

COMPLETION REPORT TO THE AUSTRALIAN FLORA FOUNDATION

Project title: Seed longevity and viability in several plant species of Box-Ironbark Forests

Corinna Orscheg
School of Anthropology, Geography and Environmental Studies
University of Melbourne, Parkville, 3010

Summary

Very little is known of ecological processes in threatened Victorian Box-Ironbark forests. This study examined patterns of *in situ* and *ex situ* seed longevity, dormancy and viability decay over three years for eight species. The species selected comprised three 'soft' seeded species (*Briza maxima*, *Eucalyptus tricarpa*, *Ozothamnus obcordata*) and five 'hard' seeded species of the Mimosaceae (three common species, *Acacia genistifolia*, *A. pycnantha* and *Pultenaea prostrata*, and two rare or threatened species *A. ausfeldii* and *A. williamsonii*).

Soft-seeded species all displayed *in situ* longevity patterns typical of species with a transient soil seedbank. For all three species *in situ* seed loss was greatest after 12 months, however the source of seed loss varied. Seed was lost to decay for the two native species, while for the sole exotic species most seed was lost to germination. *Briza maxima* was also the only species for which seed was recovered after three years of *in situ* burial, albeit a very small fraction of the original amount buried (2.5%). Under *ex situ* storage the proportion of viable seed declined little over three years for three species examined (between 1.7% and 2.5%). For the two native species this suggests their soil seedbanks have the potential to contribute to regeneration beyond a year, however *in situ* conditions affecting seed decay prevent seed remaining in the soil seedbank for greater than a year.

For all hard-seeded species seed was recovered after three years of *in situ* burial, but the proportion of seed varied between species. The majority of seed from *Acacia ausfeldii*, *A. genistifolia* and *Pultenaea prostrata* was recovered after three years and viability differed little to that prior to burial. However, for *A. pycnantha* and *A. williamsonii* considerable seed was lost *in situ*, mostly due to germination.

Levels of dormancy also varied among hard-seeded species. Dormancy levels were initially high for all species prior to burial (c.98-100%), however proportions of dormant seed declined considerably for *A. pycnantha* and *A. williamsonii* (61.6±9.1% and 50.4±7.4% non-dormant seed respectively after three years of burial). Proportions of dormant seed also declined for *A. ausfeldii* and *A. genistifolia*, but not to the same degree (4.5±1.3% and 15±3.3% non-dormant seed after three years respectively). As heat associated with fire is a dormancy breaking cue in these species (Brown *et al.* 2000). This has consequences for species persistence considering that current fuel loads and accumulation rates in Box-Ironbark forest suggest infrequent fire events.

Introduction

The Victorian box-ironbark system, which extends from Stawell in the west to Chiltern in the northeast of the state, represents a typical anthropogenic disturbance pattern found following European settlement in temperate Australia. Following initial exploration the natural resources of the system were exploited heavily through grazing, agriculture, mining and logging. Most current remnants have regenerated from more or less complete clearance during the 1850's goldrush and have since been cut over at least once (Neuman, 1961). The soils of the box-ironbark system have been extensively degraded, a product of alluvial mining during the goldrush, as well as later topsoil extraction for road-making. As a result current profiles are largely undifferentiated and an A₁ horizon is present at few localities. A policy of fire suppression has been in place since the 1920's, which included understorey clearing in the early 19th century and prescription burning for asset protection, the latter continues today. The effect that this extensive disturbance history has had on regeneration processes is unclear.

The soil seed-bank can form an important component of community regeneration and its composition at any one time is largely a product of individual species seed-longevity and dormancy status. Seed longevity has been used to classify two broad seed-bank traits; transient (≤ 12 months longevity) and persistent (≥ 12 months longevity) (Thompson & Grime, 1979). Longevity also varies within these two traits. Transient seed-banks can have very short longevity whereby seed that does not germinate on seedfall is lost quickly to predation or decay (e.g. Morgan, 1995; Yates *et al.*, 1995). Among species regarded as persistent, seed-banks can be further categorised into short-term (1-5 years) and long-term (> 5 years) persistence, although the division is arbitrary and in reality a continuum best describes the range of seed-persistence (Thompson, 1992).

Seed dormancy status contributes to the variation in longevity patterns. Dormancy can be generated by morphological, or physiological means (Fenner & Thompson, 2005). The non-dormant fraction of transient and persistent seed-banks will germinate readily once water and temperature requirements are met, while the dormant fraction can require one or more specific cues to break physical or chemical dormancy mechanisms (Baskin & Baskin, 1989; Murdoch & Ellis, 1992). The proportions of dormant and non-dormant seed can vary seasonally (Vleeshouwers *et al.*, 1995; Baskin & Baskin, 1998; Fenner & Thompson, 2005) and with seed age (Morrison *et al.*, 1992; Auld *et al.*, 2000). Seasonal release from dormancy is likely to be a response to a specific maximum and minimum temperature regime and if environmental cues required for germination, such as light, are not met while seed is non-dormant, dormancy may be re-imposed when that specific regime returns later in the year (Vleeshouwers *et al.*, 1995). Levels of dormancy may also decline after initial seed release (Bradbeer, 1988). In a sample of Australian legumes Morrison *et al.* (1992) found species where the proportion of dormant seed declined over time as well as species whose dormant fraction did not differ significantly over the four years of laboratory

storage. They attribute the variation in dormancy dynamics partly to a variation in the physical and chemical structure of the seed testa, but suggest that seed size and embryo age may also play a role.

Several studies have examined seed-longevity and persistence dynamics in southeastern Australian vegetation (Lunt, 1995; Morgan, 1995; Leishman & Westoby, 1998; Auld *et al.*, 2000). Studies of dry sclerophyll communities have focused on fire-prone NSW communities. None have addressed longevity patterns in the box-ironbark system. While broad longevity patterns might be extrapolated from generic or familial patterns observed in other communities, exploring patterns more specifically provides an opportunity to add to the very limited ecological understanding of box-ironbark forests especially for characteristic species or those that may represent a management issue. Further, while little is known of the fire ecology of box-ironbark forests current fuel loads and fuel accumulation rates suggest fires are likely to occur infrequently and be of low intensity, which contrasts to the usual fire regimes associated with dry sclerophyll forests. Notwithstanding, these forests support a considerable number of species with traits that suggest an adaptation to fire. Particularly common are hard-seeded species of the Fabaceae and Mimosaceae that typically require heat to break physical dormancy (Cavanagh, 1987; Auld & O'Connell, 1991). Understanding seed longevity of these fire-cued obligate-seeding species is particularly important where fires are infrequent. Species may become locally extinct as the time between fires exceeds both species' life spans and seed longevity (Keith, 1996). For Australian species of Fabaceae and Mimosaceae little is known of whether their dormancy varies with the amount of time seed remains in the soil seed-bank (Morrison *et al.*, 1992). If dormancy decays over time then there is the potential for inter-fire recruitment in these hard seeded species.

This study aimed to characterise the longevity and dormancy dynamics of eight species of the Victorian box-ironbark system, which included hard- and soft-seeded species (*Acacia ausfeldii*, *A. genistifolia*, *A. pycnantha*, *A. williamsonii*, *Briza maxima*, *Eucalyptus tricarpa*, *Ozothamnus obcordata*, *Pultenaea prostrata*). Species were selected to represent common components of the box-ironbark forest, or to inform the management of the species. Specifically the study used an *in situ* burial experiment to examine how seed loss, dormant and non-dormant fractions varied over time.

Methods

Study species

Mature seed was collected from box-ironbark populations of all species in spring and summer of 2001/2002 (Table 1). Seed was collected from over 50 individuals and bulked for each species. For *Acacia ausfeldii*, *A. genistifolia* and *Briza maxima*, seed collected in 2000/2001 was also used in trials to identify if viability varied between one year old seed and fresh seed. Mean seed mass for each species were estimated from 5 replicates of 50 seeds. For species with dispersal structures such as eliasomes, pappus or membranes, seed masses were inclusive.

Table 1. Provenance, regeneration traits, life-form seed mass and sample size of the eight box-ironbark species studied. Conservation status v = vulnerable in Victoria, r = rare in Victoria (Victorian flora information system April 2004, Department of Sustainability and Environment). Flora Reserve (FR), National Park (NP), State Forest (SF).

Family / species	Provenance	Seeds per replicate		Species characters		Life-form	Conservation status
		2000	2001	Mean seed mass \pm SE (mg)	Regeneration trait		
Poaceae							
<i>Briza maxima</i>	Rushworth SF	30	25	5.3 \pm 0.1	Obligate seeder	Annual grass	Exotic
Asteraceae							
<i>Ozothamnus obcordata</i>	Greater Bendigo NP	-	25	0.061 \pm 0.002	Obligate seeder	Perennial shrub	-
Fabaceae							
<i>Pultenaea prostrata</i>	Deep Lead FR	-	20	1.81 \pm 0.01	Obligate seeder	Perennial shrub	-
Mimosaceae							
<i>Acacia ausfeldii</i>	Greater Bendigo NP	30	25	8.4 \pm 0.1	Obligate seeder	Perennial shrub	v
<i>Acacia genistifolia</i>	Rushworth SF	30	25	27.5 \pm 0.2	Obligate seeder	Perennial shrub	-
<i>Acacia pycnantha</i>	Rushworth SF	30	-	20.8 \pm 0.3	Obligate seeder	Perennial shrub	-
<i>Acacia williamsonii</i>	Rushworth SF	25	-	8.8 \pm 0.1	Obligate seeder	Perennial shrub	r
Myrtaceae							
<i>Eucalyptus tricarpa</i>	Rushworth SF	-	25	0.72 \pm 0.02	Resprouter	Tree	-

Acacia ausfeldii Regal. (Plate 1)

A medium perennial shrub (2-4m) that relies on seed for regeneration. The species is listed as vulnerable in Victoria and is currently known from scattered sites in central Victoria where it can form dense local stands (Fig 1). Department of Sustainability and Environment records suggest the species distribution extended to Inglewood in 1975, however the population has not been relocated. A recent study examining seed-banks preserved under mullock heaps deposited during the 1850's gold rush found an *A. ausfeldii* seed from St Arnaud samples (Parkinson, 2003). However, extant populations have not been located in the area.

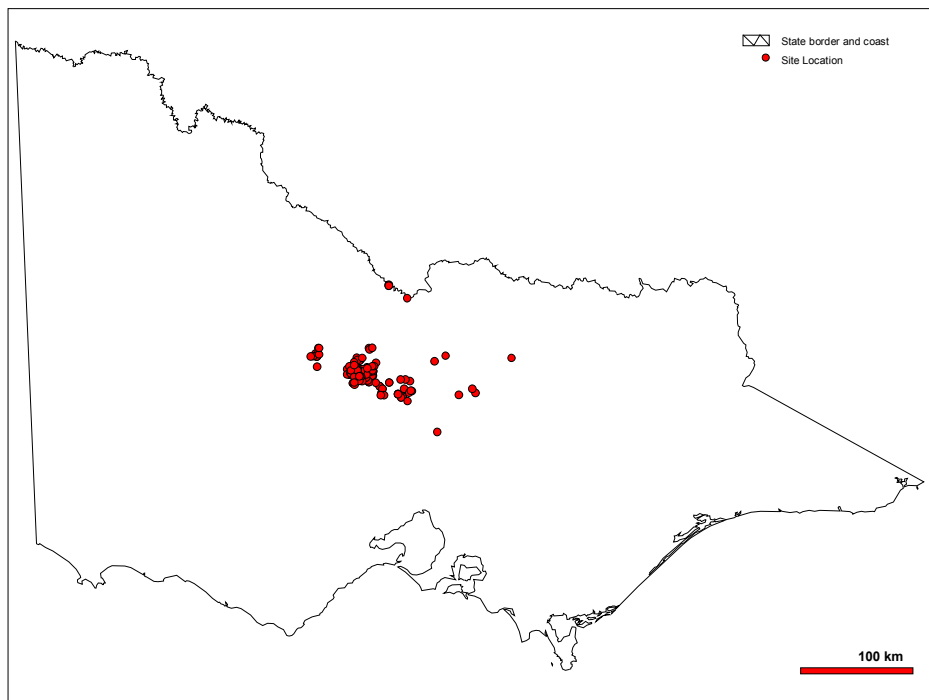
Brown *et al.* (2003) suggest the rarity of *A. ausfeldii* may be partly attributed to a combination of smaller seed size limiting the depth from which seed may successfully germinate, and the higher temperatures required to break seed dormancy (c.100°C).

The species may flower from August to October (Walsh & Entwisle, 1996) and mature seed was available in the canopy in December to early January. The seed is distributed by ants and has a small cream coloured eliasome.



Photo by: Paul Gullan/Viridans Images

Plate 1. *Acacia ausfeldii*. Data Source: 'Victorian Flora Site Database', © The State of Victoria, Department of Sustainability and Environment (accessed via the 'Flora Information System', [October, 2006] - © Viridans Biological Databases).



Data: Flora Information System, Biodiversity and Natural Resources, DSE - May 2005 - © Viridans Biological Databases

Figure 1. Current known distribution of *Acacia ausfeldii* in Victoria. Data Source: 'Victorian Flora Site Database', © The State of Victoria, Department of Sustainability and Environment (accessed via the 'Flora Information System', [July, 2006] - © Viridans Biological Databases).

Acacia genistifolia Link. (Plate 2)

A common and widespread obligate seeding medium shrub (0.6-3m) whose distribution in the box-ironbark system extends from Stawell in the west to Chiltern in the northeast (Fig. 2). The species flowers from February to October (Walsh & Entwisle, 1996) and in box-ironbark mature seed was available in the canopy in December to early January. The seed is distributed by ants and has a cream coloured eliasome.



Plate 2. *Acacia genistifolia* inflorescence, Castlemaine, Central Victoria.

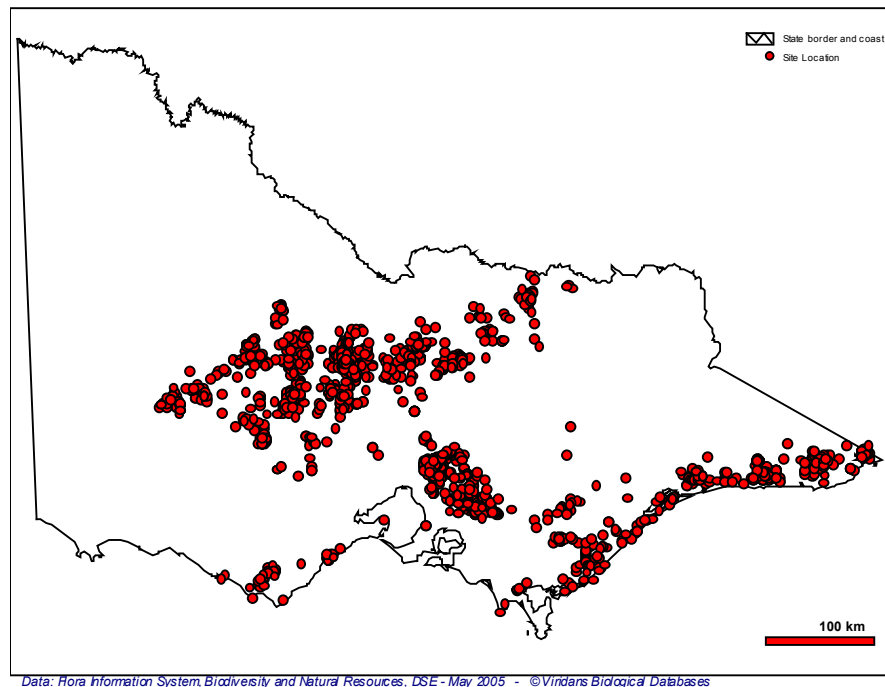


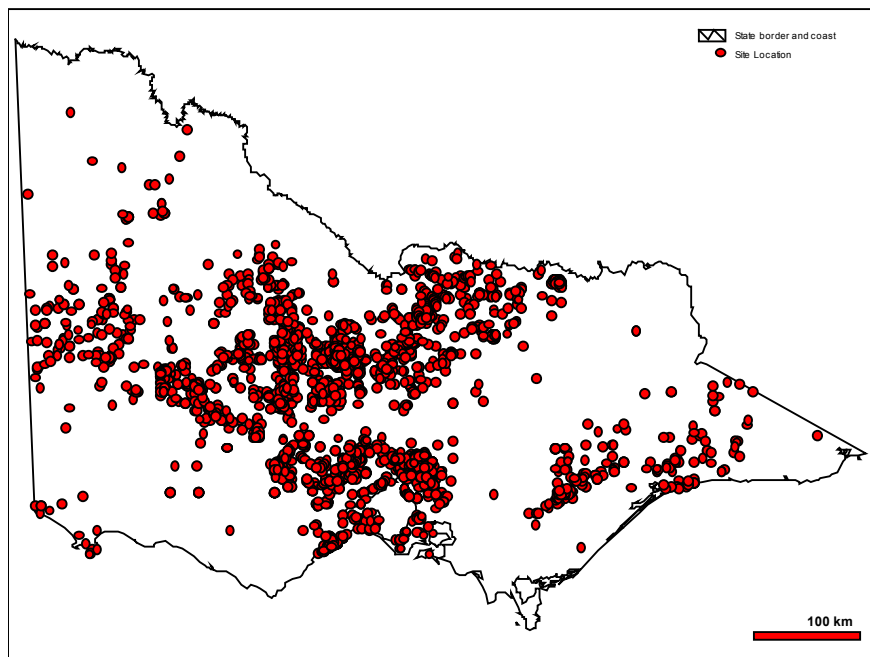
Figure 2. Current known distribution of *Acacia genistifolia* in Victoria. Data Source: 'Victorian Flora Site Database', © The State of Victoria, Department of Sustainability and Environment (accessed via the 'Flora Information System', [July, 2006] - © Viridans Biological Databases).

Acacia pycnantha Benth. (Plate 3 a & b)

A common and widespread obligate seeding shrub that may reach 8m in parts of Victoria (Walsh & Entwisle, 1996), but averages 2-3m in the Box-Ironbark region (pers. ob.). It occurs throughout the box-ironbark system from Stawell in the west to Chiltern in the northeast (Fig. 4). The species is scattered throughout the understorey and following fire can form locally abundant stands. The species flowers from August to October (Walsh & Entwisle, 1996). In the box-ironbark mature seed was in the canopy from December to early January. The seed is distributed by ants and has a cream coloured eliasome.



Plate 3 a & b. *Acacia pycnantha* life form (a) and inflorescence (b), Castlemaine, Central Victoria.



Data: Flora Information System Biodiversity and Natural Resources, DSE - May 2005 - ©Viridans Biological Databases

Figure 3. Current known distribution of *Acacia pycnantha* in Victoria. Data Source: 'Victorian Flora Site Database', © The State of Victoria, Department of Sustainability and Environment (accessed via the 'Flora Information System', [July, 2006] - © Viridans Biological Databases).

Acacia williamsonii Court. (Plate 4)

An obligate seeding medium shrub to 2m, which is listed as rare at the state level (Victorian Flora Information System, April 2004). It is restricted to the understorey of dry sclerophyll forests around Bendigo and Rushworth where it forms dense stands locally (Fig 4.). Rarity of the species is probably a consequence of restricted habitat, but high abortion rates (possible self-incompatibility) and considerable granivory may contribute to the species rarity (Brown *et al.*, 2003).

Flowers are borne in August to September (Walsh & Entwisle, 1996) and mature seed was available in the canopy in December to early January. The seed is distributed by ants and has a small cream coloured eliasome.

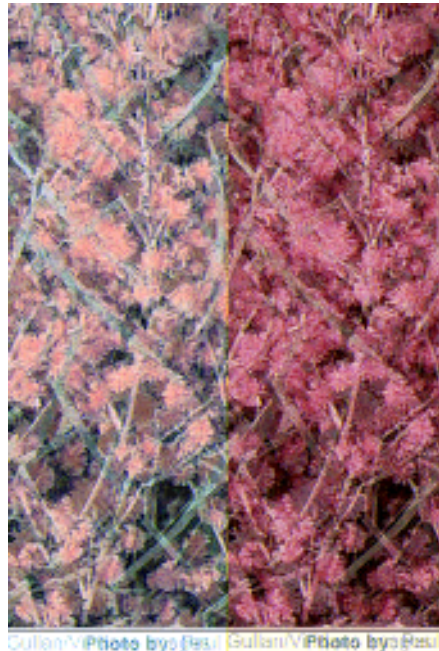
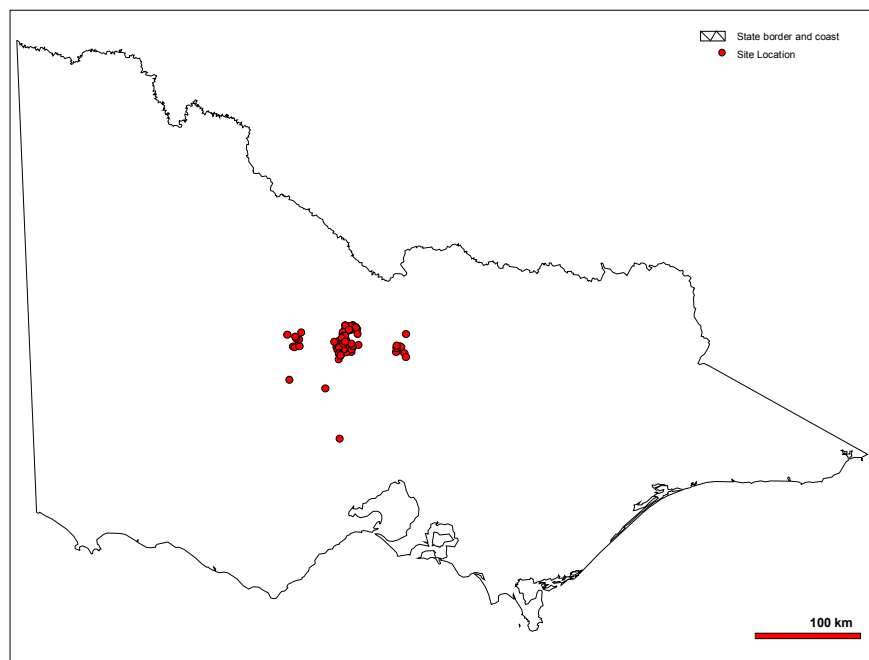


Plate 4. *Acacia williamsoni*. Data Source: 'Victorian Flora Site Database', © The State of Victoria, Department of Sustainability and Environment (accessed via the 'Flora Information System', [October, 2006] - © Viridans Biological Databases).



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Figure 4. Current known distribution of *Acacia williamsonii* in Victoria. Data Source: 'Victorian Flora Site Database', © The State of Victoria, Department of Sustainability and Environment (accessed via the 'Flora Information System', [July, 2006] - © Viridans Biological Databases).

Briza maxima L. (Plate 5 a & b)

A naturalised obligate seeding annual grass of Mediterranean origin that is widely distributed in Victoria (Walsh & Entwisle, 1994, Fig. 5). While it is not considered a major agricultural weed, it is capable of reducing native species richness by c.75% by displacing native geophytes and herbs (Auld & Medd, 1992; Blood, 2001). Where it occurs in box-ironbark forests it can form a considerable component of the soil seed-bank (Orscheg *et al.* in prep.). Flowering in the species occurs from August to December (Walsh & Entwisle, 1994) and in the box-ironbark mature seed was available in November. The seed is anemocochorous.

(a)

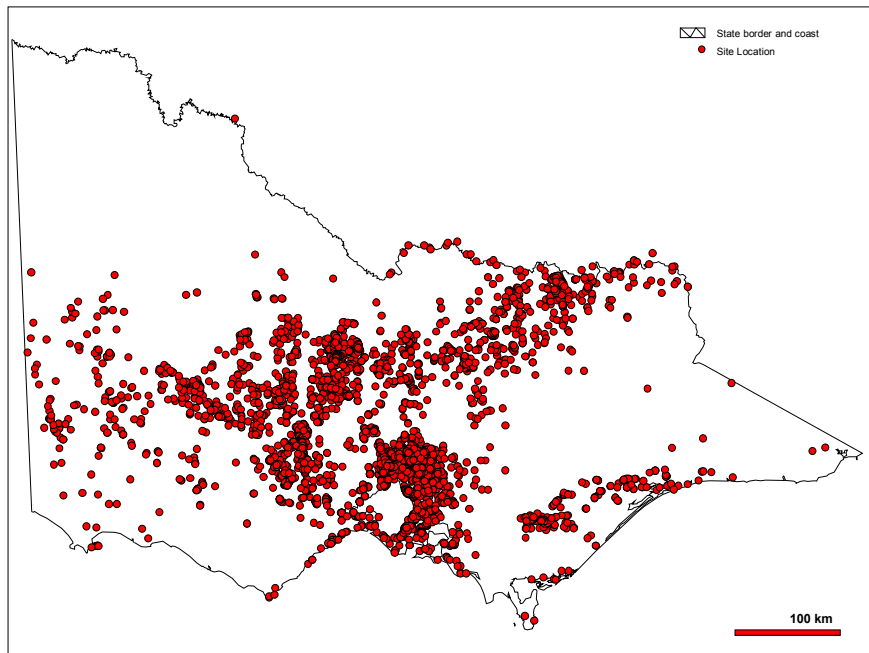


Plate 5 a & b. *Briza maxima* scattered amongst rocks, litter and the tussock grass *Chionochloa pallida*, Castlemaine, Central Victoria (a) and life form (b). Data Source for (b): 'Victorian Flora Site Database', © The State of Victoria, Department of Sustainability and Environment (accessed via the 'Flora Information System', [October, 2006] - © Viridans Biological Databases).



Photo by: Paul Gullan/Viridans Images

(b)



Data: Flora Information System, Biodiversity and Natural Resources, DSE - May 2005 - © Viridans Biological Databases

Figure 5. Current known distribution of *Briza maxima* in Victoria. Data Source: 'Victorian Flora Site Database', © The State of Victoria, Department of Sustainability and Environment (accessed via the 'Flora Information System', [July, 2006] - © Viridans Biological Databases).

Eucalyptus tricarpa (L.A.S. Johnson) L.A.S. Johnson & K.D. Hill. (Plate 6)

A perennial facultative sprouting tree to 35m, which is a member of the subgenus *Symphyomyrtus* and is the most common Victorian Ironbark. It is common through out the Victoria box-ironbark forests north of the Great Dividing Ranges and also occurs in the dry foothills forests south of the range in Gippsland (Fig. 6). Flowering in the species occurs through most of the year (June – February) (Walsh & Entwisle, 1996), but locally flowering can be patchy (Wilson & Bennett, 1999). Mature seed can be obtained from capsules at any time of year.

Seed based regeneration in box-ironbark forests is limited. While seed germinates readily in darkness at 18°C *ex situ* and seed production and viability is high at the tree and population level, conditions for *in situ* germination are yet to be identified (Orscheg *et al.* in prep.). The species was more or less absent from the soil seed-bank (Orscheg *et al.* in prep.), thus characterising its longevity pattern will add to the current understanding surrounding seed-based recruitment in the species.

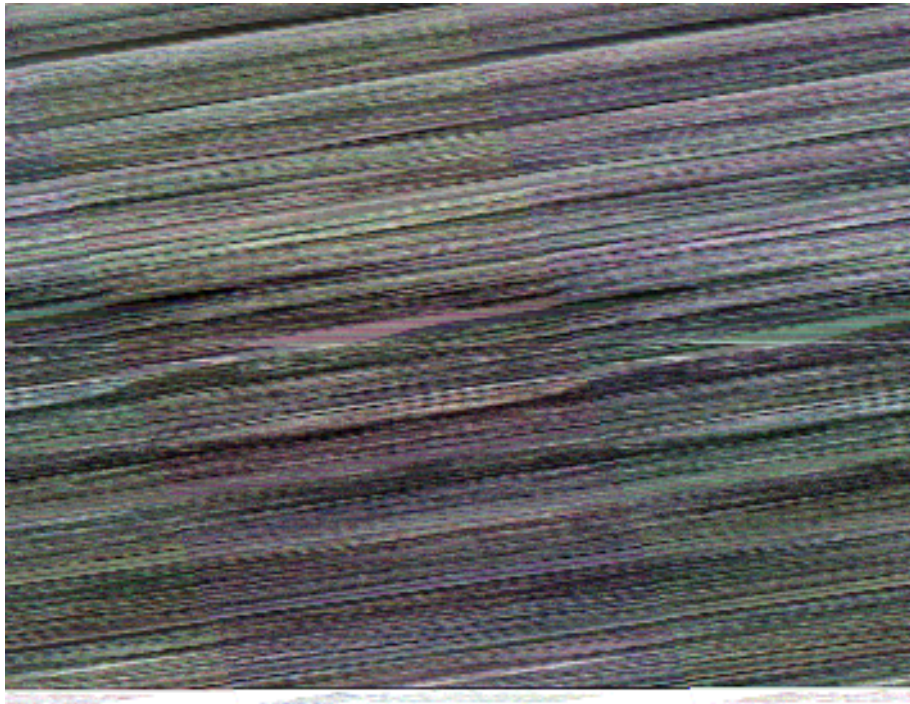


Plate 6. *Eucalyptus tricarpa* life form and details of infructescence, leaves, inflorescence and bark. Data Source: 'Victorian Flora Site Database', © The State of Victoria, Department of Sustainability and Environment (accessed via the 'Flora Information System', [October, 2006] - © Viridans Biological Databases).

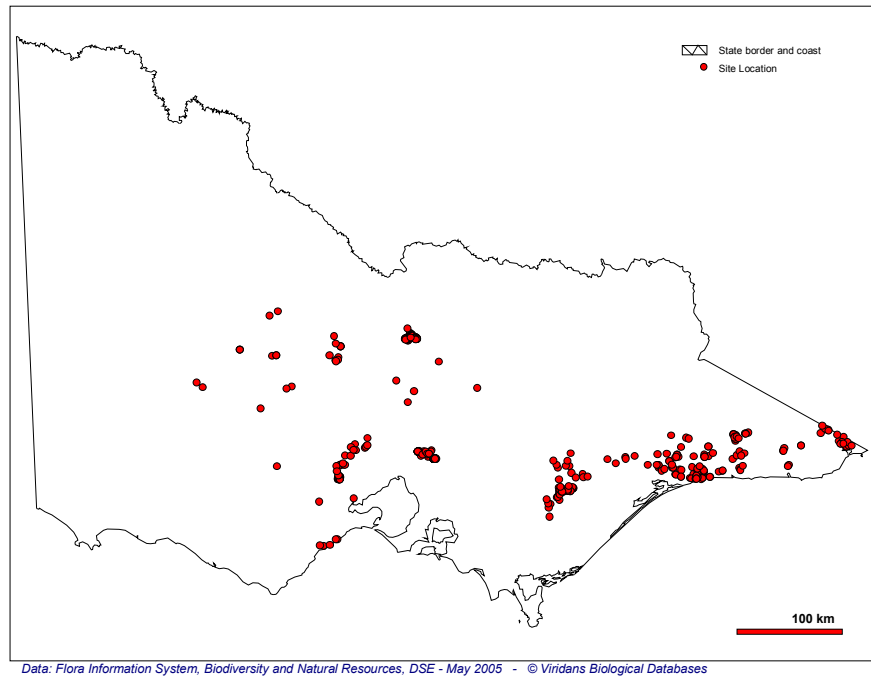


Figure 6. Current known distribution of *Eucalyptus tricarpa* in Victoria. Data Source: 'Victorian Flora Site Database', © The State of Victoria, Department of Sustainability and Environment (accessed via the 'Flora Information System', [July, 2006] - © Viridans Biological Databases).

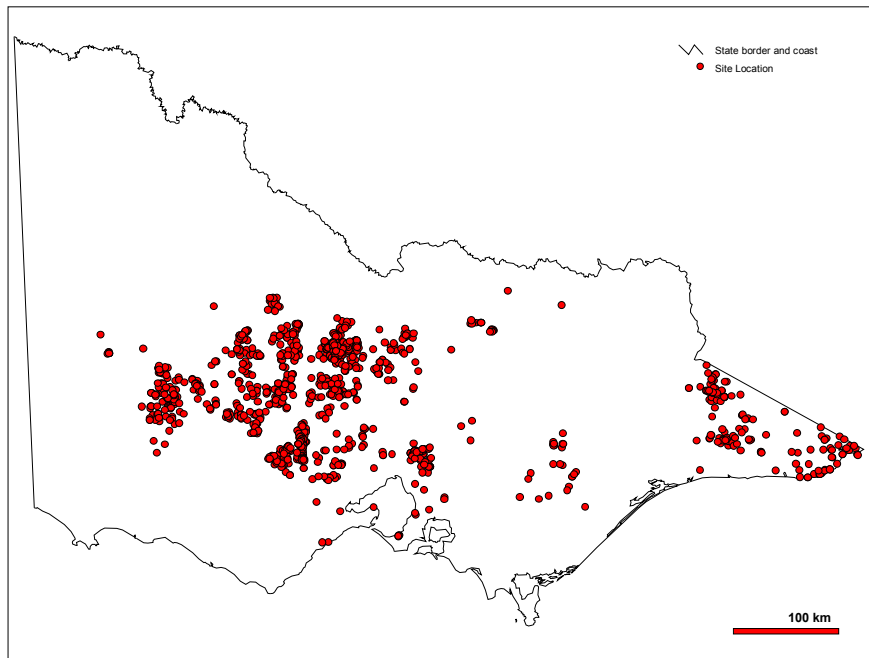
Ozothamnus obcordatus D.C. (Plate 7 a & b)

A perennial obligate seeding shrub that can reach 1m in box-ironbark forests. The species here represents the smaller leafed variant formerly corresponding to *O. obcordatus* ssp. *obcordatus* that occurs throughout central Victoria (Walsh & Entwisle, 1999, Fig. 7).

Flowers are borne from November to December (Walsh & Entwisle, 1999) and in the box-ironbark mature seed was collected in January. With a pappus of fine bristles the seed is anemochorous.



Plate 7 a & b. *Ozothamnus obcordata* life form (a) and inflorescence (b), Castlemaine, Central Victoria.

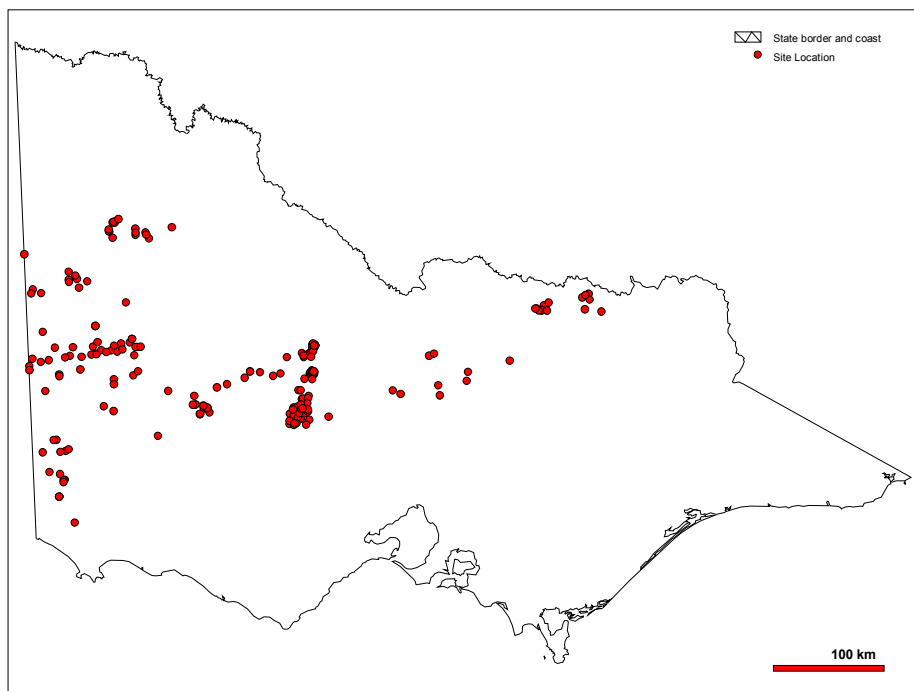


Data: Flora Information System, Biodiversity and Natural Resources, DSE - May 2005 - © Viridans Biological Databases

Figure 7. Current known distribution of *Ozothamnus obcordata* in Victoria. Data Source: 'Victorian Flora Site Database', © The State of Victoria, Department of Sustainability and Environment (accessed via the 'Flora Information System', [July, 2006] - © Viridans Biological Databases).

Pultenaea prostrata Benth. ex Hook. f.

A low perennial shrub to 0.5m, which in the box-ironbark system is found in heathier understoreys from Stawell in the west to Chiltern in the northeast (Fig. 8). Flowers are borne from September to November (Walsh & Entwisle, 1996). Mature seed was available in box-ironbark forests from December to early January. Seed has a small cream coloured eliasome.



Data: Flora Information System, Biodiversity and Natural Resources, DSE - May 2005 - © Viridans Biological Databases

Figure 8. Current known distribution of *Pultenaea prostrata* in Victoria. Data Source: 'Victorian Flora Site Database', © The State of Victoria, Department of Sustainability and Environment (accessed via the 'Flora Information System', [July, 2006] - © Viridans Biological Databases).

Ex situ germination trials were used to assess the initial proportion of non-dormant and dormant seed for each species. Four replicates of 20-30 seeds were plated into 9cm diameter plastic petri dishes on Whatman no. 40 filter-paper, watered with 10mL of distilled water and sealed with Parafilm. Seed was screened to select only that which appeared full and viable. Previous trials found most of the study species germinated under constant darkness and 18°C in a controlled temperature cabinet. *Ozothamnus obcordata* seed required a light cue. The total germination of the other species did not differ between the temperature cabinet and laboratory bench so all plates were kept on a laboratory bench under a natural light regime at 17-22°C. Plates were checked every third day and germination recorded on radicle emergence. Additional water was added when needed. Where fungal infection was evident, the plate was treated with Mancozeb. Plates were monitored for four weeks (non-dormant fraction) following which ungerminated seed was nicked with a scalpel to expose endosperm and monitored for an additional four weeks (dormant fraction). Germination was recorded on radical emergence. Viability of remaining seed was assessed under a dissecting microscope using squash tests or dissection, where the presence of a white intact embryo was taken to represent viable seed.

Burial site

All seed was buried in June 2002 at Rushworth State Forest (36°41'45"S; 144°59'15"E). The site has an undifferentiated orange dispersible silty clay soil, the result of extensive disturbance due to alluvial mining in the 1850's and a long history of erosion and clearing activities. Soils are developed from thinly bedded marine sediments (siltstone and sandstone) of the Broadford Formation (Bendigo Sheet, Geological Map Series 1997) and support a dry sclerophyll open forest dominated by *Eucalyptus tricarpa* and *E. macrorhyncha*, with *Acacia acinacea*, *A. pycnantha*, *A. genistifolia*, *Astroloma humifusum*, *Austrodanthonia* spp. and *Cassinia arcuata* common in the understorey.

Mean annual rainfall is 584mm (based on 29 years of records for Mangalore Airfield located 30km to the southeast). Rainfall occurs in all months but shows a late winter peak (Meteorology, 1995). Temperature records collected over 27 years give an average annual temperature of 20.8°C, with the highest mean maximum daily temperature of 29.3°C recorded for January and February and lowest mean daily minimum of 2.9°C for July. Temperature and rainfall conditions during the period of this study are summarized with mean climatic data in Figure 9. Average monthly rainfall over 2002-2004 was below the long-term average; 53% of the average falling in 2002, 97% in 2003 and 75% in 2004.

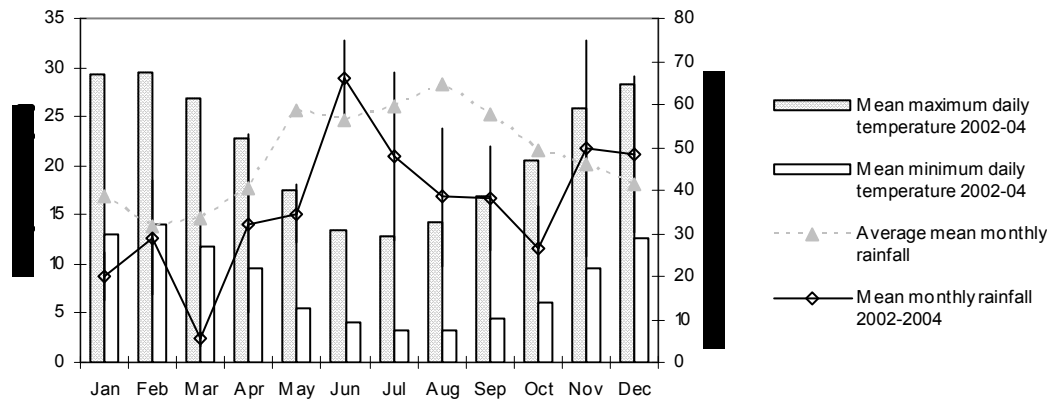


Figure 9. Summary of average climatic data for Mangalore Airfield (rainfall 29 years, temperature 27 years) and mean monthly rainfall data from 2002-2004 (\pm S.E.).

Seed longevity

For *in situ* storage, the requisite seed number (see Table 1) was placed into 20 nylon voile bags for each species. Bags were colour coded for species and cohort. A total of 40 bags were used for species with one year old and fresh seed; 20 for each cohort.

Five 0.36m² plots were established and marked at the site and in each plot four bags of each species were buried to 3cm deep. The thin leaf litter layer removed prior to digging each hole was re-distributed over each plot after filling. All bags from one plot were retrieved at one of four points over two years except for two plots in the final retrieval; spring 2002, autumn 2003, spring 2003, spring 2004 (two plots retrieved). Bag contents were examined to identify the proportion of seed that had germinated (remnants of roots or cotyledons), decayed (absent) or was intact. Intact seed was plated up using the procedure outlined above to assess the proportion of dormant and non-dormant seed.

Seed stored *ex situ* was kept in paper bags under low light and moisture conditions, without fruit or pods but with dispersal structures. After three years of *ex situ* storage total viability, dormant and non-dormant fractions were assessed for seven of the eight species using the procedure used to assess initial viability. *Ozothamnus obcordata* seed for *ex situ* storage was misplaced during a relocation and thus total viability, dormant and non-dormant fractions after three years of storage could not be assessed.

Data analysis

One way ANOVA with Bonferroni post-hoc tests adjusted for multiple comparison were used to assess the effect of time *in situ* on total viability, dormant and non-dormant fractions of each species. Where assumptions of normality and/or variance heterogeneity were not met and transformation did not alleviate the problem, the Kruskal-Wallis non-parametric ANOVA with the Tukey-type post-hoc test was applied (Zar, 1996). For species with two seed cohorts, germination variables were compared between collection periods using students t-test or Mann-

Whitney U test. If no significant difference was found, data for the two cohorts were pooled and tested for a time *in situ* effect.

The students t-test was used to compare levels of total viability, dormant or non-dormant fractions in seed buried for three years to that of seed stored *ex situ* for three years. Where data violated test assumptions, the Mann-Whitney U test was applied.

Species with low variability for lost, non-dormant or dormant fractions were not submitted to statistical analyses.

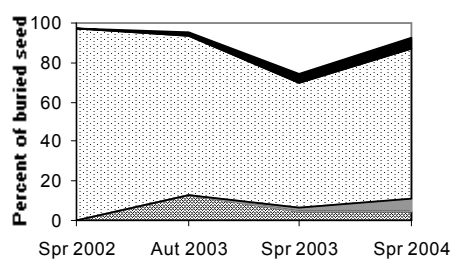
Results

At burial, viability was high for all species (Table 2). Large non-dormant fractions were only evident for *Briza maxima* and *Eucalyptus tricarpa*; 100%±0 and 95.8%±0.6 respectively. For remaining species most seed was dormant prior to burial (Table 2). For species with two seed cohorts, at the time of burial the proportion of dormant and non-dormant fractions differed little if at all between ‘fresh’ and one-year old seed. For each of the eight species the proportion of seed lost *in situ* and the dormancy status of retrieved seed for each of the retrieval times are summarised in Figure 3a-k.

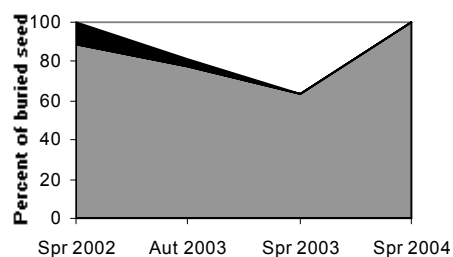
Table 2. Pre-burial seed viability and dormancy status of the eight Victorian box-ironbark species used in the study. Standard error in parentheses.

Species (cohort)	Viability (%)	Dormant (%)	Non-dormant (%)
Poaceae			
<i>Briza maxima</i> (2001)	100±0	0 (0)	100 (0)
<i>Briza maxima</i> (2002)	100±0	0 (0)	100 (0)
Asteraceae			
<i>Ozothamnus obcordata</i>	72±1.3	96.5 (1.2)	5 (2.5)
Fabaceae			
<i>Pultenaea prostrata</i>	100±0	99.2 (0.8)	0.8 (0.8)
Mimosaceae			
<i>Acacia ausfeldii</i> (2001)	99.5±0.1	100 (0)	0 (0)
<i>A. ausfeldii</i> (2002)	99.5±0.1	100 (0)	0 (0)
<i>A. genistifolia</i> (2001)	100±0	99.3 (0.6)	0.7 (0.7)
<i>A. genistifolia</i> (2002)	100±0	100 (0)	0 (0)
<i>A. pycnantha</i>	100±0	98.0 (0.9)	2.0 (0.9)
<i>A. williamsonii</i>	98.0±0.3	100 (0)	0 (0)
Myrtaceae			
<i>Eucalyptus tricarpa</i>	100±0	0 (0)	100

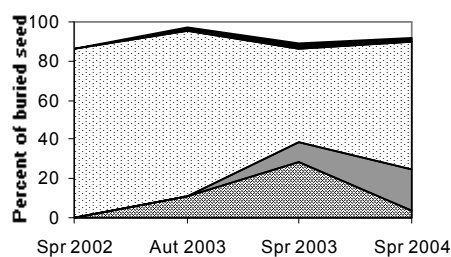
a. *Acacia ausfeldii* 2001 cohort



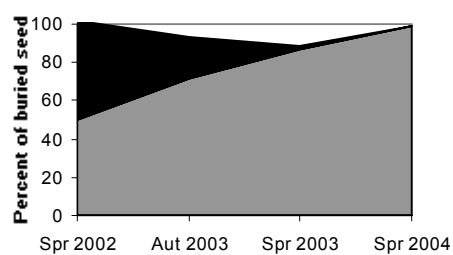
g. *Briza maxima* 2001 cohort



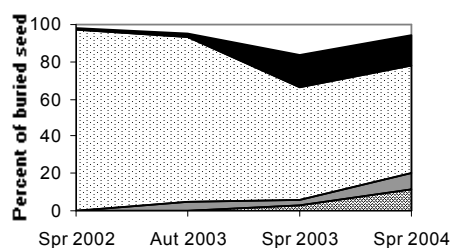
b. *Acacia ausfeldii* 2002 cohort



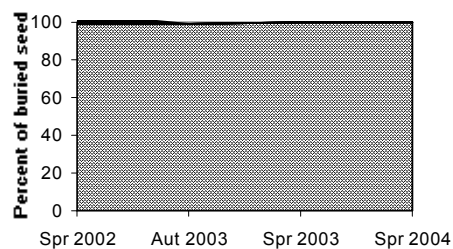
h. *Briza maxima* 2002 cohort



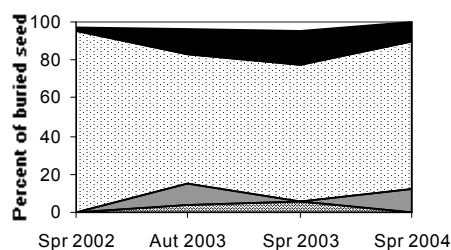
c. *Acacia genistifolia* 2001 cohort



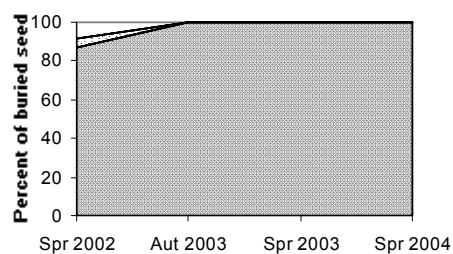
i. *Eucalyptus tricarpa*



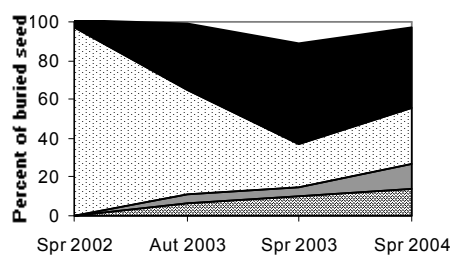
d. *Acacia genistifolia* 2002 cohort



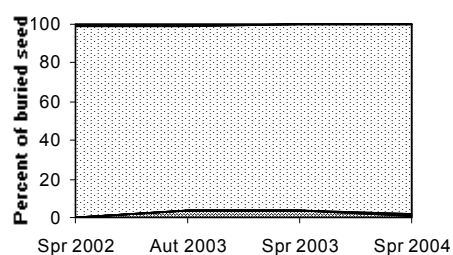
j. *Ozothamnus obcordata*



e. *Acacia pycnantha*



k. *Pultenaea prostrata*



f. *Acacia williamsonii*

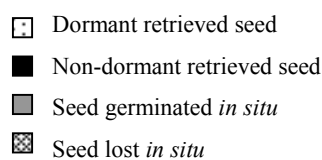
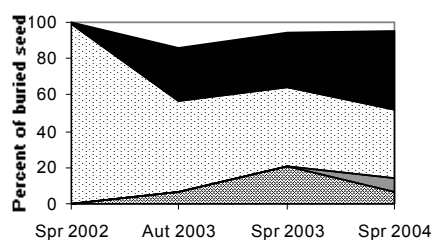


Figure 10. The fate of buried seed. Proportions of seed lost in situ and dormancy status of retrieved seed.

For the four species that could be submitted to statistical analysis (*Acacia ausfeldii*, *A. genistifolia*, *A. pycnantha* and *A. williamsonii*), the proportion of dormant seeds differed with length of burial (Table 3, Fig. 10a-k). *Acacia pycnantha* recorded the lowest proportion of dormant seed ($27\% \pm 10$ at 15 and 27 months). After three years *A. ausfeldii* and *A. genistifolia* had the highest proportion of dormancy among retrieved seeds. While the proportion of dormant seed tended to decline with time buried for *A. pycnantha* and *A. williamsonii*, the pattern was not clear for *A. ausfeldii* and *A. genistifolia*. Mean dormancy levels in these latter two species were lowest in spring 2003 and levels were higher in spring 2004. However, post-hoc testing found this trend was only significant for *A. ausfeldii*.

Table 3. Mean percent of dormant and non-dormant seed at each retrieval period (\pm standard error). Columns with differing superscripts differed significantly.

	Spring 2002	Autumn 2003	Spring 2003	Spring 2004	P
Dormant					
<i>Acacia ausfeldii</i>	98.8 \pm 0.9 ^a	93.3 \pm 2.0 ^{ac}	69.1 \pm 5.6 ^b	85.7 \pm 4.3 ^{bc}	0.019
<i>Acacia genistifolia</i>	99.2 \pm 0.5 ^a	83.9 \pm 4.2 ^b	71.0 \pm 4.3 ^b	82.9 \pm 3.5 ^b	0.006
<i>Acacia pycnantha</i>	97.5 \pm 1.6 ^a	69.1 \pm 10.6 ^b	27.7 \pm 10.2 ^b	35.7 \pm 7.6 ^b	0.001
<i>Acacia williamsonii</i>	100 \pm 0 ^a	53.5 \pm 3.9 ^{ab}	56.7 \pm 8.5 ^{ab}	43.4 \pm 4.5 ^b	0.024
<i>Briza maxima</i>	-	-	-	-	NA
<i>Eucalyptus tricarpa</i>	-	-	-	-	NA
<i>Ozothamnus obcordata</i>	0	-	-	-	NA
<i>Pultenaea prostrata</i>	100 \pm 0	98.8 \pm 1.3	100 \pm 0	100 \pm 0	NA
Non-dormant					
<i>Acacia ausfeldii</i>	0.0 \pm 0.0 ^a	2.2 \pm 1.5 ^a	4.1 \pm 1.5 ^b	4.5 \pm 1.3 ^b	0.047
<i>Acacia genistifolia</i>	0.4 \pm 0.4 ^a	8.0 \pm 2.5 ^b	18.7 \pm 3.7 ^c	15 \pm 3.3 ^c	<0.001
<i>Acacia pycnantha</i>	3.3 \pm 1.37 ^a	29.9 \pm 10.5 ^{ab}	61.9 \pm 10.5 ^b	61.6 \pm 9.1 ^b	0.002
<i>Acacia williamsonii</i>	1.0 \pm 1.0 ^a	31.6 \pm 6.2 ^b	37.0 \pm 6.4 ^b	50.4 \pm 7.4 ^b	<0.001
<i>Briza maxima</i>	3.5 \pm 3.0	36.2 \pm 7.2	19.7 \pm 5.4	25.0 \pm N ^A	NA
<i>Eucalyptus tricarpa</i>	-	-	-	-	NA
<i>Ozothamnus obcordata</i>	47.2 \pm 12.1	-	-	-	NA
<i>Pultenaea prostrata</i>	0 \pm 0	1.3 \pm 1.3	0 \pm 0	0 \pm 0	NA

Four of the five hard-seeded species had buried seed that appeared to be non-dormant. For all *Acacia* spp. a proportion of seed germinated readily with the addition of water at each retrieval period. *Pultenaea prostrata* did not display this pattern; only in a few instances did a seed germinate without scarification. Among the *Acacia* spp. the portion of non-dormant seed differed between retrieval times (Table 3). For *A. pycnantha* and *A. williamsonii* post-hoc testing suggested this was due to the lower portion of non-dormant seed in spring 2002, as proportions did not differ between later retrieval dates. While in *A. ausfeldii* and *A. genistifolia* differences were due to lower proportions of non-dormant seed in the first two retrieval periods (spring 2002 and autumn 2003) compared to the last two (spring 2003 and spring 2004).

Briza maxima also appeared to retain a non-dormant seed fraction in the soil for greater than 12 months, though most seed was lost within the first year of burial. The loss of *B. maxima* seed to germination over time reduced replication and therefore precluded testing for a time effect. The

For *E. tricarpa* and *O. obcordata* the lack of any seed after 12 months burial prevented examining the dynamics of a non-dormant fraction in these species.

A time effect on dormancy could not be tested for *Ozothamnus obcordata* and *Pultenaea prostrata*. For *O. obcordata* high rates of *in situ* loss meant seed were not available for testing, while for *P. prostrata* little variation in the high proportion of dormant seeds at each retrieval prevented statistical testing, but suggested dormancy did not degrade over the course of the study. A lack of dormancy in *Briza maxima* and *Eucalyptus tricarpa* negated testing for a declining dormancy effect in these species.

***In situ* seed loss**

Proportion of seed lost *in situ* varied between retrieval times for four of the eight species (Table 4). Hard- and soft-seeded species were represented among those with a significant time effect, as well as those whose proportion of seed lost *in situ* did not vary between retrieval times. For species whose seed lost *in situ* varied over time buried, greatest losses were recorded in later retrieval periods.

After three years no seed remained *in situ* for two of the soft-seeded species (*Eucalyptus tricarpa*, *Ozothamnus obcordata*) and only 2.5% of seed remained for *Briza maxima*. For *B. maxima* loss was due to germination, while for both *E. tricarpa* and *O. obcordata* all loss was the consequence of decay/predation (Fig 10i & j). For the three species most seed was lost by the first retrieval period. The small proportion of *B. maxima* seed that was retrieved at three years germinated readily *ex situ*.

Table 4. Mean percent of seed lost *in situ* at each retrieval period (\pm standard error). Columns with different superscripts differed significantly ($P < 0.05$).

Species	Spring 2002	Autumn 2003	Spring 2003	Spring 2004	P
<i>Acacia ausfeldii</i>	6.9 \pm 3.8 ^a	12.3 \pm 3.9 ^a	19.5 \pm 5.3 ^a	18.1 \pm 2.7 ^b	0.023
<i>Acacia genistifolia</i>	2.0 \pm 1.1 ^a	6.5 \pm 1.5 ^a	7.4 \pm 1.7 ^a	17.3 \pm 5.2 ^b	0.004
<i>Acacia pycnantha</i>	0 \pm 0 ^a	9.2 \pm 4.4 ^{ab}	15.0 \pm 6.5 ^{ab}	27.1 \pm 10.1 ^b	0.015
<i>Acacia williamsonii</i>	0 \pm 0	7.0 \pm 2.5	21.0 \pm 14.5	14.5 \pm 3.6	0.077
<i>Briza maxima</i>	69.0 \pm 9.0 ^a	62.5 \pm 6.7 ^a	74.0 \pm 5.4 ^a	98.0 \pm 1.2 ^b	<0.001
<i>Eucalyptus tricarpa</i>	100 \pm 0	100 \pm 0	100 \pm 0	100 \pm 0	NA
<i>Ozothamnus obcordata</i>	88.0 \pm 5.2	100 \pm 0	100 \pm 0	100 \pm 0	NA
<i>Pultenaea prostrata</i>	0 \pm 0	3.8 \pm 2.4	3.8 \pm 3.8	1.9 \pm 0.9	0.489

Among hard-seeded species far less seed was lost *in situ*, though seed was still lost to germination and predation. In the first two years of burial, *A. ausfeldii* recorded the greatest losses and *P. prostrata* the least. Among the *Acacia* spp., *A. genistifolia* had the least loss while *A. pycnantha* and *A. williamsonii* fell midway between. However after three years seed losses of 20% or more had been recorded in all *Acacia* spp. Seed loss in *P. prostrata* seed loss remained very low over the course of the study.

Among the *Acacia* spp. only *A. genistifolia* and *A. pycnantha* displayed a trend for increasing proportions of seed loss with time buried. For *A. ausfeldii* and *A. williamsonii* seed loss fluctuated but displayed no distinct trend, indeed for *A. williamsonii* the amount of seed lost *in situ* did not differ between retrieval periods (Table 4).

Storage effect

After three years of *ex situ* storage, viability remained high for all species (Table 5).

Table 5. Viability and dormant and non-dormant fractions under *ex situ* storage initially and after three years.

	Viability (%)		Dormant (%)		Non-dormant (%)	
	Initial	Final	Initial	Final	Initial	Final
<i>Acacia ausfeldii</i>	99.5±0.1	96.5±0.5	100±0	78.1±6.2	0±0	21.0±4.8
<i>Acacia genistifolia</i>	100±0	100±0	100±0	56.0±4.2	0±0	44.0±4.2
<i>Acacia pycnantha</i>	100±0	98.0±0.3	91.0±2.9	15.0±3.3	7.5±2.8	85.0±3.4
<i>Acacia williamsonii</i>	98.0±0.3	94.5±0.6	98.7±1.1	70.4±4.3	2.0±1.1	30.0±4.3
<i>Briza maxima</i>	100±0	97.5±0.3	0	0	100±0	100±0
<i>Eucalyptus tricarpa</i>	100±0	97.5±1.3	0	0	95.8±0.6	97.5±1.3
<i>Ozothamnus obcordata</i>	72±1.3	-	100	-	0±0	-
<i>Pultenaea prostrata</i>	100±0	98.3±0.3	100±0	100±0	0±0	0±0

Among species with *in situ* seed remaining after three years the dormant fractions differed between control and buried seed only for *A. genistifolia* and *A. williamsonii* ($t_{A. genistifolia} = 4.30$, $P=0.0003$; $t_{A. williamsonii} = -3.69$, $P=0.002$). Dormancy was greater in buried seed for *A. genistifolia* ($x_{in situ} = 87.3±2.4\%$, $x_{control} = 78.1±6.2\%$), while control seed had a far greater proportion of dormant seed for *A. williamsonii* ($x_{in situ} = 43.4±5.5\%$, $x_{control} = 70.0±4.3\%$).

Discussion

Longevity patterns of box-ironbark species examined are consistent with those observed elsewhere. Species seed persistence in the soil seed-bank included transient seed (types I and II, Thompson & Grime, 1979), with seed loss attributable either to germination or decay, as well as persistent seed (types III and IV, Thompson & Grime, 1979). As expected seed of soft-seeded species was lost most rapidly from the soil seed-bank, while hard-seed species were at least moderately long-term persistent. Initial viability was high among all species (72-100%) and the initial proportion of dormant seed was high for all species (91-100%), except *Briza maxima* and *Eucalyptus tricarpa*, both of which had no dormant seed.

Soft-seeded species

Two species displayed a pattern typical of transient seed. For *E. tricarpa* and *Ozothamnus obcordata*, while seed viability remained high after three years of *ex situ* storage, *in situ* seed had degraded or was predated within 12 months. Therefore seed-based recruitment in both these

species requires recent seed release. While the lack of *in situ* germination in *O. obcordata* may be explained by the high levels of dormancy recorded, the lack of germination in *E. tricarpa* despite the high levels of non-dormant seed is curious. However, while the study found no dormant seed in *E. tricarpa* under laboratory conditions, the fact that *Eucalyptus* spp. germination may be reduced or inhibited by non-optimum temperatures or moisture conditions may mean that *in situ* seed was either physiologically dormant due to inappropriate temperature conditions or it had not received appropriate environmental stimuli (Bell & Williams, 1997; Fenner & Thompson, 2005).

Being woody perennials both *E. tricarpa* and *O. obcordata* are not reliant on annual seed-based recruitment for persistence in the community. Thus the low recruitment probability presented by the combination of transient seed and limited germination probability is buffered by the perennial life-cycle of these species. Other characters of these species reduce the need for persistent seed. The production of copious amounts of anemochorous seed in *O. obcordata* may partly overcome the need for local seed persistence, although further investigations are required to clarify whether dispersal from off-site sources may provide sufficient seed to re-establish a local population. For *E. tricarpa* while non-dormant seed appears to be transient in the soil seed-bank, seed is also held in a canopy seed-bank under physical dormancy in woody capsules and is thus persistent for at least the moderate term. The species is also capable of resprouting. So while the transience of soil-stored *E. tricarpa* seed may be a factor contributing to the limited seed-based recruitment, other traits of the species ensure that its persistence is not currently under threat.

Briza maxima was the only soft-seeded species for which seed was recovered after three years. While the amount of seed recovered was just 0.5-3.5% of the initial number of seeds buried, all were still viable and non-dormant. The minimal amount of seed remaining after three years suggests that its persistence is optimised by annual seed input. Consequently this exotic species may be minimised by interrupting seed input. From the rates of longevity decline documented, it would appear that 2-3 years of stemming seed input would be sufficient to exhaust local soil seed-banks. Further investigations into the species propagule dispersal range are required to assess the whether local management is a feasible option for reducing local occurrences of the species.

Hard-seeded species

For seed to persist in the soil seed-bank it requires either a form of dormancy, or specific environmental cues for germination (Vleeshouwers *et al.*, 1995; Fenner & Thompson, 2005). In this study long-term persistence was found in those species whose dormancy was largely imbued by a hard-seed coat, however the proportion of dormant seed varied over time and between species. At three years less than half of recovered seeds of *Acacia pycnantha* (35%±8) and *A. williamsonii* (43%±6) seeds were dormant, while most seeds were dormant in *A. ausfeldii*

(86%±7), *A. genistifolia* (83%±6) and *Pultenaea prostrata* (100%±0). Only for *P. prostrata* was all seed dormant, other species had a combination of dormant and non-dormant seed that remained persistent.

A high level of dormancy is widely recorded for Australian native legumes (Cavanagh, 1987). While low levels of non-dormant seed have been recorded in some species, it is not uncommon for species to have considerable fractions of non-dormant seed (Auld & O'Connell, 1991; Morrison *et al.*, 1992; Auld *et al.*, 2000). For three of the *Acacia* spp. examined here the non-dormant fraction varied over time. Variation in the non-dormant fraction over time has been observed in a number of native legumes of the Sydney region for seed stored under laboratory conditions (Morrison *et al.*, 1992). However, this was not found for any of the *Acacia* spp. they examined. In species where the non-dormant fraction varied through time, they suggested that the dormancy decay may be the consequence of the physical or chemical structure of the seed testa layers in combination with seed size and embryo age. *In situ*, environmental factors such as mechanical abrasion, fungal and microbial attack, high temperatures, fluctuating temperatures and humidity may also contribute to dormancy decay (Baskin & Baskin, 1998; Fenner & Thompson, 2005). Auld & Bradstock (1996) suggest that soil heating may play a role in breaking dormancy cues in Australian legumes. They mention that while the possibility of reaching dormancy breaking temperatures of c.60°C is greater following summer fires, soil temperatures of 40°C for eight hours may be sufficient to release a portion of seed from dormancy. While this may be a possibility in the box-ironbark legumes examined here, highest levels of germination in these species required at least 80°C rather than the 60°C most commonly found in the NSW species (Brown *et al.*, 2003, Auld, 1991 #198). However, daily temperature fluctuations in excess of 20°C over several weeks have been found to generate cracks in the seed coat of legumes, which in several species has facilitated germination (Hagon, 1971; Moreno-Casasola *et al.*, 1994). However, it has been suggested that the cracks are not deep enough to permit water uptake in Mimosaceous species (Cavanagh, 1980; Morrison *et al.*, 1998) and duration of heat exposure had no effect on the dormancy of a sample of Australian legumes (Auld & O'Connell 1991). This possibility requires examination to explore its relevance to Box-Ironbark species.

A non-dormant yet persistent seed fraction is said to be associated with environments where the intra- or inter-annual timing of optimal germination conditions is unpredictable (Baskin & Baskin, 1998; Auld *et al.*, 2000). The size of the non-dormant fraction can vary seasonally, whereby a portion of the seed becomes non-dormant in response to environmental cues and awaits secondary cues such as light or soil moisture to trigger germination (Vleeshouwers *et al.*, 1995; Baskin & Baskin, 1998; Fenner & Thompson, 2005). In this study the high proportion of non-dormant *A. pycnantha* and *A. williamsonii* seed recovered may be explained by the lack of suitable secondary germination cues during the study period. Rainfall over 2002-2004 was below

average, though for 2003 97% of the long-term mean annual rainfall fell compared to just 53% in 2002 and 75% in 2004. The highest proportion of non-dormant seed for all four *Acacia* spp. tended to occur in spring 2003, so it may be that adequate rainfall or soil moisture conditions act as a secondary trigger.

Hard-seeded legumes of the Fabaceae and Mimosaceae are known for their persistence in the soil seed-bank and for their association with fire due to the heat cue often required to break their dormancy (e.g. Auld & O'Connell, 1991). The variation in the proportion of non-dormant seed found in the leguminous species of this study has implications for inter-fire recruitment capacity and species persistence. The fuel characters in the box-ironbark forests suggest fires are most likely to occur infrequently and be of a low intensity (Chatto, 1996). A long period between fires may not be an issue for the persistence of *Acacia pycnantha* and *A. williamsonii* in the community, as while these species do have a portion of dormant seed in the soil seed-bank that may be available to germinate following the next fire, three years after seed release about half their seed was non-dormant. These non-dormant seeds are therefore available to germinate without fire. The limited proportion of seed lost to germination suggests that successful inter-fire recruitment will still depend on breaking secondary dormancy mechanisms or the occurrence of specific environmental stimuli (Fenner & Thompson, 2005). However, to confirm that inter-fire recruitment of these species is sufficient for population survival, seedling survival will need to be monitored. Auld (1986) found that while the non-dormant fraction of *A. suaveolens* was capable of germinating between fire events, survivorship was low. If this is the case for *A. pycnantha* and *A. williamsonii*, both the species will rely on rather regular input into the soil seed-bank to sustain adequate levels of dormant seed in the soil seed-bank to respond to the next fire event.

Proportions of non-dormant seed were far less in the remaining three hard-seeded species (0-18%). The possession of a non-dormant seed fraction in both *Acacia ausfeldii* and *A. genistifolia* suggests that they, like *A. pycnantha* and *A. williamsonii*, are able to recruit between fires. However, as they had a smaller fraction of non-dormant seed it may be that the survival probability of inter-fire recruits is lower. Again, monitoring seedling survival would reveal whether germination success equated to successful recruitment. As both *A. ausfeldii* and *A. genistifolia* had higher fractions of dormant seed remaining after three years, it seems that compared to *A. pycnantha* and *A. williamsonii* these species do not require as frequent input into the soil seed-bank to maintain sufficient levels of dormant seed available to respond to a fire event. However, it may also mean that successful recruitment of these species is more contingent upon fire than *A. pycnantha* and *A. williamsonii*. A further consideration that is applicable to all the *Acacia* spp. examined is that a single fire event may not break the dormancy of all soil-stored *Acacia* seed (Auld, 1996), and thus understanding the maximum length of time that seed of each

of the species might remain dormant will also aid in identifying appropriate fire intervals for their persistence.

As all *Pultenaea prostrata* seed remained dormant after three years of burial it might be concluded that the recruitment of this species is more or less reliant on fire. Considering the seemingly infrequent occurrence of fire in this system, it seems that persistence of this species is reliant on the longevity of soil-stored seed. In NSW *Pultenaea* spp. the amount of dormant seed did not vary over four years of *ex situ* storage (Morrison *et al.* 1992), so tracking seed longevity in *P. prostrata* over a longer period of time may clarify whether seed longevity is greater than current fire intervals, or if a portion of its soil seed-bank becomes non-dormant over greater time and available for inter-fire recruitment.

Conclusion

The patterns of persistence observed in the Box-ironbark species examined are consistent with those observed elsewhere. The strategies recorded included transient and persistent seed. The species with transient seed possess plant traits that moderate the seemingly risky strategy of short-lived seed in a dry sclerophyll community. While the weed species examined had seed that persisted for greater than 12 months, very little seed remained after three years *in situ*. This suggests that preventing seed input over a few years may be sufficient to exclude the species locally. However, identifying the species dispersal range will be required to ascertain if such actions are a realistic option.

Four of the five hard-seeded species had non-dormant seed and all were *Acacia* spp. The other species, *Pultenaea prostrata*, maintained a high proportion of dormant seed, with virtually no non-dormant fraction, which suggests the species may require fire for recruitment. Examining specific heat cues required for germination in the species would confirm this possibility. Levels of dormant seed varied over time for three of the *Acacia* spp. The dormancy dynamics of the *Acacia* spp. examined suggest that they are able to recruit between fires as well as retain a portion of seed in the soil seed-bank that is available to respond to fire events. Ecologically the combination of persistent seed with non-dormant and dormant fractions provides an ecological strategy suited to unpredictable environments. This pattern has also been a strategy that enabled persistence under a rather intensive anthropogenic disturbance regime. Identifying mean seed longevity ranges among such hard seeded species may contribute to quantifying maximum fire-intervals.

Further investigations are required to determine if the obligate seeders examined are able cope with the long periods between fire suggested by current fuel dynamics in the box-ironbark forests. Identifying upper limits of seed longevity would clarify whether seed-banks may permit

persistence of hard-seeded species in particular. Tracking the survival of inter-fire recruits and identifying dispersal ranges would clarify whether species are able to persist locally between fire events.

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