

Germination responses of a dry sclerophyll forest soil-stored seedbank to fire related cues

Penman, T.D.^{1,3,4}, Binns, D.L.², Allen, R.M.¹, Shiels, R.J.¹ and Plummer, S.H.³

¹ Forest Science Centre, Dept of Primary Industries, PO Box 100, Beecroft, NSW 2119 AUSTRALIA.

² Forests NSW, PO Box J19, Coffs Harbour Jetty, NSW 2450 AUSTRALIA.

³ Bushfire Co-operative Research Centre, 5/340 Albert Street, East Melbourne Vic 3002, AUSTRALIA.

⁴ Corresponding author: Trent Penman email: trentp@sf.nsw.gov.au

Abstract: Fire is an integral component of many ecosystems worldwide. Many plant species require fire-related cues, primarily heat and smoke, to trigger germination. Despite the importance of this process, the responses of many Australian species to these cues are unknown. Without this knowledge fire management strategies may be developed that are inappropriate for individual species and vegetation communities. In this study we examined the responses of a dry sclerophyll forest seed bank to heat and smoke germination cues. Analysis was possible for 48 taxa within the soil seedbank with 34 of these showing a response to one or both of the germination cues. 10 species responded to the heat treatment, 11 species responded to the smoke treatment and 13 species responded to both the heat and smoke treatments. Germination cues acted independently for all species considered. Results in this study were consistent with published reports for most species, although some differences were seen at the species and genus level. The study highlights the importance of fire-related cues in enhancing germination of a large proportion of the species occurring in dry sclerophyll forests.

Cunninghamia (2008) 10(4): 547–555

Introduction

Many plant species accumulate a soil-stored seedbank, an important mechanism of survival for obligate-seeding species particularly in fire prone environments (Gill 1981). One important factor which influences distribution and abundance of plant species in relation to fire is the response of this seedbank (Keith 1996). The well-known pulse of post-fire germination is at least partly due to seeds being released from dormancy by fire-related cues (Noble & Slatyer 1981).

Heat and smoke are considered the primary fire related cues for triggering germination. Heat has been shown to stimulate germination in a wide range of species, from a number of families including Fabaceae (Auld & O'Connell 1991; Enright *et al.* 1997), Convolvulaceae (Read *et al.* 2000) and Cyperaceae (Thomas *et al.* 2003). Heating fractures the seed coat enhancing germination, particularly in hard-seeded species. The optimum range of temperatures for germination varies between species (e.g., Kenny 2000; Morris 2000; Read *et al.* 2000; Hill & French 2003), with short term exposures (of only a few minutes) to high temperatures (>100°C) resulting in seed mortality in some species (Keeley & Keeley 1987; Auld & O'Connell 1991). The role of smoke or smoke compounds in triggering germination has received increasing attention in recent years (Clarke *et al.* 2000). Smoke has

been found to trigger germination in native species from South Africa (e.g., Brown *et al.* 1994), North America (e.g., Keeley & Fotheringham 1997), Europe (e.g., Rivas *et al.* 2006) and Australia (e.g., Roche *et al.* 1997a; Read & Bellairs 1999; Clarke *et al.* 2000; Enright & Kintrup 2001). For many species the combined application of smoke and heat significantly increases germination (Keith 1997; Kenny 2000; Tieu *et al.* 2001). These changes can be independent and additive, synergistic or unitive (Thomas *et al.* 2003).

Germination responses of species within some native vegetation communities have been well studied, though many remain poorly studied. Heath and woodland communities have received the most attention (Enright *et al.* 1997; Benwell 1998; Enright & Kintrup 2001; Wills & Read 2002; Wills & Read 2007) particularly in the Sydney basin area in eastern Australia (Auld & O'Connell 1991; Kenny 2000; Hill & French 2003; Thomas *et al.* 2003). Similarly heath and forest communities in south-western Australia have received considerable attention (e.g., Bell *et al.* 1987; Enright & Lamont 1989; Meney *et al.* 1994; Dixon *et al.* 1995; Roche *et al.* 1997b; Smith *et al.* 1999; Tieu *et al.* 2001; Baker *et al.* 2005). Fewer studies have been conducted in other vegetation communities such as savannas (Williams *et al.* 2005) and dry forests (Wang 1997; Read *et al.* 2000).

Understanding how individual species respond to fire-derived cues will result in improved predictions regarding the impacts of fire management practices on individual species, hence communities. In this paper, we tested the effect of a single heat treatment (80°C), a smoke treatment, and an interaction of the two, on a soil seedbank from a dry sclerophyll forest in south-eastern New South Wales (NSW).

Materials and Methods

Soil samples were collected from the Eden Burning Study Area (EBSA) in south-eastern NSW, Australia (lat 37° 14'S, long 149° 38'E). The EBSA is a 1080 ha area of southeast dry sclerophyll forests in Yambulla State Forest, managed by Forests NSW. Dominant canopy species in the site are *Eucalyptus consideriana*, *Eucalyptus sieberi*, *Eucalyptus agglomerata*, *Eucalyptus globoidea*, *Eucalyptus muellerana* and *Eucalyptus cytellocarpa*. Established in 1986, the EBSA was designed to examine the effects of timber harvesting and repeated prescribed burning on a range of ecological attributes (for more details see Binns & Bridges (2003) and Penman *et al.* (2008)).

In April 2006, soil was collected from 213 permanently marked understorey vegetation plots, at a distance of 6 m from the plot centre (routine vegetation measurements are taken within a 5.64 m radius and we did not wish to interfere with these). Nine samples were taken from each plot starting from a random bearing from the plot centre and then at 40° intervals or approximately 4.2m arcs. Each sample was taken from the top 10 cm of the soil profile using an auger (8 cm diameter), resulting in a total of approximately 3.5 kg of soil per plot. During collection, soil samples were combined in a breathable calico bag and mixed together. Soil samples were air-dried, to prevent mould-damage to the soil-stored seeds, and to ensure the subsequent heat treatment (see below) was dry heat and not wet heat.

In the laboratory, the combined soil samples from each plot were mixed thoroughly a second time then divided into four equal sub-samples. Sub-samples were then randomly assigned to one of four germination treatments – Control, Heat, Smoke, and combined Heat plus Smoke. The heat treatment involved placing the soil in aluminium trays which were then placed in a dry oven at 80°C for one hour. For the Smoke and Heat plus Smoke treatments, samples were placed in a semi-sealed (3m x 3m) room with a smoke generator in one corner which was run continuously for two hours fuelled by native vegetation. The samples were then left in the room for another hour while the smoke settled. Temperatures in the smoking room were monitored throughout the smoking process and did not rise by more than 5°C above ambient temperatures (20–25°C).

All treated and control samples were then placed in seedling trays (350 x 295 x 50 mm), which were placed randomly in a glasshouse. For each plot, samples were placed into two

seedling trays, each divided into two discrete sections using an aluminium divider. The first tray held the control and heat treatments and the second the smoke and the combined heat plus smoke treatments. For the first five days following the smoking treatment, all trays were lightly watered for five minutes once a day. Following this period, samples were watered using misting spray for five minutes every 12 hours. The glasshouse was kept at ambient temperature, except during the peak of summer where an air-conditioner was used to keep temperatures below 35° C. Germinating seedlings were identified at approximately two monthly intervals from June 2006 through to June 2007. Nomenclature used was that accepted by the National Herbarium of New South Wales, Sydney (Royal Botanic Gardens & Domain Trust 2007). After being identified, each specimen was removed from the tray to prevent double counting.

We used a general linear model to determine the influence of each germination cue in which we included only the plots on which each species germinated. Only species recorded in ten or more sub-samples (out of the 213 plots with four sub-samples from each) were considered in the analysis. For each plot, we calculated the proportion of seedlings, of a given species, that germinated in each of the four treatments. We then compared these proportions using a two factor general linear model with heat and smoke as the two factors. Scores were weighted using the square root of the number of seedlings germinating from the plot. A square root transformation was used to ensure plots with extremely large numbers of seedlings did not have undue influence on the analysis. Tukey's HSD test was used for post-hoc comparisons where significant interactions were recorded (Quinn & Keough 2002). All analyses were conducted in the R-package v 2.5.0 (R-Development Core Team 2007).

Results

A total of 8510 seedlings germinated during the 12 month study, comprising 103 species, with a further 6 taxa only identified to genus level or higher (Appendix 1). There were 42 shrub and sub-shrub species (hereafter termed shrubs), 62 herbs, 2 vines, 1 tree species (*Allocasurina littoralis*) and an aggregate group of eucalypt taxa (species of *Eucalyptus* and *Corymbia*). The eucalypts were not identified to species level and are not considered further in this paper. Several species of orchids also appeared in the trays, but these were all resprouts from tubers and not counted as germinants. The most common taxa occurring in the seedbank were *Epacris impressa* (1165 seedlings at 161 plots), *Gonocarpus teucrioides* (1055 seedlings) and *Wahlenbergia spp.* (909 seedlings). These three species made up 37% of the total germinants. Three introduced species were recorded amongst the germinants albeit in low numbers – *Centaurium erythraea* (21 seedlings), *Cirsium vulgare* (1 seedling) and *Conyza sp.* (1 seedling).

Table 1: Summary of the germination response to Heat and Smoke treatments for all species with more than 10 seedlings. Values presented are for parameter estimates in the model with positive estimates indicating a positive response to the germination cue and negative estimates indicating a negative response, i.e. reduced germination in the treatment compared to the controls. * indicates significance at the 0.05 level, ** significance at the 0.01 level, * significance at the 0.001 level and ^m indicates a marginally significant result with p values between 0.05 and 0.1.**

a) Herb species

Family	Species	Heat	Smoke	Interaction	Num. of germinants
Apiaceae	<i>Hydrocotyle</i> spp.	0.078	0.175	-0.232	45
Asteraceae	<i>Chrysocephalum baxteri</i>	-0.025 *	0.340 ***	-0.170 ^m	85
	<i>Euchiton gymnocephalus</i>	0.046	0.042	-0.177 *	218
	<i>Euchiton sphaericus</i>	0.325	0.024	-0.201	29
	<i>Lagenifera stipitata</i>	0.11	0.184 *	0.059	27
Campanulaceae	<i>Wahlenbergia</i> spp.	0.039	0.072 ^m	-0.073 ^m	909
Centrolepidaceae	<i>Centrolepis strigosa</i>	0.250 *	0.098	-0.019	181
Clusiaceae	<i>Hypericum</i> spp.	0.011	-0.004	0.02	171
Convolvulaceae	<i>Dichondra repens</i>	0.492 *	0.001	0.017	16
Cyperaceae	<i>Caustis flexuosa</i>	0.001	0.325 **	0.06	17
	<i>Gahnia clarkei</i>	0.207	-0.105	-0.073	21
	<i>Gahnia radula</i>	0.076	-0.043	0.117	38
	<i>Lepidosperma laterale</i>	0.328 ***	0.210 ^m	-0.181	56
	<i>Schoenus apogon</i>	0.167 **	0.067	-0.059	384
	<i>Schoenus maschalinus</i>	0.122	0.167	-0.174	101
Droseraceae	<i>Drosera</i> spp.	-0.009	-0.072	0.245	110
Euphorbiaceae	<i>Poranthera microphylla</i>	0.143 ***	0.136 ***	0.039	292
Gentianaceae	<i>Centaurium erythraea</i>	0.027	0.095	-0.03	71
Haloragaceae	<i>Gonocarpus micranthus</i>	0.123 *	0.009	0.21	66
Iridaceae	<i>Patersonia</i> spp.	0.030	0.032	0.009	46
Juncaceae	<i>Juncus planifolius</i>	0.035	0.124 **	0.024	150
Oxalidaceae	<i>Oxalis</i> spp.	0.062	0.123	-0.025	19
Poaceae	<i>Dichelachne rara</i>	0.202 *	0.045	-0.065	68
	<i>Microlaena stipoides</i>	0.263 ^m	0.145	-0.263 ^m	52
	<i>Tetrarrhena juncea</i>	0.123	0.184 **	-0.177 *	200
Rubiaceae	<i>Galium</i> spp.	0.036	0.083 ^m	0.064	68
Selaginellaceae	<i>Selaginella uliginosa</i>	0.260	0.257	-0.253	17
Violaceae	<i>Viola hederacea</i>	-0.005	0.018	-0.029	187

b) Shrub and sub-shrub species

Family	Species	Heat	Smoke	Interaction	Num. of germinants
Apiaceae	<i>Platysace lanceolata</i>	0.149 **	0.244 ***	-0.11	263
	<i>Xanthosia tridentata</i>	-0.035	0.248 ***	0.086	64
Asteraceae	<i>Cassinia longifolia</i>	0.107 ^m	0.103	-0.003	101
Dilleniaceae	<i>Hibbertia empetrifolia</i>	0.212 *	0.146 ^m	-0.022	32
Ericaceae (Epacridaceae)	<i>Epacris impressa</i>	0.136 ***	0.135 ***	-0.024	1165
	<i>Monotoca scoparia</i>	0.208 **	0.143 ^m	-0.021	60
Euphorbiaceae	<i>Amperea xiphioclada</i>	0.078	0.383 ***	0.079	25
Fabaceae (Faboideae)	<i>Aotus ericoides</i>	0.101 ^m	0.22 **	0.096	29
	<i>Daviesia buxifolia</i>	0.117 ***	-0.132	0.205	59
Fabaceae (Mimosoideae)	<i>Acacia longifolia</i>	0.380 **	0.152	-0.064	15
	<i>Acacia myrtifolia</i>	0.688 ***	-0.047 ***	-0.471 **	25
	<i>Acacia terminalis</i>	0.517 ***	0.000	-0.033	14
Haloragaceae	<i>Gonocarpus teucroides</i>	0.022	0.101 ***	-0.035	1055
Myrtaceae	<i>Kunzea ambigua</i>	-0.01	0.083 **	0.021	801
	<i>Kunzea ericoides</i>	-0.225	0.170 ^m	0.211	36
	<i>Leptospermum scoparium</i>	0.062	-0.046	-0.125	13
Pittosporaceae	<i>Billardiera procumbens</i>	0.144 *	0.224 ***	-0.032	90
Rubiaceae	<i>Opercularia aspera</i>	0.086 ^m	0.256 ***	-0.002	120
	<i>Opercularia varia</i>	0.091 ***	0.194 ***	0.027	498
Tremandraceae	<i>Tetratheca pilosa</i>	0.103 *	0.26 ***	0.123	35

Five herbaceous species that had not been previously recorded on the study site (Binns & Bridges 2003) were recorded in the soil seedbank, four in very low numbers – *Deyeuxia parviseta* (10 seedlings), *Lobelia alata* (3 seedlings) and *Luzula* spp. (8 seedlings) and the weed *Cirsium vulgare* (1 seedling). The fifth species, *Schoenus apogon*, with 384 seedlings, occurred in 24 plots (11%).

Forty one obligate seeders (27 shrubs, 13 herbs, 1 vine) that have been identified in the above-ground vegetation in the plots (Binns & Bridges 2003) did not germinate in any of the trays during this study (Appendix 1). Three of these species have canopy stored seedbanks (*Banksia marginata*, *Hakea eriantha* and *Hakea sericea*) and were unlikely to be present in soil seedbank. The remainder of these species are relatively rare as adults, with 36 of the missing species having been recorded on less than 5% of the plots during the study period, of these 32 have been recorded on less than 2% of the plots. The remaining two species *Pultenaea linophylla* (20 plots) and *Olearia ramulosa* (26 plots) were each recorded from about 10% of the plots.

Analysis of the effect of treatment on germination was conducted for 48 taxa (41 species and 7 identified only to genus) of which 34 responded to one or both of the treatments (Table 1). 18 species (11 shrubs and 7 herbs) had significantly higher germination in the Heat treatment when compared to the unheated Control samples. A further four species (3 shrubs, 1 herbs) had marginally higher germination in the Heat treatment. One herb *Chrysocephalum baxteri* had significantly lower germination in the Heat treatment ($p=0.004$). Eighteen species had significantly higher germination in the Smoke treatment (12 shrubs, 6 herbs) with 3 shrubs and 3 herbs having marginally higher germination in the Smoke treatment. Of the Smoke responsive species, 10 shrubs and 3 herbs had also shown a significant or marginally significant heat response.

Significant Heat plus Smoke treatment interactions were recorded for six species. Of these, for *Acacia myrtifolia*, germination in the Heat only treatment was significantly higher than all other treatments ($p<0.001$ for all comparisons). *Chrysocephalum baxteri* recorded a marginal interaction which was due to significantly higher germination in the Smoke only treatment when compared with the Heat only treatment ($p<0.001$) and the control ($p<0.001$). For *Tetrarrhena juncea* germination was higher in the Smoke treatment than the control ($p=0.009$) with no other significant differences recorded. Interactions were recorded for *Euchiton gymnocephalus*, *Microleana stipoides* and *Wahlenbergia* spp. but post-hoc comparisons found no significant differences between any of the four treatments.

Discussion

The results of this study highlight the importance of fire in promoting germination in dry sclerophyll forest communities. Fire cues increased the rate of germination in 34 of the 48 taxa with sufficient data for analysis. Heat and smoke acted independently for all species, occasionally in an additive manner but never in a synergistic or unitive manner. The mechanisms by which fire related cues, i.e. heat and smoke, trigger germination are relatively well understood (e.g., Bell 1999; Kenny 2000; Thomas *et al.* 2003) and are not discussed further here.

Many of the species responses to fire-related germination cues were consistent with those reported by other studies. Fabaceae are well-known for their germination responses to heating (e.g., Auld & O'Connell 1991; Morrison *et al.* 1992; Bell 1999; Read *et al.* 2000). In this study, all the Fabaceae species, *Acacia longifolia*, *Acacia myrtifolia*, *Acacia terminalis*, *Daviesea buxifolia* and *Aotus ericoides*, responded positively to the Heat treatment. The positive responses of *Epacris impressa* to Smoke and Heat treatments (Enright & Kintrup 2001), *Tetratheca pilosa*, *Opercularia varia* and *Kunzea ambigua* responses to Smoke treatments, and *Dichondra repens* and *Poranthera microphylla* responses to Heat treatments, were consistent with published data (Roche *et al.* 1997b; Coates 2003; Thomas *et al.* 2003; Read *et al.* 2000; Hill & French 2003 respectively)

A number of species exhibited identical responses to other species within the same genus. To our knowledge responses of these species have not been reported in previous studies. Positive responses to smoke have been reported within *Billardiera* (Dixon *et al.* 1995; Roche *et al.* 1997b), *Hibbertia* (Dixon *et al.* 1995; Roche *et al.* 1997b; Clarke *et al.* 2000), *Platysace* (Roche *et al.* 1997b) and *Xanthosia* (Dixon *et al.* 1995; Roche *et al.* 1997b). *Opercularia* species responded positively and independently to smoke and heat treatments (Read *et al.* 2000; Enright & Kintrup 2001; Hill & French 2003). The lack of responses to both heat and smoke treatments has been reported previously for the *Hydrocotyle* and *Oxalis* species (Hill & French 2003).

Three species in this study did not respond to germination cues that had been reported previously in the literature. *Centrolepis strigosa* has been reported to respond to both smoke and heat (Enright & Kintrup 2001) whereas we found only the Heat treatment increased germination. *Microleana stipoides* has been reported as having a negative response to smoke treatments (Read & Bellairs 1999) but a positive response to heat and smoke (Clarke *et al.* 2000). In our study, the effect of Heat was marginal for this species with no Smoke response recorded. *Wahlenbergia* spp. responded to our Smoke treatment but not to our Heat treatments, whereas Enright & Kintrup (2001) reported positive responses to both these cues. The lack of response in our study may have been

a result of different Heat treatment. Enright & Kintrup (2001) placed soil samples in a 100° C oven for an hour, Clarke *et al.* (2000) placed seeds in an 80° C oven for 15 minutes and our study placed soil samples in an 80° C oven for an hour. Similarly, both Enright & Kintrup (2001) and Clarke *et al.* (2000) applied smoke related compounds through smoked water whereas we used a direct application of smoke from native fuels.

Four species exhibited responses different to published data for their respective genera. *Euchiton involucratus* has been recorded as responding positively to heating treatments (Tang *et al.* 2003), but we found no responses recorded for either *Euchiton* species in this study. *Drosera glanduligera* responded independently to the effects of heat and smoke in a study by Enright & Kintrup (2001). However, neither cue increased the level of germination for the *Drosera* species group in this study. Thomas *et al.* (2003) found *Gahnia sieberiana* increased germination in heat and smoke treatments, but neither *Gahnia* species in this study, *Gahnia radula* and *Gahnia clarkei*, responded to either treatment. These differences are not unexpected as responses to germination cues can vary between species within a genus (Bell 1999).

Heat or smoke increased germination in over 70% of species in this study. For some species, such as species of *Acacia*, there was little or no germination in untreated soil, but the extent of the increase in treated soil was dramatic, consistent with the post-fire recruitment pulse which is often reported from field observations. However, other species responded in both the treated and control samples with only a relatively small increase in response to treatment. In the field, such species may appear to rapidly increase after fire to a greater extent than implied by our results. The difference may be attributed to increased survival of germinants of these species in the post-fire environment due to the removal of competitive effects from other species. Species for which germination is enhanced by fire or smoke may increase in relative abundance over time, if fires occur at intervals less than age to senescence but greater than time to maturity. In contrast, the long-term absence of fire will favour those species which germinate independently of heat or smoke treatments and which can survive and mature in intact vegetation.

The differing responses of species suggest that there is likely to be spatial variation in germination in the post-fire environment. Species only responding to the heat cues will only have increased germination within the burnt area, if sufficient temperatures have been reached. Current data suggests that temperatures used in this study to trigger germination (>80° C) are rarely reached in prescribed burns (e.g., Bradstock & Auld 1995; Penman *et al.* 2006; Penman & Towerton 2008); these species require hotter fires (e.g., medium to high intensity wildfires) to trigger germination. While it might be argued that these temperatures may be achieved on hot days, data suggests that this is only possible

in the upper 0.5 cm post-fire (Auld & Bradstock 1996) where successful germination is rarely recorded (Auld & Denham 2006). In contrast, those species that germinate in response to smoke would be expect to exhibit increased germination both within and adjacent to the burnt area (regardless of the soil temperature), as the smoke disperses. To our knowledge, no study has recorded the distance from a fire at which smoke can increase germination in the field situation, although this warrants further attention.

Few species in this study recorded any synergistic effects of heat and smoke, although some additive effects were recorded (cf Thomas *et al.* 2003). Most species responded independently to one of the germination cues tested, although some species (e.g., *Poranthera microphylla* and *Epacris impressa*) responded to both independently. In a field situation, these species are expected to exhibit increased germination across a much larger area than those species responding to only one cue. The greatest germination for these species would be within the burn area, with increased germination still expected in adjacent areas affected only by smoke.

Forty-one obligate seeder species that have been recorded previously in the above-ground vegetation at the EBSA were not recorded in this study. These species occur in only a small proportion of plots at the study site, and may have correspondingly low numbers of soil-stored seed; the limited soil-stored seedbank sampling regime may not have captured them in this study. Alternatively, it is possible that different germination cues are required for some of these species.

This study has contributed to our knowledge of germination responses for a range of dry sclerophyll forest species. For many species we have reported results which are consistent with previous studies, but we have also reported on some previously undocumented species and some for which the response varied from that previously described. Knowledge of germination response can aid in interpreting plant community changes after fire. Combined with knowledge of other plant life history attributes, and information on interactions with other species and the physical environment, it is also an important factor in predicting changes in plant communities with respect to different management strategies.

Acknowledgements

This work is based upon a long-term Forests NSW study site established by Bob Bridges and Doug Binns. Roy Shiels and Ruth Allen collected and compiled the historic species data used in the analysis. The Bushfire CRC provided funding for the soil seedbank study including a scholarship for Sandra Plummer to assist in the establishment of the experiment. We thank Rod Kavanagh, Alison Towerton, Alan York, Richard Thornton, Huw Morgan and one anonymous referee for comments on an earlier draft of this manuscript.

References

- Auld T.D. & Bradstock R.A. (1996) Soil temperatures after the passage of a fire: do they influence the germination of buried seeds? *Australian Journal of Ecology* 21: 106–109.
- Auld T.D. & Denham A.J. (2006) How much seed remains in the soil after a fire? *Plant Ecology* 187: 15–25.
- Auld T.D. & O'Connell M.A. (1991) Predicting patterns of post-fire germination in 35 eastern Australian Fabaceae. *Australian Journal of Ecology* 16: 53–70.
- Baker K.S., Steadman K.J., Plummer J.A. & Dixon K.W. (2005) Seed Dormancy and Germination Responses of Nine Australian Fire Ephemerals. *Plant and Soil* 277: 345–358.
- Bell D.T. (1999) Turner Review No. 1 – the Process of Germination in Australian Species. *Australian Journal of Botany* 47: 475–517.
- Bell D.T., Vlahos S. & Watson L.E. (1987) Stimulation of seed germination of understorey species of the northern jarrah forest of Western Australia. *Australian Journal of Botany* 35: 593–599.
- Benwell A.S. (1998) Post-fire seedling recruitment in coastal heathland in relation to regeneration strategy and habitat. *Australian Journal of Botany* 46: 75–101.
- Binns D.L. & Bridges R.G. (2003) *Ecological impacts and sustainability of timber harvesting and burning in coastal forests of the Eden area: Establishment and progress of the Eden Burning Study. Technical Paper 67.* (Research and Development Division, State Forests of New South Wales: Sydney)
- Bradstock R.A. & Auld T.D. (1995) Soil temperatures during experimental bushfires in relation to fire intensity: Consequences for legume germination and fire management in south-eastern Australia. *Journal of Applied Ecology* 32: 76–84.
- Brown N.A.C., Jamieson H. & Botha P.A. (1994) Stimulation of seed germination in South African species of Restionaceae by plant-derived smoke. *Plant Growth Regulation* 15: 93–100.
- Clarke P.J., Davison E.A. & Fulloon L. (2000) Germination and dormancy of grassy woodland and forest species: effects of smoke, heat, darkness and cold. *Australian Journal of Botany* 48: 687–700.
- Coates T. (2003) The effect of concentrated smoke products on the restoration of highly disturbed mineral sands in southeast Victoria. *Ecological Management & Restoration* 4: 133–139.
- Dixon K.W., Roche S. & Pate J.S. (1995) The promotive effect of smoke derived from burnt native vegetation on seed germination of Western Australian plants. *Oecologia* 101: 185–192.
- Enright N.J., Goldblum D., Ata P. & Ashton D.H. (1997) The independent effects of heat, smoke and ash on emergence of seedlings from the soil seed bank of a healthy Eucalyptus woodland in Grampians (Gariwerd) National Park, western Victoria. *Australian Journal of Ecology* 22: 81–88.
- Enright N.J. & Kintrup A. (2001) Effects of smoke, heat and charred wood on the germination of dormant soil-stored seeds from a Eucalyptus baxteri heathy-woodland in Victoria, SE Australia. *Austral Ecology* 26: 132–141.
- Enright N.J. & Lamont B.B. (1989) Seed Banks, Fire Season, Safe Sites and Seedling Recruitment in Five Co-Occurring Banksia Species. *The Journal of Ecology* 77: 1111–1122.
- Gill A.M. (1981) Adaptive Responses of Australian Vascular Plant Species to Fires. In *Fire and the Australian Biota*. eds. AM Gill, RH Groves & IR Noble pp. 243–272. (Australian Academy of Science: Canberra)
- Hill S.J. & French K. (2003) Response of the soil seed-bank of Cumberland Plain Woodland to heating. *Austral Ecology* 28: 14–22.
- Keeley J.E. & Fotheringham C.J. (1997) Trace gas emissions and smoke-induced seed germination. *Science* 276: 1248–1250.
- Keeley J.E. & Keeley S.C. (1987) Role of fire in the germination of chaparral herbs and suffrutescents. *Madrono* 34: 240–249.
- Keith D.A. (1996) Fire-driven extinction of plant populations: A synthesis of theory and review of evidence from Australian vegetation. *Proceedings of the Linnean Society of New South Wales* 116: 37–78.
- Keith D.A. (1997) Combined Effects of Heat Shock, Smoke and Darkness on Germination of *Epacris Stuartii* Stapf., An Endangered Fire-Prone Australian Shrub. *Oecologia* 112: 340–344.
- Kenny B.J. (2000) Influence of Multiple Fire-Related Germination Cues on Three Sydney Grevillea (Proteaceae) Species. *Austral Ecology* 25: 664–669.
- Meneilly K.A., Nielsen G.M. & Dixon K.W. (1994) Seed bank patterns in Restionaceae and Epacridaceae after wildfire in kwongan in southwestern Australia. *Journal of Vegetation Science* 5: 5–12.
- Morris E.C. (2000) Germination Response of Seven East Australian Grevillea Species (Proteaceae) to Smoke, Heat Exposure and Scarification. *Australian Journal of Botany* 48: 179–189.
- Morrison D.A., Auld T.D., Rish S., Porter C. & McClay K. (1992) Patterns of testa-improved seed dormancy in native Australian legumes. *Annals of Botany* 70: 157–163.
- Noble I.R. & Slatyer R.O. (1981) Concepts and models of succession in vascular plant communities subject to recurrent fire. In *Fire and the Australian Biota*. eds. AM Gill, RH Groves & IR Noble pp. 311–335. (Australian Academy of Science: Canberra)
- Penman T.D., Binns D.L., Shiels R.J., Allen R.M. & Kavanagh R.P. (2008) Changes in understorey plant species richness following logging and prescribed burning in shrubby dry sclerophyll forests of south-eastern Australia. *Austral Ecology* 33: 197–210.
- Penman T.D., Lemckert F.L. & Mahony M.J. (2006) A preliminary investigation into the potential impacts of fire on a forest dependent burrowing frog species. *Pacific Conservation Biology* 12: 78–83.
- Penman T.D. & Towerton A.L. (2008) Are soil temperatures during autumn prescribed burning sufficient to trigger germination in fire responsive species? *International Journal of Wildland Fire* in press.
- Quinn G.P. & Keough M.J. (2002) *Experimental Design and Data Analysis for Biologists*. (Cambridge University Press: Cambridge)
- R-Development Core Team (2007) R: A language and environment for statistical computing. In (R Foundation for Statistical Computing: Vienna, Austria)
- Read T.R. & Bellairs S.M. (1999) Smoke affects the germination of native grasses of New South Wales. *Australian Journal of Botany* 47: 563–576.
- Read T.R., Bellairs S.M., Mulligan D.R. & Lamb D. (2000) Smoke and heat effects on soil seed bank germination for the re-establishment of a native forest community in New South Wales. *Austral Ecology* 25: 48–57.
- Rivas M., Reyes O. & Casal M. (2006) Influence of heat and smoke treatments on the germination of six leguminous shrubby species. *International Journal of Wildland Fire* 15: 73–80.
- Roche S., Dixon K.W. & Pate J.S. (1997a) Seed ageing and smoke: partner cues in the amelioration of seed dormancy in selected Australian native species. *Australian Journal of Botany* 45: 783–815.
- Roche S., Koch J.M. & Dixon K.W. (1997b) Smoke enhanced seed germination for mine rehabilitation in the southwest of western Australia. *Restoration Ecology* 5: 191–203.

- Royal Botanic Gardens & Domain Trust (2007) PlantNET. In 'The Plant Information Network System of the Botanic Gardens Trust Version 2.0.' (Sydney, Australia)
- Smith M.A., Bell D.T. & Loneragan W.A. (1999) Comparative Seed Germination Ecology of *Austrostipa Compressa* and *Ehrharta Calycina* (Poaceae) in a Western Australian Banksia Woodland. *Australian Journal of Ecology* 24: 35–42.
- Tang Y.B., Boulter S.L. & Kitching R.L. (2003) Heat and smoke effects on the germination of seeds from soil seed banks across forest edges between subtropical rainforest and eucalypt forest at Lamington National Park, south-eastern Queensland, Australia. *Australian Journal of Botany* 51: 227–237.
- Thomas P.B., Morris E.C. & Auld T.D. (2003) Interactive Effects of Heat Shock and Smoke on Germination of Nine Species Forming Soil Seed Banks Within the Sydney Region. *Austral Ecology* 28: 674–683.
- Tieu A., Dixon K.W., Meney K.A. & Sivasithamparam K. (2001) The interaction of heat and smoke in the release of seed dormancy in seven species from Southwestern Western Australia. *Annals of Botany* 88: 259–265.
- Wang L. (1997) The soil seed bank and understorey regeneration in *Eucalyptus regnans* forest, Victoria. *Australian Journal of Ecology* 22: 404–411.
- Williams P.R., Congdon R.A., Grice A.C. & Clarke P.J. (2005) Germinable soil seed banks in a tropical savanna: seasonal dynamics and effects of fire. *Austral Ecology* 30: 79–90.
- Wills T.J. & Read J. (2002) Effects of Heat and Smoke on Germination of Soil-Stored Seed in a South-Eastern Australian Sand Heathland. *Australian Journal of Botany* 50: 197–206.
- Wills T.J. & Read J. (2007) Soil Seed Bank Dynamics in Post-Fire Heathland Succession in South-Eastern Australia. *Plant Ecology* 190: 1–12.

Manuscript accepted 11 June 2008

Appendix 1: All understorey species recorded within the Eden Burning Study Area, highlighting those that have been recorded in the soil seedbank study. *= exotic

Family	Scientific Name	Seed bank	Obligate-Seeder
Adiantaceae	<i>Cheilanthes austrotenuifolia</i>	No	No
	<i>Cheilanthes sieberi</i>	No	No
Anthericaceae	<i>Arthropodium milleflorum</i>	Yes	No
Anthericaceae	<i>Caesia parviflora</i>	Yes	No
	<i>Thysanotus tuberosus</i>	Yes	No
Apiaceae	<i>Daucus glochidiatus</i>	No	Yes
	<i>Platysace lanceolata</i>	Yes	No
	<i>Xanthosia dissecta</i>	No	No
	<i>Xanthosia pilosa</i>	Yes	Yes
	<i>Xanthosia tridentata</i>	Yes	Yes
Araliaceae	<i>Polyscias sambucifolia</i>	No	No
Asclepiadaceae	<i>Tylophora barbata</i>	No	No
Asteraceae	<i>Arrhenechthites mixta</i>	No	Yes
	<i>Cassinia aculeata</i>	No	Yes
	<i>Cassinia longifolia</i>	Yes	Yes
	<i>Cassinia trinerva</i>	No	Yes
	* <i>Conyza albida</i>	No	Yes

Family	Scientific Name	Seed bank	Obligate-Seeder
	<i>Euchiton gymnocephalum</i>	Yes	Yes
	<i>Helichrysum argophyllum</i>	No	Yes
	<i>Helichrysum baxteri</i>	Yes	Yes
	<i>Helichrysum leucopsidium</i>	Yes	No
	<i>Helichrysum obcordatum</i>	No	Yes
	<i>Helichrysum scorpioides</i>	No	No
	* <i>Hypochaeris radicata</i>	No	No
	<i>Lagenifera stipitata</i>	Yes	No
	<i>Leptorhynchus nitidulus</i>	No	No
	<i>Olearia erubescens</i>	No	No
	<i>Olearia ramulosa</i>	Yes	Yes
	<i>Ozothamnus cuneifolius</i>	Yes	Yes
	<i>Ozothamnus diosmifolius</i>	No	Yes
	<i>Senecio linearifolius</i>	No	Yes
Baueraceae	<i>Bauera rubioides</i>	No	No
Bignoniaceae	<i>Pandorea pandorana</i>	No	No
Blechnaceae	<i>Blechnum cartilagineum</i>	No	No
	<i>Blechnum nudum</i>	No	No
Boraginaceae	<i>Heliotropium brachygyne</i>	No	Yes
Campanulaceae	<i>Wahlenbergia gracilis</i>	Yes	No
Caryophyllaceae	<i>Stellaria flaccida</i>	No	Yes
Casuarinaceae	<i>Allocasuarina littoralis</i>	Yes	No
Centrolepidaceae	<i>Centrolepis strigosa</i>	Yes	No
Clusiaceae	<i>Hypericum gramineum</i>	No	No
	<i>Hypericum japonicum</i>	Yes	No
Colchicaceae	<i>Burchardia umbellata</i>	No	No
Convolvulaceae	<i>Dichondra repens</i>	Yes	No
Crassulaceae	<i>Crassula helmsii</i>	No	Yes
Crassulaceae	<i>Crassula sieberiana</i>	Yes	Yes
Cyatheaceae	<i>Cyathea australis</i>	No	No
Cyperaceae	<i>Caustis flexuosa</i>	Yes	No
	<i>Cyperus tenellus</i>	No	Yes
	<i>Gahnia clarkei</i>	Yes	No
	<i>Gahnia melanocarpa</i>	No	No
	<i>Gahnia radula</i>	Yes	No
	<i>Gahnia sieberiana</i>	No	No
	<i>Lepidosperma filiforme</i>	No	No
	<i>Lepidosperma gladiatum</i>	No	No
	<i>Lepidosperma laterale</i>	Yes	No
	<i>Lepidosperma lineare</i>	No	No
	<i>Lepidosperma urophorum</i>	No	No
	<i>Schoenus maschalinus</i>	Yes	No
	<i>Schoenus melanostachys</i>	Yes	No
Dennstaedtiaceae	<i>Pteridium esculentum</i>	No	No
Dicksoniaceae	<i>Calochlaena dubia</i>	No	No
Dilleniaceae	<i>Hibbertia empetrifolia</i>	Yes	No
	<i>Hibbertia obtusifolia</i>	No	No
	<i>Hibbertia serpyllifolia</i>	No	No
Droseraceae	<i>Drosera auriculata</i>	Yes	No
Elaeocarpaceae	<i>Elaeocarpus reticulatus</i>	No	No
Ericaceae (Epacridaceae)	<i>Acrotriche serrulata</i>	No	No
	<i>Astroloma humifusum</i>	No	No
	<i>Brachyloma daphnoides</i>	No	No
	<i>Epacris impressa</i>	Yes	No
	<i>Leucopogon ericoides</i>	Yes	Yes
	<i>Leucopogon lanceolatus</i>	Yes	No

Family	Scientific Name	Seed bank	Obligate-Seeder	Family	Scientific Name	Seed bank	Obligate-Seeder
	<i>Leucopogon microphyllus</i>	Yes	Yes		<i>Juncus planifolius</i>	Yes	No
	<i>Leucopogon virgatus</i>	No	No	Lamiaceae	<i>Scutellaria mollis</i>	No	Yes
	<i>Monotoca scoparia</i>	Yes	No	Lauraceae	<i>Cassytha glabella</i>	Yes	Yes
Euphorbiaceae	<i>Amperea xiphioclada</i>	Yes	No		<i>Cassytha pubescens</i>	No	Yes
	<i>Poranthera microphylla</i>	Yes	Yes	Lindsaeaceae	<i>Lindsaea linearis</i>	No	No
Fabaceae (Faboideae)	<i>Aotus ericoides</i>	Yes	No		<i>Lindsaea microphylla</i>	No	No
	<i>Bossiaea buxifolia</i>	No	No	Lobeliaceae	<i>Lobelia gibbosa</i>	No	No
	<i>Bossiaea obcordata</i>	No	No		<i>Mitrasacme pilosa</i>	Yes	Yes
	<i>Bossiaea prostrata</i>	Yes	No	Lomandraceae	<i>Mitrasacme polymorpha</i>	No	Yes
	<i>Daviesia buxifolia</i>	Yes	No		<i>Lomandra confertifolia</i>	No	No
	<i>Daviesia ulicifolia</i>	Yes	No		<i>Lomandra filiformis</i>	Yes	No
	<i>Dillwynia sericea</i>	No	Yes		<i>Lomandra glauca</i>	No	No
	<i>Glycine clandestina</i>	Yes	No		<i>Lomandra longifolia</i>	Yes	No
	<i>Gompholobium glabratum</i>	No	Yes	Lycopodiaceae	<i>Lomandra multiflora</i>	No	No
	<i>Gompholobium huegelli</i>	No	Yes		<i>Lycopodium deuterodensum</i>	No	No
	<i>Hardenbergia violacea</i>	Yes	No	Myrtaceae	<i>Baeckea virgata</i>	No	No
	<i>Hovea heterophylla</i>	No	No		<i>Callistemon citrinus</i>	No	No
	<i>Hovea linearis</i>	No	No		<i>Kunzea ambigua</i>	Yes	Yes
	<i>Indigofera australis</i>	No	No		<i>Kunzea ericoides</i>	Yes	No
	<i>Kennedia prostrata</i>	No	Yes		<i>Leptospermum attenuatum</i>	No	No
	<i>Kennedia rubicunda</i>	No	Yes		<i>Leptospermum juniperinum</i>	No	No
	<i>Oxylobium ilicifolium</i>	No	No		<i>Leptospermum scoparium</i>	Yes	No
	<i>Platylobium formosum</i>	No	No		<i>Melaleuca squarrosa</i>	Yes	No
	<i>Pultenaea daphnoides</i>	Yes	Yes	Onagraceae	<i>Epilobium billardierianum</i>	No	No
	<i>Pultenaea linophylla</i>	No	Yes		<i>Acianthus exsertus</i>	No	No
	<i>Pultenaea retusa</i>	Yes	Yes	Orchidaceae	<i>Caladenia carnea</i>	Yes	No
	<i>Pultenaea viscosa</i>	No	Yes		<i>Caleana major</i>	No	No
Fabaceae (Mimosoideae)	<i>Sphaerolobium vimineum</i>	No	Yes		<i>Chiloglottis gunnii</i>	No	No
	<i>Acacia dealbata</i>	Yes	Yes		<i>Chiloglottis reflexa</i>	No	No
	<i>Acacia falciformis</i>	No	No		<i>Cymbidium suave</i>	No	No
	<i>Acacia floribunda</i>	No	Yes		<i>Dipodium variegatum</i>	No	No
	<i>Acacia implexa</i>	No	Yes		<i>Diuris sulphurea</i>	No	No
	<i>Acacia longifolia</i>	Yes	Yes		<i>Eriochilus cucullatus</i>	No	No
	<i>Acacia mearnsii</i>	No	Yes		<i>Lyperanthus suaveolens</i>	No	No
	<i>Acacia mucronata</i>	No	No		<i>Pterostylis longifolia</i>	No	No
	<i>Acacia myrtifolia</i>	Yes	Yes		<i>Pterostylis nutans</i>	No	No
	<i>Acacia obtusifolia</i>	No	Yes		<i>Pterostylis parviflora</i>	No	No
	<i>Acacia rubida</i>	No	Yes	Oxalidaceae	<i>Oxalis radicata</i>	No	No
	<i>Acacia terminalis</i>	Yes	Yes	Phormiaceae	<i>Dianella caerulea</i>	No	No
	<i>Acacia ulicifolia</i>	No	Yes		<i>Dianella revoluta</i>	No	No
	<i>Acacia verticillata</i>	No	Yes		<i>Dianella tasmanica</i>	No	No
Gentianaceae	<i>Centaurium erythraea</i>	Yes	Yes		<i>Stypantra glauca</i>	Yes	No
Geraniaceae	<i>Pelargonium inodorum</i>	Yes	Yes	Pittosporaceae	<i>Billardiera procumbens</i>	Yes	Yes
Gleicheniaceae	<i>Gleichenia microphylla</i>	No	No		<i>Billardiera scandens</i>	Yes	No
Goodeniaceae	<i>Coopernookia barbata</i>	Yes	No		<i>Bursaria spinosa</i>	No	No
	<i>Dampiera stricta</i>	Yes	No	Plantaginaceae	<i>Plantago debilis</i>	Yes	Yes
	<i>Goodenia elongata</i>	Yes	No	Poaceae	<i>Anisopogon avenaceus</i>	No	No
	<i>Goodenia ovata</i>	Yes	Yes		<i>Austrostipa nervosa</i>	No	No
	<i>Scaevola ramosissima</i>	Yes	No		<i>Danthonia pallida</i>	No	No
Haloragaceae	<i>Gonocarpus tetragynus</i>	No	No		<i>Danthonia pilosa</i>	No	No
	<i>Gonocarpus teucroides</i>	Yes	Yes		<i>Deyeuxia quadriseta</i>	No	No
Iridaceae	<i>Diplarrena moraea</i>	Yes	No		<i>Dichelachne rara</i>	Yes	No
	<i>Patersonia fragilis</i>	No	No		<i>Entolasia stricta</i>	Yes	No
	<i>Patersonia glabrata</i>	No	No		<i>Hierochloe rariflora</i>	Yes	No
	<i>Patersonia longifolia</i>	No	No		<i>Imperata cylindrica</i>	No	No
Juncaceae	<i>Juncus pauciflorus</i>	No	No				

	<i>Microlaena stipoides</i>	Yes	No		<i>Xanthorrhoea resinifera</i>	No	No
	<i>Oplismenus imbecillis</i>	Yes	No				
	<i>Poa labillardieri</i>	No	No				
	<i>Poa meionectes</i>	No	No				
	<i>Stipa pubescens</i>	No	No				
	<i>Tetrarrhena juncea</i>	Yes	No				
	<i>Themeda australis</i>	No	No				
Polygalaceae	<i>Comesperma ericinum</i>	No	Yes				
	<i>Comesperma volubile</i>	No	No				
Proteaceae	<i>Banksia marginata</i>	No	Yes				
	<i>Banksia serrata</i>	No	No				
	<i>Banksia spinulosa</i>	No	No				
	<i>Hakea eriantha</i>	No	Yes				
	<i>Hakea sericea</i>	No	Yes				
	<i>Lomatia ilicifolia</i>	No	No				
	<i>Persoonia confertiflora</i>	No	No				
	<i>Persoonia levis</i>	No	No				
	<i>Persoonia linearis</i>	Yes	No				
	<i>Persoonia lucida</i>	No	No				
Ranunculaceae	<i>Clematis aristata</i>	No	No				
Restionaceae	<i>Empodisma minus</i>	Yes	No				
	<i>Leptocarpus tenax</i>	No	No				
Rhamnaceae	<i>Pomaderris andromedifolia</i>	No	Yes				
	<i>Pomaderris lanigera</i>	Yes	Yes				
	<i>Pomaderris ligustrina</i>	No	Yes				
	<i>Pomaderris multiflora</i>	No	Yes				
Rubiaceae	<i>Coprosma quadrifida</i>	No	No				
	<i>Galium binifolium</i>	Yes	Yes				
	<i>Galium liratum</i>	No	Yes				
	<i>Opercularia aspera</i>	Yes	Yes				
	<i>Opercularia varia</i>	Yes	Yes				
	<i>Pomax umbellata</i>	Yes	Yes				
Family	Scientific Name	Seed bank	Obligate-seeder				
Rutaceae	<i>Correa reflexa</i>	Yes	No				
Santalaceae	<i>Choretrum pauciflorum</i>	No	No				
	<i>Exocarpos cupressiformis</i>	No	No				
	<i>Exocarpos strictus</i>	No	No				
Santalaceae	<i>Omphacomeria acerba</i>	No	No				
Sapindaceae	<i>Dodonaea triquetra</i>	Yes	Yes				
Schizaeaceae	<i>Schizaea bifida</i>	No	No				
Scrophulariaceae	<i>Gratiola peruviana</i>	No	Yes				
	<i>Veronica calycina</i>	Yes	No				
	<i>Veronica plebeia</i>	No	No				
Selaginellaceae	<i>Selaginella uliginosa</i>	Yes	No				
Solanaceae	<i>Solanum pungetium</i>	Yes	Yes				
Stackhousiaceae	<i>Stackhousia monogyna</i>	No	No				
Sterculiaceae	<i>Lasiopetalum ferrugineum</i>	No	No				
	<i>Lasiopetalum macrophyllum</i>	Yes	No				
Stylidiaceae	<i>Stylidium graminifolium</i>	Yes	No				
Thymelaeaceae	<i>Pimelea curviflora</i>	No	No				
Tremandraceae	<i>Tetratheca pilosa</i>	Yes	No				
	<i>Tetratheca thymifolia</i>	No	Yes				
Uvulariaceae	<i>Schelhammera undulata</i>	No	No				
Violaceae	<i>Viola hederacea</i>	Yes	Yes				
	<i>Viola sieberiana</i>	No	No				
Xanthorrhoeaceae	<i>Xanthorrhoea concava</i>	No	No				