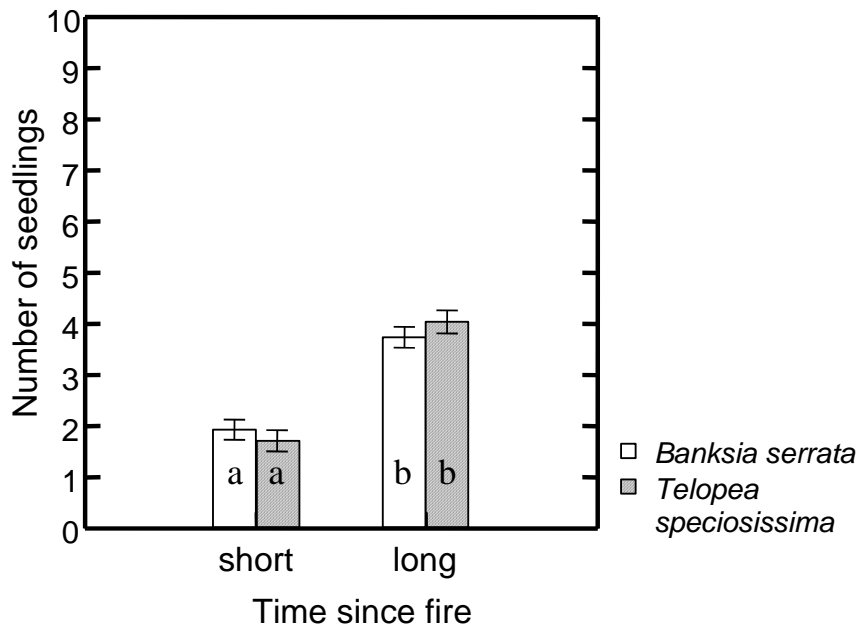


Figure 4.10. The mean number of seedlings that ever occurred, determined by direct observation (census) or inferred from seed remains. Different letters represent significantly different means in pair-wise comparisons. Errors are 95% confidence intervals.

There was no evidence of greater establishment of *B. serrata* seedlings soon after fire than after 2 years. The reverse was in fact apparent, with greater establishment at later post-fire sites than early post-fire sites, with one early post-fire site having very low levels of establishment. This is in contrast to findings for other *Banksia* spp in the Sydney region, where establishment in sites 3 or more years post-fire was considerably poorer than in sites recently burnt (Zammit & Westoby 1988). There was also no evidence that *B. serrata* has greater establishment success in microsites with low amounts of litter.

For *T. speciosissima* there were significantly more seedlings established in later post-fire sites, but again, no evidence of an influence of litter on establishment success. I found more seedlings of *B. serrata* than of *T. speciosissima* at both TSF categories (Fig. 4.7) suggesting that although *T. speciosissima* does not have seeds adapted for seedling establishment soon after fire, it is not better adapted to establishment later after fire than *B. serrata*. Conflicting evidence based on seed remains (Fig. 4.10), suggests that seedlings of *T. speciosissima* were very short-lived and disappeared between

censuses or that they did not emerge from the litter. However, it is important to note that vertebrate seed predators were prevented from gaining access to the seeds. This is because the aim was to maximise the power to detect a general time-since-fire effect and a specific litter effect. The loss of most seeds to vertebrate predators may obscure these effects. In other studies, vertebrate seed predation on *T. speciosissima* in late post-fire habitats was intense (Denham & Auld 2002; Chapter 3) with the impact influenced by litter cover (Chapter 3). Here I was unable to determine if the levels of vertebrate predation would differ between the study species or between litter treatment levels, but I was able to measure predation by invertebrates. This did not differ between the two litter treatment levels, suggesting that the foraging success of invertebrates was not affected by the amounts of litter in this treatment. Litter increased the susceptibility of seeds and seedlings to invertebrate predation in old fields in New Jersey USA (Facelli 1994), but had no effect in prairie grasslands (Reed *et al.* 2006).

Very high mortality of both species was observed between the third and fourth censuses. This coincided with the highest temperatures of the summer, including a very high maximum for the 1st of January (Fig. 4.8), and a period of drought. Although the decline was remarkable, lack of replication of planting years makes it impossible to determine whether the extreme temperatures influenced the shape of the survival curve or whether such declines are common. Other studies have reported similar summer losses (e.g., Lamont *et al.* 1993; Lamont & Groom 1998; Ordonez & Retana 2004), although these were in Mediterranean climates where summer drought and high temperatures are part of an annual cycle. Lamont & Groom (1998) predicted that for woody-fruited Proteaceae, less than 10% of seeds released after fire become seedlings and < 50% of these survive their first summer. Final seed / seedling survival maxima of about 7% (*B. serrata*) and 2% (*T. speciosissima*) are consistent with these predictions and comparable with Chapter 3 and the findings of Denham & Auld (2002).

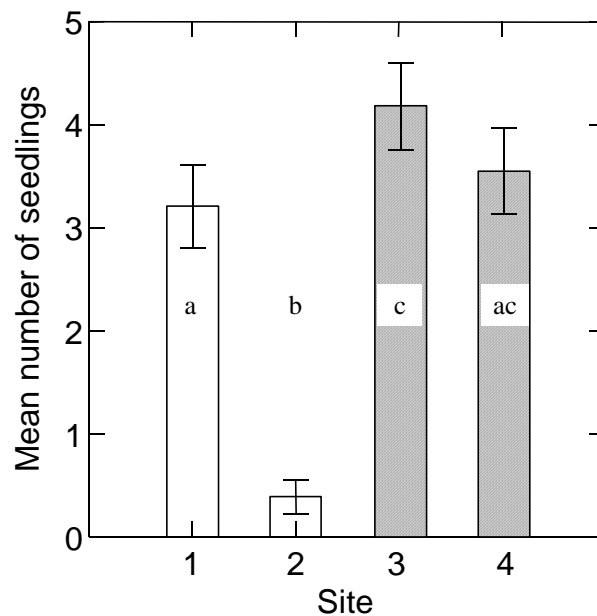


Figure 4.11. The mean number of seedlings for *B. serrata* and *T. speciosissima* combined, that ever occurred at each site. Totals include those directly observed by census or inferred from seed remains. Open bars for early time-since-fire, hatched bars for later time-since-fire. Different letters represent significantly different means in pair-wise comparisons. Errors are 95% confidence intervals.

Seedling establishment of both species was negligible at Site 2 and this strongly influenced the overall time-since-fire comparisons. It seems likely that conditions at Site 2 were considerably harsher than at other sites. Unlike all the other sites, I observed that Site 2 had been subjected to a high intensity fire (as evidenced by the complete scorch of the shrub layer and the death of all fire sensitive plants). It is also on a westerly aspect and would experience greater soil temperatures and aridity than the other sites. Sites 1, 3 and 4 were all similar in both the number of observed seedlings and the pattern of seedling establishment and loss over time.

Analysis of seed remains provides a different perspective of the course of the experiment, although the evidence is more inferential than direct observation. The analysis of seedling establishment based on seed remains provided more weight to the argument that both species favour recruitment in later post-fire habitats (Fig. 4.7).

Despite the large differences between the two early TSF sites, the trend still supported

greater establishment in later TSF sites; there was a significant difference between the early TSF site with greater seedling establishment (Site 1) and one of the later TSF sites (Fig. 4.9). I also observed a TSF x species interaction on the proportion of seeds eaten by invertebrates, with seeds of *T. speciosissima* more prone to predation in early post-fire sites (Fig. 4.9). This was the only clear indication of a mechanism producing a benefit of establishing seedlings in the time frame usually observed for either species.

4.6 Conclusions

Both species were more successful at establishing seedlings in late post-fire habitats, with more seedlings of *B. serrata* observed at all sites. Overall establishment success was low and few seedlings survived to the end of the study period. Since most individuals of both species are likely to survive fire by resprouting, their reliance on seedling recruitment to maintain populations after any one fire is reduced compared to fire-sensitive species. Nevertheless, the aim of this study was to identify difference between these two species. One major difference was detected - *Telopea speciosissima* suffered greater predation in early post-fire sites than in later ones and greater predation than *B. serrata* in early post-fire sites. *Banksia serrata* did not show this variation in predation across TSF categories. Neither species was affected by the amount of litter surrounding their seeds. Thus while seedling establishment of *T. speciosissima* was poorer in early post-fire habitats, litter (in the amounts used in this experiment) was not the mechanism that differentiated it from *B. serrata*. In contrast *B. serrata* was flexible in its recruitment strategy and able to establish seedlings long after the process of post-fire seed fall in the species. This is consistent with evidence of successful inter-fire recruitment in this species as observed by Whelan *et al.* (1998) and in some other canopy seed bank species (Zammit & Westoby 1987; Lamont & Enright 2000). Thus far I have failed to identify any mechanism that facilitates late post-fire seedling establishment in *T. speciosissima*, although invertebrate predation reduces its ability to establish seedlings soon after fire. Differential exclusion of vertebrate and invertebrate seed predators may highlight other differences among the two species or time-since-fire categories, although it would require increased replication of experimental microsites

and more seeds. Further examination of the conditions in microsites where these species have and have not established seedlings may provide insights into the possible mechanisms that allow establishment (e.g., Lamont *et al.* 1993; Chambers 2001; Purdy *et al.* 2002; Garcia & Houle 2005). Manipulations to mimic these conditions in both early and late post-fire habitats may then confirm or refute their relevance. The use of species with contrasting post-fire recruitment strategies reduces the likelihood of making generalisations that are only relevant for individual species.

Chapter 5 - General discussion and conclusions

5.1 Summary of results

In this study, I examined the following questions (Chapter 1, part 1.7), in order to understand some of the ecological factors influencing the recruitment of new individuals in populations of plants in fire-prone habitats, with a particular focus on the shrubby pyrogenic flowering species *Telopea speciosissima*:

1. Do seedlings establish under shade and litter and tolerate competition from existing plants, or must they establish in open spaces?
2. Does post-dispersal seed predation in *T. speciosissima* strongly influence seedling recruitment?
3. Does *T. speciosissima* have particular characteristics that tie seedling establishment to the late post-fire environment or is it only its life history (constrained by its phylogeny) that prevents earlier seed release?

In this chapter, I examine the contribution I have made to answering each of these questions in this study. I then discuss the characteristics that lead to the persistence of populations of pyrogenic flowering species in the light of these findings, review the limitations of the study and suggest areas for further research in this field.

5.1.1 Establishment of seedlings

During the period of natural recruitment in *T. speciosissima*, I placed its seeds into experimental microsites in each of three different microhabitat classes (Chapter 3). These classes were based on the amount of litter and vegetation cover observed at the start of the experiment. I also manipulated the amount of cover in an experiment, by removing litter and vegetation from half of these microsites and by modifying the degree of access of vertebrate predators. Seedlings were observed in all microhabitat classes, with some surviving to the end of the experiment. More seeds or seedlings survived long enough to germinate in microhabitats with high levels of litter and vegetation cover than those with low levels of cover (Fig. 3.5). These differences were not significant when I considered the proportion of seedlings that survived to the end of the experiment. However, in one of the two years of the experiment, removing all the

litter and vegetation significantly reduced the proportion of seedlings that survived to the end of the experiment (Fig. 3.6). The seedlings that I observed in locations from which cover had been removed did not establish on bare ground, but occurred near the edges of the confining plastic cylinder or against other obstructions.

I manipulated the amount of litter in microsites in habitats differing in time-since-fire, using seeds of both *T. speciosissima* and *B. serrata* (Chapter 4). Both species germinated and established seedlings in each of the litter treatments and in each of the TSF categories. The amount of seedling establishment did not differ significantly between different levels of the litter treatment. Thus, it is apparent that *T. speciosissima* (and *B. serrata*) is able to establish in microsites that have both vegetation and litter cover. Indeed, seedlings of *T. speciosissima* were able to establish in microsites with litter cover in excess of 1kg/m^2 (Fig. 3.3), and both species established seedlings in microsites with litter cover in excess of 0.7 kg/m^2 , which was the mean litter amount in sites 2-3 years after fire (Fig. 2.6, Chapter 4). Long-term monitoring would be required to determine if these seedlings become effective in the population by flowering or at least surviving until after the next fire.

5.1.2 Seed predation

Post-dispersal seed predation in *T. speciosissima* was high, with significant losses to both vertebrate and invertebrate predators. Seeds that were protected from vertebrate predation were likely to be eaten by invertebrates, if they did not escape by germinating. While litter appeared to reduce the impact of predation by vertebrates, it had little effect on the level of predation by invertebrates. It also seems that the species' susceptibility to seed predation, at least by invertebrates, is increased when seeds appear early in the post-fire environment. In contrast, the seeds of *Banksia serrata*, which has a canopy-stored seed bank released soon after fire, suffered consistent levels of predation by invertebrates regardless of when they were placed into post-fire habitats. These levels of predation were lower than for *T. speciosissima* in recently burnt habitats.

Seed predation strongly influenced seedling establishment in both *T. speciosissima* and of *B. serrata*. Similar impacts of predators have been observed in other studies in fire-prone areas (e.g., Wellington & Noble 1985a; Andersen 1987; Botha & Le Maitre 1992; Clarke & Davison 2001; Denham & Auld 2002; Cote *et al.* 2003; Campbell & Clarke 2006). Ants were surprisingly important as predators, given

the large size of these seeds (mass approximately 75 mg cf. *Eucalyptus baxteri*, 1.9 mg or *Casuarina pusilla*, 2.2 mg, Andersen & Ashton 1985), especially when vertebrates were excluded. Further assessment of their impact on seed establishment could be obtained by using treatments that exclude ants (e.g., Clarke & Davison 2001) or that deter ants from eating seeds (e.g., Ordonez & Retana 2004).

Differences in levels of seed predation between *B. serrata* and *T. speciosissima* may relate to characteristics of their seeds and seed coats. These characteristics influence food value and palatability, and the ability of predators to detect the seeds (e.g., Willott *et al.* 2000; Crowley & Garnett 2001). The seeds of *B. serrata* and *T. speciosissima* are similar in size and mass, but strikingly different in colour, with the former being charcoal grey and the latter light brown. The seeds of *B. serrata* correspond in colour remarkably well to the charcoal dominated landscape of early post-fire sites; while the seeds of *T. speciosissima* correspond in colour with the fallen leaves of eucalypts characteristic of later post-fire sites (see Figs 4.3 and 4.4). This suggests that visual cues may have allowed predators to detect them when they occur in the contrasting habitats set up in this experiment. Seed (or seed plus aril) colour influences seed removal (Whitney 2005) and seed predation rates (Nystrand & Granstrom 1997; Saracino *et al.* 2004) by birds. Few studies have examined the influence of fruit colour on food selection in mammals (e.g., Urbani 2002) and I know of none that examined seed colour. However, vertebrates were excluded in the experiment contrasting *B. serrata* and *T. speciosissima*. The only available data on invertebrates suggests that they may not use colour to distinguish among seeds (Whitney 2005), so it seems unlikely that this characteristic resulted in the different levels of predation I observed. Nevertheless, investigation of the importance of seed colour on seed predation and seedling establishment in these habitats is warranted.

5.1.3 Characteristics of *T. speciosissima* that facilitate its delayed post-fire recruitment

Using *Banksia serrata* in the seed-planting experiment described in Chapter 4 enabled a comparison between *T. speciosissima* and a sympatric serotinous (bradysporous) resprouter of similar seed mass. I found that *B. serrata* was able to establish more seedlings in all combinations of litter treatment and TSF categories. Thus, for the factors that I considered, *T. speciosissima* appears not to have evolved unique

characteristics that enable its seedlings to establish in microsites, or at times after fire that preclude establishment by other species. However, due at least in part to increased levels of invertebrate seed predation, seeds of *T. speciosissima* were less likely to become established in early TSF categories than in late ones, indicating that natural seed release occurs at a time when establishment is more likely. Invertebrate seed predation may thus contribute to the selective pressure that prevents a more rapid post-fire seed release in this species.

From a phylogenetic perspective, the Proteaceae are a distinct family, with ancestors in moist forests (Johnson & Briggs 1975). The tribe Embothrieae, of which *Telopea* is a member genus, has many species that still occur in or at the fringe of moist forests, and even those species that occur beyond moist forests are considered to be only moderately sclerophyllous (Johnson & Briggs 1975). Many species of the Proteaceae have characteristics that enable them to survive fire such as persistent seed banks that are released by fire and the ability to resprout after fire. Although resprouting after fire may be adaptive, it is so common in angiosperms that it cannot be assumed to be so (Bellingham & Sparrow 2000; Bond & Midgley 2003; Vesk & Westoby 2004; Pausas *et al.* 2006). This character is considered to be labile and may evolve or undergo reversal independently within taxonomic groups (e.g., within the genera *Banksia* and *Protea*, Bond & Midgley 2003). The multi-stemmed form and the presence of a subterranean storage organ of *T. speciosissima* are characteristics that Bellingham & Sparrow (2000) believe reflect evolution under conditions of frequent, severe disturbance such as fire. *Telopea speciosissima* and its close relatives do not appear to have seed dormancy or canopy seed storage, the other common characteristics of species in fire-prone habitats. However, these characteristics are common in other tribes within the Grevilleoideae such as the Grevilleeae or Banksieae, respectively. It is possible that *T. speciosissima* retains characteristics of its moist forest ancestors due to inflexibility in the genes that control these characters or due to its relatively recent appearance in fire-prone habitats.

5.2 How do species with delayed post-fire recruitment persist?

The question of how species with delayed recruitment persist in fire-prone habitats has not been definitively answered in this study. Seedlings of these species need to be able to establish in habitats where most post-fire seedling establishment has already occurred and vegetative resprouting is well advanced. However, this study has demonstrated that

opportunities for establishment do occur in late post-fire habitats. Indeed, this is even true for *B. serrata*, which typically recruits immediately after fire. This suggests that the habitat *per se* is capable of supporting more individuals than are recruited in the immediate post-fire period (the first 1-2 years). There are a number of non-exclusive explanations for this lack of apparent microsite limitation (Eriksson & Ehrlén 1992; Turnbull *et al.* 2000; Rey *et al.* 2006):

1. Dispersal of seeds into the soil seed bank before fire and from canopy stores after the fire does not saturate all sites (dispersal or seed limitation),
2. Post-fire weather conditions prevent germination or kill some early emerged seedlings,
3. Competition, seed predation and / or herbivory causes the death of some seeds or early emerged seedlings,
4. In some locations, fire kills soil-stored seeds and / or makes these locations inimical to seedling establishment. With the passage of time and the restoration of litter and vegetation cover, they then became more suitable for recruitment,
5. Delayed mortality of resprouting plants or the falling of limbs or dead plants creates new suitable microsites.

Separation of the regeneration from the persistence niche (Grubb 1977; Bond & Midgley 2001) may mean that sites where seedlings may establish are not suitable for long term survival and reproduction of individuals. This is particularly pertinent in fire-prone habitats where survival of new recruits through the following fire may depend on their location in the habitat. For resprouting species, reaching a fire-resistant size prior to the next fire is the key to successful recruitment. Thus it is possible that the paucity of late post-fire recruiting species results from the inability of most species to attain fire-resistance fast enough for recruitment to be successful. The corollary of this is that species with delayed seed release must attain fire-resistance in a shorter time than those that release seeds immediately after fire. A summary of the literature on the time to attain fire-resistance does not support this notion (Table 5.1). This may be because all resprouting species are less sensitive to post-fire recruitment selection pressures than fire sensitive species. However, an experimental test of this prediction is warranted.

Table 5.1. Time to attain fire-resistance in resprouting species measured in years since fire. Data in brackets are estimates of the percentage of seedlings that survive fire.

Recruitment type	Time (years)	Reference
Early post-fire recruiters		
<i>Banksia serrata</i>	5-7	Bradstock & Myerscough (1988)
<i>Banksia grandis</i>	7	Abbott (1985)
<i>Isopogon anemonifolius</i>	10-13	Bradstock & Myerscough (1988)
<i>Banksia attenuata</i>	8	Enright <i>et al.</i> (1998)
<i>Eucalyptus obstans</i>	7-10	Auld <i>et al.</i> (1993)
Late post-fire recruiters		
<i>Angophora hispida</i> ¹	8-9 (37%)	Auld (1986a), (1990)
<i>Podocarpus drouynianus</i>	>8	Chalwell & Ladd (2005)
<i>Doryanthes excelsa</i>	7 (60%)	Denham (unpubl. data)
<i>Telopea speciosissima</i>	7 (20%)	Denham (unpubl. data)
<i>Telopea speciosissima</i>	8-10 (<25%)	Bradstock (1995)

¹Although this is a pyrogenic flowering species, it establishes seedlings within two years of fire.

5.3 Limitations of the study

The most obvious limitation of this study is in the limited replication of sites or fires. Since all fires differ in some way, it is important to replicate experiments over a number of fires (Whelan 1995). However, this is beyond the scope of many research projects that have limited time and other resources. Spatial replication is also important if one is to have confidence in the generality of conclusions drawn from experimental work. Spatial replication was achieved over two small-scale experiments that drew similar conclusions, but variation within experiments, especially that in Chapter 4, was also substantial. Temporal replication is often tied up with replication of individual fires, that is, individual fires can only occur once – repeating an experiment after two different fires often also means at two different times, depending on the amount of available habitat or the extent of the fires. However, at least in one experiment, I was able to

replicate it over two years after one fire (Chapter 3). This was valid since *Telopea speciosissima* releases seeds for a number of years after fire, at least in some circumstances (Denham & Auld 2002). This may be seen as a bet-hedging strategy to allow recruitment to occur if conditions in one year are unsuitable. However, Denham & Auld (2002) found that both the amount of seed produced and the proportion of successful recruitment tended to decline after the first year of seed release.

5.4 Future work

This study provides directions for further study in a number of areas. Firstly, it is apparent that the ecology of many pyrogenic flowering species is poorly known. Although most species in the Sydney region have been the subject of some study (e.g., *Angophora hispida* - Auld 1986a, 1990; *A. inopina* - Tierney 2004; *Doryanthes excelsa* - Nash 1996; Denham & Auld 2002; *Lomatia silaifolia* - Denham & Whelan 2000; *Telopea speciosissima* - Pyke 1983; Whelan & Goldingay 1989; Goldingay & Whelan 1993; Bradstock 1995; Denham & Auld 2002; and *Xanthorrhoea* spp. Keith & Tozer unpubl), there are many unanswered questions about all these species. Some other members of these genera may also be pyrogenic flowering species (see Table 1.3). There are also potentially other species that may warrant classification as pyrogenic flowering species particularly among the monocotyledons (e.g. members of the Haemodoraceae, Iridaceae, Liliaceae *sensu lato*, Xyridaceae and Xanthorrhoeaceae).

Secondly, the role of litter in plant recruitment after fire is poorly understood, especially in Australia despite numerous related studies (e.g., Lamont *et al.* 1993; Facelli & Kerrigan 1996; Facelli & Ladd 1996; Facelli *et al.* 1999; Hastwell & Facelli 2000; Barritt & Facelli 2001; Clarke & Davison 2001). There are a number of components of this role that warrant investigation. These include the interaction of litter and vertebrate / invertebrate seed predation after fire, the dynamics and spatial distribution of litter in the early post-fire environment (preliminary investigations were presented in Chapter 2) and the direct impact of litter on recruitment of seedlings.

Better understanding of the impact of fire on populations of seed predators, especially vertebrates, would also be welcome. The predominant vertebrate seed predators in the Sydney region appear to be rats (*Rattus fuscipes* in particular – Auld & Denham 1999, 2001; Denham & Auld 2002). They are generalist feeders, who presumably eat seeds whenever they are available and particularly when other foods are

in poor supply. Their population dynamics with respect to fire *regimes* are poorly known, as is the influence of size, patchiness or intensity of individual fires (Sutherland & Dickman 1999; Whelan *et al.* 2002). Thirdly, the ability of habitats to support individuals after fire (microsite limitation), and when competitive interactions affect community composition are poorly understood. The immediate post-fire recruitment phase is likely to be highly competitive, with many new seedlings competing with each other and with resprouting vegetation. Does this competition create gaps that may be filled by late recruiting species? What is the role of competition in recruitment of pyrogenic flowering species? Exploring the temporal changes in microsite availability may reveal much about the assembly rules of fire-prone habitats (Keddy 1992).

Chapter 6 - References

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Chapter 7 - Appendices

Appendix 3.1. Repeated measures ANOVA table for the proportion of genets surviving up to 7 months after planting. Significant sources at $\alpha=0.01$ are in bold font. The factor referred to as COVER\$ is the microhabitat classification.

Between subjects

Source	SS	df	MS	F	P
SITE\$	6.723	2	3.361	19.397	<0.001
COVER\$	0.326	2	0.163	0.939	0.392
CLIP\$	1.129	1	1.129	6.513	0.011
CAGE\$	60.445	1	60.445	348.794	<0.001
YEAR	0.003	1	0.003	0.016	0.900
SITE\$*COVER\$	1.003	4	0.251	1.447	0.219
SITE\$*CLIP\$	0.761	2	0.380	2.195	0.114
SITE\$*CAGE\$	9.907	2	4.954	28.584	<0.001
SITE\$*YEAR	5.637	2	2.818	16.263	<0.001
COVER\$*CLIP\$	0.084	2	0.042	0.242	0.786
COVER\$*CAGE\$	0.247	2	0.124	0.713	0.491
COVER\$*YEAR	0.423	2	0.211	1.220	0.297
CLIP\$*CAGE\$	2.612	1	2.612	15.074	<0.001
CLIP\$*YEAR	0.073	1	0.073	0.422	0.516
SITE\$*COVER\$*CLIP\$	1.212	4	0.303	1.748	0.140
SITE\$*COVER\$*CAGE\$	0.724	4	0.181	1.044	0.385
SITE\$*COVER\$*YEAR	0.620	4	0.155	0.894	0.468
SITE\$*CLIP\$*CAGE\$	0.413	2	0.207	1.192	0.306
SITE\$*CLIP\$*YEAR	0.519	2	0.260	1.498	0.226
COVER\$*CLIP\$*CAGE\$	0.412	2	0.206	1.189	0.306
COVER\$*CLIP\$*YEAR	0.321	2	0.160	0.925	0.398
SITE\$*COVER\$*CLIP\$*CAGE\$	0.648	4	0.162	0.935	0.444
Error	41.418	239	0.173		

Within subjects

Source	SS	df	MS	F	P	G-G	H-F
Time	54.195	4	13.549	480.568	<0.001	<0.001	<0.001
Time*SITE\$	1.605	8	0.201	7.115	<0.001	<0.001	<0.001
Time*COVER\$	0.273	8	0.034	1.211	0.289	0.300	0.295
Time*CLIP\$	0.782	4	0.196	6.935	<0.001	<0.001	<0.001
Time*CAGE\$	3.389	4	0.847	30.053	<0.001	<0.001	<0.001
Time*YEAR	0.790	4	0.197	7.004	<0.001	<0.001	<0.001
Time*SITE\$*COVER\$	0.559	16	0.035	1.240	0.230	0.256	0.243
Time*SITE\$*CLIP\$	0.194	8	0.024	0.860	0.550	0.517	0.535
Time*SITE\$*CAGE\$	2.867	8	0.358	12.712	<0.001	<0.001	<0.001
Time*SITE\$*YEAR	1.824	8	0.228	8.086	<0.001	<0.001	<0.001
Time*COVER\$*CLIP\$	0.199	8	0.025	0.884	0.529	0.499	0.516
Time*COVER\$*CAGE\$	0.268	8	0.034	1.190	0.302	0.311	0.307
Time*COVER\$*YEAR	0.102	8	0.013	0.454	0.888	0.828	0.862
Time*CLIP\$*CAGE\$	0.066	4	0.016	0.581	0.676	0.614	0.647
Time*CLIP\$*YEAR	0.464	4	0.116	4.118	0.003	0.008	0.005
Time*SITE\$*COVER\$* CLIP\$	0.547	16	0.034	1.213	0.251	0.274	0.262
Time*SITE\$*COVER\$* CAGE\$	0.792	16	0.050	1.756	0.033	0.058	0.043
Time*SITE\$*COVER\$* YEAR	0.803	16	0.050	1.780	0.029	0.054	0.040
Time*SITE\$*CLIP\$* CAGE\$	0.247	8	0.031	1.095	0.364	0.363	0.364
Time*SITE\$*CLIP\$* YEAR	0.317	8	0.040	1.405	0.190	0.215	0.202
Time*COVER\$*CLIP\$* CAGE\$	0.301	8	0.038	1.333	0.223	0.244	0.234
Time*COVER\$*CLIP\$* YEAR	0.507	8	0.063	2.250	0.022	0.042	0.030
Time*SITE\$*COVER\$* CLIP\$*CAGE\$	0.276	16	0.017	0.613	0.875	0.819	0.850
Error	26.953	956	0.028				

Appendix 3.2. ANOVA table for the proportion of genets that ever had the opportunity to become seedlings. Significant sources at $\alpha=0.01$ are in bold font.

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
SITE\$	0.020	2	0.010	0.507	0.603
COVER\$	0.255	2	0.128	6.440	0.002
CAGE\$	0.330	1	0.330	16.660	<0.001
CLIP\$	0.148	1	0.148	7.484	0.007
YEAR	0.015	1	0.015	0.737	0.391
SITE\$*COVER\$	0.158	4	0.039	1.989	0.097
SITE\$*CAGE\$	0.054	2	0.027	1.354	0.260
SITE\$*CLIP\$	0.082	2	0.041	2.076	0.128
SITE\$*YEAR	0.276	2	0.138	6.971	0.001
COVER\$*CAGE\$	0.037	2	0.018	0.926	0.398
COVER\$*CLIP\$	0.050	2	0.025	1.259	0.286
COVER\$*YEAR	0.006	2	0.003	0.148	0.863
CAGE\$*CLIP\$	0.015	1	0.015	0.748	0.388
CAGE\$*YEAR	0.004	1	0.004	0.194	0.660
CLIP\$*YEAR	0.071	1	0.071	3.604	0.059
SITE\$*COVER\$*CAGE\$	0.192	4	0.048	2.416	0.050
SITE\$*COVER\$*CLIP\$	0.072	4	0.018	0.905	0.462
SITE\$*COVER\$*YEAR	0.200	4	0.050	2.528	0.042
SITE\$*CAGE\$*CLIP\$	0.000	2	0.000	0.004	0.996
SITE\$*CAGE\$*YEAR	0.080	2	0.040	2.007	0.137
SITE\$*CLIP\$*YEAR	0.006	2	0.003	0.140	0.869
COVER\$*CAGE\$*CLIP\$	0.024	2	0.012	0.593	0.553
COVER\$*CAGE\$*YEAR	0.020	2	0.010	0.497	0.609
COVER\$*CLIP\$*YEAR	0.059	2	0.030	1.499	0.226
CAGE\$*CLIP\$*YEAR	0.029	1	0.029	1.440	0.232
SITE\$*COVER\$*CAGE\$*CLIP\$	0.072	4	0.018	0.907	0.461
SITE\$*COVER\$*CAGE\$*YEAR	0.017	4	0.004	0.211	0.932
SITE\$*COVER\$*CLIP\$*YEAR	0.071	4	0.018	0.891	0.470
SITE\$*CAGE\$*CLIP\$*YEAR	0.048	2	0.024	1.220	0.297
COVER\$*CAGE\$*CLIP\$*YEAR	0.002	2	0.001	0.059	0.943
SITE\$*COVER\$*CAGE\$*CLIP\$*YEAR	0.067	4	0.017	0.845	0.498
Error	4.302	217	0.020		

Appendix 3.3. ANOVA table for the proportion of genets and that were still alive

after seven months. Significant sources at $\alpha=0.01$ are in bold font.

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
SITE\$	0.024	2	0.012	1.055	0.350
COVER\$	0.069	2	0.035	3.088	0.048
CAGE\$	0.157	1	0.157	13.959	<0.001
CLIP\$	0.060	1	0.060	5.362	0.022
YEAR	0.070	1	0.070	6.208	0.013
SITE\$*COVER\$	0.116	4	0.029	2.587	0.038
SITE\$*CAGE\$	0.003	2	0.002	0.150	0.861
SITE\$*CLIP\$	0.042	2	0.021	1.862	0.158
SITE\$*YEAR	0.073	2	0.036	3.236	0.041
COVER\$*CAGE\$	0.005	2	0.002	0.219	0.803
COVER\$*CLIP\$	0.006	2	0.003	0.262	0.770
COVER\$*YEAR	0.028	2	0.014	1.241	0.291
CAGE\$*CLIP\$	0.017	1	0.017	1.546	0.215
CAGE\$*YEAR	0.004	1	0.004	0.387	0.534
CLIP\$*YEAR	0.086	1	0.086	7.620	0.006
SITE\$*COVER\$*CAGE\$	0.076	4	0.019	1.697	0.152
SITE\$*COVER\$*CLIP\$	0.054	4	0.014	1.210	0.307
SITE\$*COVER\$*YEAR	0.083	4	0.021	1.851	0.120
SITE\$*CAGE\$*CLIP\$	0.001	2	0.001	0.057	0.945
SITE\$*CAGE\$*YEAR	0.026	2	0.013	1.178	0.310
SITE\$*CLIP\$*YEAR	0.003	2	0.001	0.119	0.888
COVER\$*CAGE\$*CLIP\$	0.023	2	0.012	1.037	0.356
COVER\$*CAGE\$*YEAR	0.003	2	0.002	0.141	0.868
COVER\$*CLIP\$*YEAR	0.018	2	0.009	0.794	0.454
CAGE\$*CLIP\$*YEAR	0.051	1	0.051	4.549	0.034
SITE\$*COVER\$*CAGE\$*CLIP\$	0.051	4	0.013	1.134	0.342
SITE\$*COVER\$*CAGE\$*YEAR	0.015	4	0.004	0.327	0.860
SITE\$*COVER\$*CLIP\$*YEAR	0.054	4	0.014	1.211	0.307
SITE\$*CAGE\$*CLIP\$*YEAR	0.013	2	0.006	0.561	0.571
COVER\$*CAGE\$*CLIP\$*YEAR	0.000	2	0.000	0.015	0.986
SITE\$*COVER\$*CAGE\$*CLIP\$*YEAR	0.069	4	0.017	1.541	0.191
Error	2.439	217	0.011		

Appendix 3.4. ANOVA table for the proportion of seeds that were eaten or missing at the end of the experiment. Significant sources at $\alpha=0.01$ are in bold font.

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
YEAR	0.576	1	0.576	12.316	0.001
SITE\$	1.104	2	0.552	11.794	<0.001
COVER\$	0.041	2	0.021	0.438	0.646
CLIP\$	0.860	1	0.860	18.387	<0.001
CAGE\$	8.967	1	8.967	191.622	<0.001
SITE\$*YEAR	0.868	2	0.434	9.271	<0.001
COVER\$*YEAR	0.026	2	0.013	0.282	0.755
CLIP\$*YEAR	0.002	1	0.002	0.037	0.848
CAGE\$*YEAR	0.325	1	0.325	6.953	0.009
COVER\$*SITE\$	0.058	4	0.014	0.307	0.873
CLIP\$*SITE\$	0.003	2	0.001	0.032	0.969
CAGE\$*SITE\$	1.005	2	0.503	10.741	<0.001
CLIP\$*COVER\$	0.211	2	0.105	2.250	0.108
CAGE\$*COVER\$	0.142	2	0.071	1.522	0.220
CAGE\$*CLIP\$	0.114	1	0.114	2.440	0.120
CLIP\$*COVER\$*SITE\$	0.207	4	0.052	1.108	0.354
CAGE\$*COVER\$*SITE\$	0.032	4	0.008	0.174	0.952
CAGE\$*CLIP\$*COVER\$	0.069	2	0.035	0.741	0.478
CLIP\$*COVER\$*YEAR	0.123	2	0.062	1.318	0.270
CAGE\$*COVER\$*YEAR	0.012	2	0.006	0.133	0.876
CAGE\$*CLIP\$*YEAR	0.097	1	0.097	2.083	0.150
COVER\$*SITE\$*YEAR	0.235	4	0.059	1.253	0.289
CLIP\$*SITE\$*YEAR	0.130	2	0.065	1.394	0.250
CAGE\$*SITE\$*YEAR	0.315	2	0.157	3.362	0.036
Error	11.184	239	0.047		

Appendix 4.1. Repeated measures analysis of the number of live seedlings present (dead seedlings don't contribute). Significant factors at $\alpha=0.01$ are marked in bold.

Between Subjects

Source	SS	df	MS	F	P
LITTER\$	0.040	1	0.040	0.192	0.661
SPECIES\$	9.910	1	9.910	47.70	0.000
TSF	5.516	1	5.516	26.55	0.000
LITTER\$*SPECIES\$	0.001	1	0.001	0.004	0.950
LITTER\$*TSF	0.058	1	0.058	0.278	0.598
SPECIES\$*TSF	0.120	1	0.120	0.575	0.449
LITTER\$*SPECIES\$*TSF	0.207	1	0.207	0.998	0.318
SITE\$(TSF)	12.66	2	6.329	30.46	0.000
LITTER\$(SITE\$(TSF))	0.082	2	0.041	0.196	0.822
SPECIES\$(SITE\$(TSF))	1.688	2	0.844	4.061	0.018
LITTER\$*SPECIES\$(SITE\$(TSF))	0.268	2	0.134	0.646	0.525
Error	96.40	464	0.208		

Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
Days	32.55	10	3.255	258.3	0.000	0.000	0.000
days*LITTER\$	0.051	10	0.005	0.404	0.946	0.770	0.778
days*SPECIES\$	2.685	10	0.269	21.31	0.000	0.000	0.000
days*TSF	5.649	10	0.565	44.83	0.000	0.000	0.000
days*LITTER\$*SPECIES\$	0.094	10	0.009	0.744	0.683	0.539	0.544
days*LITTER\$*TSF	0.040	10	0.004	0.316	0.977	0.833	0.841
days*SPECIES\$*TSF	0.190	10	0.019	1.504	0.131	0.208	0.206
days*LITTER\$*SPECIES\$*TSF	0.040	10	0.004	0.314	0.978	0.835	0.842
days*SITE\$(TSF)	5.475	20	0.274	21.73	0.000	0.000	0.000
days*LITTER\$(SITE\$(TSF))	0.144	20	0.007	0.571	0.934	0.771	0.778
days*SPECIES\$(SITE\$(TSF))	0.858	20	0.043	3.404	0.000	0.002	0.001
days*LITTER\$*SPECIES\$(SITE\$(TSF))	0.119	20	0.006	0.471	0.977	0.847	0.854
Error	58.459	4640	0.013				
Greenhouse-Geisser Epsilon:	0.3317						
Huynh-Feldt Epsilon:	0.3452						

Appendix 4.2. Repeated measures analysis of the cumulative number of seedlings (dead seedlings contribute). Significant factors at $\alpha=0.01$ are marked in bold.

Between Subjects

Source	SS	df	MS	F	P
LITTER\$	0.086	1	0.086	0.143	0.706
SPECIES\$	18.73	1	18.73	30.94	0.000
TSF	80.28	1	80.28	132.6	0.000
LITTER\$*SPECIES\$	0.055	1	0.055	0.091	0.763
LITTER\$*TSF	0.000	1	0.000	0.000	0.994
SPECIES\$*TSF	0.101	1	0.101	0.167	0.683
LITTER\$*SPECIES\$*TSF	0.173	1	0.173	0.285	0.594
SITE\$(TSF)	81.47	2	40.74	67.27	0.000
LITTER\$(SITE\$(TSF)	2.530	2	1.265	2.089	0.125
SPECIES\$(SITE\$(TSF)	1.007	2	0.504	0.832	0.436
LITTER\$*SPECIES\$(SITE\$(TSF)	0.579	2	0.290	0.478	0.620
Error	281.0	464	0.606		

Within Subjects

Source	SS	df	MS	F	P	G-G	H-F
Days	98.69	10	9.869	803.9	0.000	0.000	0.000
days*LITTER\$	0.025	10	0.002	0.200	0.996	0.717	0.725
days*SPECIES\$	4.107	10	0.411	33.46	0.000	0.000	0.000
days*TSF	12.22	10	1.222	99.54	0.000	0.000	0.000
days*LITTER\$*SPECIES\$	0.011	10	0.001	0.089	1.000	0.828	0.835
days*LITTER\$*TSF	0.026	10	0.003	0.210	0.996	0.709	0.717
days*SPECIES\$*TSF	0.124	10	0.012	1.007	0.434	0.335	0.338
days*LITTER\$*SPECIES\$*TSF	0.032	10	0.003	0.262	0.989	0.668	0.676
days*SITE\$(TSF)	16.63	20	0.831	67.71	0.000	0.000	0.000
days*LITTER\$(SITE\$(TSF)	0.373	20	0.019	1.519	0.065	0.214	0.213
days*SPECIES\$(SITE\$(TSF)	0.519	20	0.026	2.113	0.003	0.107	0.105
days*LITTER\$*SPECIES\$(SITE\$(TSF)	0.116	20	0.006	0.472	0.977	0.672	0.679
Error	56.96	4640	0.012				
Greenhouse-Geisser Epsilon:	0.1285						
Huynh-Feldt Epsilon:	0.1328						

Appendix 4.3. Results of ANOVA on the number of seeds eaten or missing, based on seed remains.

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
TSF	72.85	1	72.85	12.89	0.000
LITTER\$	2.269	1	2.269	0.401	0.527
SPECIES\$	204.1	1	204.1	36.10	0.000
SPECIES\$*LITTER\$	0.919	1	0.919	0.163	0.687
TSF*SPECIES\$	133.4	1	133.4	23.59	0.000
LITTER\$*TSF	2.852	1	2.852	0.504	0.478
TSF*SPECIES\$*LITTER\$	2.002	1	2.002	0.354	0.552
SITE\$(TSF)	17.354	2	8.677	1.535	0.217
LITTER\$*SITE\$(TSF)	7.387	2	3.694	0.653	0.521
SPECIES\$*SITE\$(TSF)	63.19	2	31.59	5.588	0.004
SPECIES\$*LITTER\$*SITE\$(TSF)	7.721	2	3.860	0.683	0.506
Error	2623	464	5.654		

Appendix 4.4. Results of ANOVA on the number of seeds establishing as seedlings, based on observed seedlings and seed remains.

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
TSF\$	512.5	1	512.5	121.4	0.000
LITTER\$	0.133	1	0.133	0.032	0.859
SPECIES\$	0.208	1	0.208	0.049	0.824
SPECIES\$*LITTER\$	0.675	1	0.675	0.160	0.689
TSF*SPECIES\$	8.008	1	8.008	1.897	0.169
LITTER\$*TSF	2.133	1	2.133	0.505	0.477
TSF\$*SPECIES\$*LITTER\$	7.008	1	7.008	1.660	0.198
SITE\$(TSF\$)	500.1	2	250.0	59.24	0.000
LITTER\$*SITE\$(TSF)	12.62	2	6.308	1.495	0.225
SPECIES\$*SITE\$(TSF)	0.533	2	0.267	0.063	0.939
SPECIES\$*LITTER\$*SITE\$(TSF)	4.333	2	2.167	0.513	0.599
Error	1958	464	4.221		