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Effects of soil temperature regimes after fire on seed dormancy and germination in six Australian Fabaceae species

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Abstract. In addition to direct fire cues such as heat, smoke and charred wood, the passage of fire leads indirectly to changes in environmental conditions which may be able to break physical dormancy in hard-coated seeds. After a fire, the open canopy and the burnt material lying on the surface alter the thermal properties of the soil, resulting in elevated soil temperatures for long periods of time. We simulated daily temperature regimes experienced at different depths of soil profile after a summer fire. Our aim was to determine whether these temperature regimes and the duration of exposure (5, 15 and 30 days) play an important role breaking physical seed dormancy in six legumes from south-eastern Australia. Our results showed that simulated temperature regimes break seed dormancy. This effect is specially pronounced at temperatures that are expected to occur near the soil surface (0–2 cm depth). The duration of exposure interacts with temperature to break dormancy, with the highest germination rates reached after the longest duration and highest temperatures. However, the germination response varied among species. Therefore, this indirect post-fire cue could play a role in the regeneration of plant communities, and could stimulate seedling emergence independent of direct fire cues as well as in interaction with direct cues.

Introduction

A flush of seedling emergence occurs immediately after fire in many fire-prone environments around the world (Kruger and Bigalke 1984; Auld 1986; Keeley 1991; Trabaud 1994; Carrington and Keeley 1999). Heat and smoke released during the passage of fire are considered to be the most important fire cues that break dormancy or promote germination in soil-stored seeds. Temperatures reached during the passage of fire can break physical dormancy of hard-coated seeds, allowing subsequent water imbibition and germination when environmental conditions are suitable (Auld and O'Connell 1991; Keeley 1991; Cocks and Stock 1997; Bell 1999). In addition, smoke can also affect the physiology of seeds and directly stimulate germination (Brown 1993; Dixon *et al*. 1995; Keeley and Fotheringham 1998; Van Staden *et al*. 2000; Moreira *et al*. 2010) or act in combination with heat (Keeley 1991; Keith 1997; Morris 2000; Thomas *et al*. 2003). Other direct fire cues, such as charred wood, can also act to stimulate seed germination in some species (Keeley 1987). These factors all play a key role in determining vegetation recovery after fire, especially in ecosystems dominated by obligate seeders.

Most management strategies used to control fuel load and/or maintain biodiversity in fire-prone ecosystems throughout the world are dependent on a good understanding of the relationship between direct fire cues and germination (Bradstock and Auld 1995; Baeza and Roy 2008), and for this reason, they have been widely studied both in field and laboratory experiments. In particular, the relationship between high but short-term temperature conditions experienced by seeds during fire have been tested, identifying optimal and lethal temperature thresholds for a range of species (e.g. Keeley 1987; Auld and O'Connell 1991; Baeza and Vallejo 2006; Paula and Pausas 2008; and references therein).

However, the passage of fire also leads indirectly to changes in environmental conditions, particularly those experienced by seeds on or within the soil. After fire, the layer of black ash and the partially burnt organic material lying on the soil surface can alter the thermal properties of the soil (Walker *et al*. 1986), particularly where an opening in the canopy has occurred and increased solar radiation reaches the soil surface. As a consequence, a shift in the range of daily soil temperatures may occur (Sharrow and Wright 1977; Raison *et al*. 1986), in some cases exceeding the thresholds for breaking physical seed dormancy (Auld and Bradstock 1996).

This indirect fire cue may acquire special relevance after summer fires, when daily soil temperatures reach high levels and fluctuate most widely. These high temperatures can be

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sustained for significant lengths of time (i.e. up to several hours a day) in comparison to the high temperatures induced by the fire itself, which only remain for a few minutes or hours (Bradstock and Auld 1995). Furthermore, regimes of high daily temperatures may continue for several weeks after the fire. In Mediterranean ecosystems, this indirect fire cue may be quite important, ensuring that a flush of germination in some hard-seeded species occurs in the wet season after summer, irrespective of the season of fire. This germination strategy has been proposed as an adaptive trait, as it avoids germination and subsequent seedling establishment failures during the dry period (Baeza and Roy 2008).

The role that daily soil temperature regimes play as an indirect fire cue for breaking seed dormancy has been scarcely studied. However, the implications for population dynamic processes in fire-prone regions are potentially significant. Additionally, soil temperatures after fire are strongly correlated with air temperatures (Auld and Bradstock 1996; Ooi *et al*. 2009) and climate change forecasts predict significant increases in air temperatures over the next few decades throughout the world (IPCC 2007). To both inform management and help to predict the long-term consequences of climate change, it is necessary to link future environmental changes to mechanisms that can control population processes.

The aim of our work is to therefore test whether regimes of daily soil temperatures, experienced by seeds after the passage of fire, play an important role in breaking seed dormancy. An understanding of this will provide insight into the potential impact that changing climatic conditions will have on germination patterns promoted by this indirect fire cue. We simulated this indirect fire cue in the laboratory and examined its effect on germination in six Australian Fabaceae species commonly found in fire-prone vegetation in south-eastern Australia. More specifically, we asked two questions: (i) can the daily variations in temperatures that occur post-fire, at different depths in the soil, break physical dormancy in six different Fabaceae species; and (ii) does the amount of time seeds are exposed to such regimes of temperature (in terms of days) affect seed dormancy?

Materials and methods

The six study species are typical shrubs or subshrubs from the Fabaceae family, a significant understorey component of sclerophyll vegetation in the Sydney region of Australia. These species are characterised by having soil-stored seed banks and by having seeds with physical dormancy which is broken by heat (Auld and O'Connell 1991; Ooi 2007). The study species used were *Acacia suaveolens* (Sm.) Willd., *Bossiaea obcordata* (Vent.) Druce, *B. rhombifolia* Sieber ex DC., *Dillwynia retorta* (J.C. Wendl.) Druce, *Gompholobium grandiflorum* Sm. and *Pultenaea ferruginea* Rudge.

Seeds of the six study species were collected from the Blue Mountains National Park (33°48′S, 150°35′E) at some 200 m elevation, near the western outskirts of Sydney. Vegetation ranges from open heath to open forest, with the overstorey dominated by *Eucalyptus*/*Corymbia* species. Soils are derived from Hawkesbury sandstone. Average annual rainfall for the nearby Glenbrook Bowling Club Meteorological station is ~971 mm distributed throughout the year, with a peak in summer. Average summer temperatures (maximum/minimum) for Springwood Bowling Club Meteorological station (some 7 km W of Glenbrook) are 29/17°C and average winter temperatures 16/6°C. Field collections were made in summer during December of 2007. Several hundred ripe fruits were collected from at least 30 plants in each population. Seeds were stored in paper bags at laboratory temperatures (~22°C) until they were processed for treatment applications in August 2008.

The direct effects of fire in breaking physical dormancy of most of our study species have been previously studied in laboratory experiments by Auld and O'Connell (1991). The most important factor breaking dormancy was temperature, whereas the time of exposure had variable effects (1–120 min). All species experienced their maximum of germination (~90%) after treatments of 80−100°C. Further increases in temperature had deleterious effects on seed viability. However, the threshold of temperature for enhanced germination (cf. untreated seeds) differed between species. Seed dormancy was broken in *G. grandiflorum* after seeds were exposed to 40°C, whereas for the rest of our study species seed dormancy was largely unaffected at this temperature. *B. obcordata*, *B. rhombifolia* and *D. retorta* had seed dormancy broken from 60°C. One population of *A. suaveolens* had seed dormancy broken at 60°C, while a second did not respond until 80°C. The species *P. ferruginea* was not studied; however, the response of seven species of the same genus was variable, with four species having seed dormancy broken at 40°C and three species at 60°C.

Our experiment was designed to test the effects of regimes of post-fire daily temperature in the soil on physical dormancy. We used soil temperatures measured in the Sydney region after a summer fire (Auld and Bradstock 1996) to determine the range of temperatures to be applied. Auld and Bradstock (1996) found that the soil temperatures exceeded 40°C in burnt areas over summer, down to a depth of 4.5 cm, with the highest temperatures of above 60°C recorded near the soil surface, at 0.4-cm depth. Thus, temperatures reached after the passage of a fire may in some cases exceed the thresholds for breaking physical seed dormancy of the study species (Auld and O'Connell 1991). In contrast, soil temperatures after a winter fire or in unburned vegetation during summer did not rise above 40°C. Thus, we simulated daily temperature regimes using approximate summer conditions from three different depths down the soil profile.

Two incubators and two ovens were set up to apply dry heat at 12/12 h maximum/minimum temperature cycles. Three temperature ranges were chosen: 40/18°C, 50/18°C and 60/18°C. In order to test the effect of exposure time, temperature treatments were factorially combined with three durations of exposure: 5, 15 and 30 days. A fourth temperature range of 28/18°C, simulating unburned vegetation conditions during summer, was set up as a control (Auld and Bradstock 1996). Temperatures within each chamber were measured with a thermocouple and recorded every 15 min with a data logger. Although we attempted to achieve temperature regimes of 50/18°C and 60/18°C, due to technical difficulties the regimes we achieved were 47/16°C and 61/16°C. While the temperature regimes that were applied do not exactly mimic actual temperature fluctuations within a soil profile (i.e. in the field fluctuations of temperatures may occur throughout the day and the exposure to maximum temperatures can be variable depending on the depth of soil) the treatments can provide insight about the additive effect of post-fire temperatures regimes.

The control and the 30-day treatment started first, the 15-day treatment started 15 days later and the 5-day treatment started 25 days after the first one. This was done so that germination could start simultaneously for all treatments with identical elapsed time from the end of the pretreatments.

For each species, 60 seeds were divided into three replicates and used for each combination of temperature and duration during the experiment. Seeds were placed on one layer of filter paper in 9-cm Petri dishes. For the 15- and 5-day treatments, dishes were placed into the control incubator until their treatment started. For two species the number of treatments was limited by seed availability. For *B. rhombifolia* only the 30-day treatments were possible while for *B. obcordata*, the only treatment possible was 47/16°C for 30 days.

In order to estimate the potential maximum germination of seeds of each species, three additional replicates were established with no heat treated seeds individually scarified using a scalpel. For germination assessment, all seeds were kept in two germination chambers at 25°C-day temperature and 18°C-night temperature in darkness. Seeds were checked every 4 days for the first month, then once a week in the second month and only once in the third month. Petri dishes were watered with distilled water when required. A seed with a 1-mm-long radicle was scored as a germinant and removed.

Proportional data (number of germinants as a fraction of the total number of viable seeds per dish) were analysed using a one-way ANOVA. We used the results of the scalpel treatment to estimate the number of viable seeds per dish. Duncan's *post-hoc* tests were used to detect any pairwise differences among treatments ($\alpha = 0.05$) for each species. The data were checked for normality using the Kolmogorov–Smirnov test and for homogeneity of variances by the Levene's test and arcsine-transformed when necessary. We used a two-way ANOVA to determine the significance of the two fixed factors (temperature fluctuation ranges and exposure time) on germination percentage for each species. This analysis was only possible for the four species with the complete set of treatments.

To examine the variation in germination between temperature treatments with regard to increasing time of exposure, we applied a regression to the germination data for each temperature treatment (40/18°C, 47/16°C and 61/16°C) against the numbers of days of exposure (5, 15 and 30 days) for each species. Then, we compared the slopes of the regressions using an *F*-test. Only regressions with slopes significantly different from zero were compared. Germination values from the control treatment were used as common starting point (0 days of exposure) in all regressions.

Results

The mechanical scarification treatment showed that viability and potential maximum germinability of seeds used in the experiment was very high (96.7% for *A. suaveolens*, 100% for *G. grandiflorum*, and 98.3% for *D. retorta* and *P. ferruginea*). Only *B. obcordata* and *B. rhombifolia* had lower values (83.3 and 86.7%, respectively).

The response to heat treatments differed depending on the species. Daily temperature regimes and exposure duration influenced germination response in all species, except for *A. suaveolens* (Table 1, Fig. 1). Neither of these factors significantly affected germination in *A. suaveolens* (Table 1), where germination values were low for all treatments. The control treatment reached 5% germination, while the maximum in any treatment was 22.4% (Fig. 1).

The output from the one-way ANOVA showed that germination in *D. retorta* was significantly greater than the control (11.9% germinated) at 61/16°C after 15 and 30 days, reaching 37.3 and 62.7% respectively, but was not influenced by lower temperatures or 5 days' exposure at 61/16°C (Fig. 1). The slope of the relationship between germination and exposure duration at 61/16°C temperature regime was considerably greater than one, suggesting that further exposure may further increase germination (Table 2).

A similar pattern was apparent for *G. grandiflorum*, with significantly greater germination than the control treatment (23.3% germinated) at the 47/18°C 30-day treatment (50% germinated), and at 61/16°C after 15 and 30 days of exposure, with values of 53.3 and 80% respectively (Fig. 1). The regression slope for the 47/18°C treatment was less than 1, while at 61/16°C with the regression slope was almost 2 times higher and comparable with *D. retorta* at this temperature regime (Table 2).

There was a significant interaction between temperature and exposure duration for *P. ferruginea* (Table 1). For all treatments, germination increased with exposure duration (Fig. 1), but the greatest effect was found at 61/16°C, with a regression slope ~5 times higher than at 40/18°C and 47/18°C (Table 2). One-way ANOVA showed that germination was significantly enhanced over the control (10.2% germinated) at 61/16°C after 15 and 30 days of exposure, reaching values of 37.3 and 88.1%, respectively (Fig. 1).

Table 1. Results from the two-way ANOVA for the four species with complete experimental design

Variable	d.f.	Mean square	*F*	*P*
Acacia suaveolens				
Time	2	0.008	0.964	0.4
Temperature	2	0.023	3	0.075
Time*Temperature	4	0.01	1.29	0.312
Residual	18	0.008	–	–
Dillwynia retorta				
Time	2	0.155	8.92	0.002
Temperature	2	0.175	10.11	0.001
Time*Temperature	4	0.026	1.53	0.236
Residual	18	0.017	–	–
Gompholobium grandiflorum				
Time	2	0.115	6.37	0.008
Temperature	2	0.209	11.63	0.001
Time*Temperature	4	0.047	2.63	0.068
Residual	18	0.018	–	–
Pultenaea ferruginea				
Time	2	0.223	17.735	<0.001
Temperature	2	0.319	25.301	<0.001
Time*Temperature	4	0.065	5.18	0.006
Residual	18	0.013	–	–

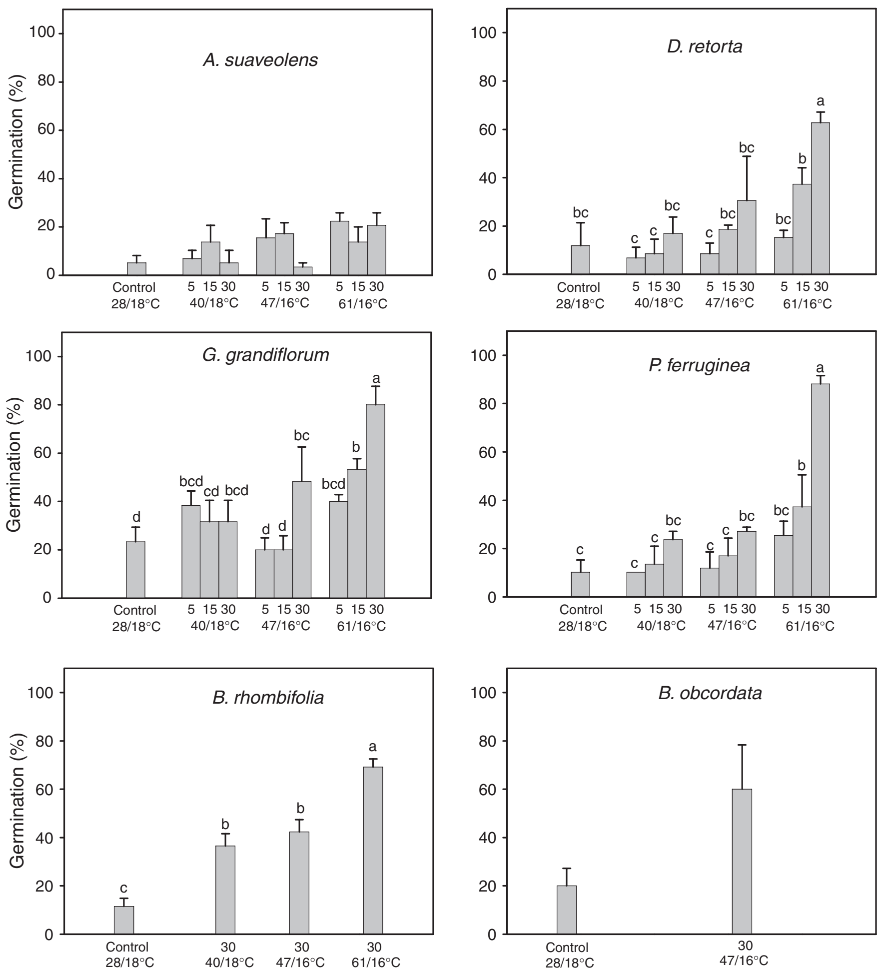

Fig. 1. Effect of treatments simulating daily soil temperature regimes in summer-burned stands upon the germination of some Australian legumes. Different lower case letters above columns indicate significant differences between treatments (Duncan's *post-hoc* test, $P < 0.05$). Error bars indicate standard error. Control = 28/18°C treatment with 30 days of exposure, simulating soil temperature regime under unburnt vegetation. The numbers 5, 15 and 30 beneath columns indicate the different heat exposure periods (in days) used in the experiment.

Table 2. Results of linear regression approach between percent germination and duration of heat treatments (5, 15 and 30 days) for the different species and daily temperature regimes

Species	Treatment	Slope	Intercept	r^2	*F*	*P*	*n*
Acacia suaveolens	40/18°C	0.01	7.55	0.01	0.006	0.940	12
	47/16°C	–0.15	12.19	0.03	0.350	0.567	12
	61/16°C	0.31	11.61	0.14	1.672	0.225	12
Dillwynia retorta	40/18°C	0.23	8.19	0.06	0.641	0.442	12
	47/16°C	0.7	8.59	0.22	2.81	0.125	12
	61/16°C	1.77	9.68	0.83	47.665	<0.001	12
Gompholobium grandiflorum	40/18°C	0.27	29.13	0.08	0.875	0.372	12
	47/16°C	0.92	16.83	0.39	6.413	0.03	12
	61/16°C	1.79	26.75	0.86	61.449	<0.001	12
Pultenaea ferruginea	40/18°C	0.46	8.55	0.37	5.982	0.035	12
	47/16°C	0.57	9.36	0.4	6.614	0.028	12
	61/16°C	2.51	8.87	0.84	53.98	<0.001	12

Although all treatments were not possible for *B. obcordata* and *B. rhombifolia*, both species also showed a trend of enhanced germination in relation to increasing daily temperatures (Fig. 1). One-way ANOVA for *B. rhombifolia* showed significant differences for all temperature treatments compared with the control, reaching germination of 69.2% for the 61/16°C

30-day treatment, while *B. obcordata* showed no significant increase in germination after exposure to 47/16°C for 30 days.

Discussion

Soil temperature regimes after summer fires could play a key role in breaking physical seed dormancy, independently of temperatures experienced during fire. We observed a significant increase in germination for several legume species after treatment at a range of temperatures representative of soil conditions in open post-fire areas. This effect would be especially pronounced on seeds present in shallow or sandy soil profiles, where temperatures reach their widest ranges (Auld and Bradstock 1996).

Although few studies have investigated the effect of post-fire soil temperature regimes on native Australian species, there is evidence from other regions that have shown similar responses by members of the Fabaceae. In European heath in the Mediterranean, daily temperature cycles occurring in vegetation gaps promoted germination in the gorse *Ulex parviflorus* (Baeza and Roy 2008). In temperate European ecosystems, Van Assche *et al*. (2003) found that slight seasonal changes in daily temperature fluctuations were key to breaking physical dormancy of many herbaceous legumes. Other evidences have been highlighted from studies on invasive species, such as the gap recruitment displayed by the tropical shrub *Mimosa pigra* (Lonsdale 1993) and the European gorse, *U. europaeus* in New Zealand (Ivens 1983). Several studies in agricultural systems found that the hard seeds of clover, *Trifolium subterraneum*, softened in response to daily temperature regimes between 30 and 60°C, if treated for several weeks or months (Hagon 1971; Taylor 1981).

Auld and O'Connell (1991) observed that many leguminous species from south-eastern Australia had their physical dormancy broken to varying degrees by temperatures experienced during fire. The most important factor breaking dormancy was temperature, with a few species reaching significant germination levels after treatment at 40 and 60°C, but most reaching their maximum germination after treatment at 80–100°C. The duration of exposure did not significantly change the effect on dormancy, however, it should be noted that temperatures maintained in the soil during fire are short and exposure duration was tested over a scale of only minutes (Bradstock and Auld 1995). In contrast, daily temperature regimes over the threshold for breaking dormancy can remain after a summer fire for weeks or months (Raison *et al.* 1986; Auld and Bradstock 1996). Our work has shown that duration of treatment (5–30 days) interacts with temperature to break physical seed dormancy in some species, with the highest germination levels reached after the longest treatment durations in some cases. The strength of this interaction increased with increasing temperature ranges. Not surprisingly, the germination response to heat treatments varied between species. For example, *A. suaveolens*, a species whose physical dormancy is broken from 60 to 80°C (Auld and O'Connell 1991), was not influenced by any of the temperature ranges or duration tested; it is unlikely that seeds would experience longer durations of exposure to the treatment temperatures in a natural setting, so germination and recruitment of this species may be more tightly bound to direct fire cues. In contrast, for other species with a lower threshold for breaking physical dormancy (40–60°C), such as *G. grandiflorum*, *D. retorta*, *P. ferruginea*, *B. obcordata* and *B. rhombifolia* (Auld and O'Connell 1991), germination has the potential to be determined by both direct and indirect cues.

Our results suggest that indirect fire cues could have more influence than expected on the germination response of some physically dormant species, especially after summer fires. Additionally, the influence of post-fire temperature regimes within the soil may behave in an additive and/or synergistic way with the direct fire cues heat and smoke in overcoming seed dormancy. For example, low intensity fires may not provide adequate heat to break dormancy in seeds, with temperatures greater than 40°C reached only in the upper 2 cm of the soil profile, and temperatures of 60–70°C occurring for only a few minutes at 1-cm depth (e.g. Auld 1986; Bradstock and Auld 1995). However, significant post-fire germination levels could still be reached if the litter layer was consumed and daily soil temperature regimes were enhanced. Other indirect fire cues such as the removal of canopy vegetation could increase both soil temperatures and the red : far-red light ratio, which can also promote germination in leguminous species (Baeza and Roy 2008). The combination of these factors may explain the higher than expected emergence of *Acacia* seedlings observed after fires studied in south-eastern Australia (Monk *et al*. 1981; Auld 1986; Bradstock and Auld 1995). It is nevertheless true that high intensity fires and the opening of litter and canopy gaps are highly correlated (Bradstock and Auld 1995; Whight and Bradstock 1999). Thus, the rupture of physical dormancy via both fire temperatures or via daily temperature regimes after fires are probably conflated and further field studies taking into consideration both effects are needed to put our experimental findings into context. This mechanism, in addition, could play a key role in inter-fire recruitment, promoting shrub regeneration in gaps opened in the canopy vegetation. In fact, other studies in fire-prone ecosystems have contrasted these cues on seedling establishment by comparing cleared with burned plots, and observed, for example, that in California chaparral germination was more tied to direct effects of fire (Tyler 1995) whereas in other Mediterranean Basin shrublands indirect effects may increase their significance (Baeza and Roy 2008; V. M. Santana, unpubl. data).

Enhanced germination resulting from summer daily temperature regimes could be considered adaptive for many physically dormant species in Mediterranean fire-prone vegetation. This may ensure that a flush of germination occurs predominantly in autumn, independently of fire season, avoiding germination during the summer drought (Trabaud 1994; Bell 1999; Baeza and Roy 2008). While a strong seasonal pattern of rainfall does not occur in south-eastern Australia, time periods with adequate soil moisture to allow seedling germination and emergence are much more common in the cooler seasons (Bradstock and Bedward 1992). Seeds with released physical dormancy germinate, independently of season, as soon as moisture conditions are suitable (Hodgkinson 1991; Bell 1999). Therefore, there is also the potential for an adaptive advantage in these non-seasonal rainfall habitats. Probably, advantages of this mechanism on these habitats could be determined by the spreading germination over time. Rupture of dormancy several weeks or months after fire could be an advantage avoiding unsuitable conditions in the immediate post-fire period, which could limit the success of seedling establishment or survival (Frazer and Davis 1988; Carrington 1999; De Luis *et al*. 2005). Hodgkinson (1991) found in semiarid woodland with no seasonal rainfall pattern in inner south-eastern Australia higher germination and survival rates for leguminous species regenerated after spring and summer fires than in winter fires.

The rupture of seed dormancy by the soil temperature regime could have implications on seeds and seed bank dynamics within the framework of predicted impacts of climate change, where significant increases in mean air temperature are forecast for the latter half of the 21st century (CSIRO 2007; IPCC 2007). In south-eastern Australia, Auld and Bradstock (1996) found that daily soil temperatures were significantly related to air temperature at all soil depths tested after a summer fire. In addition, Ooi *et al*. (2009) found a relationship between maximum air temperature and soil temperature in bare soils in arid environments, where an air temperature increase of 4°C resulted in an increase of ~10°C in soil temperature. Predicted increases in temperatures may therefore promote germination in soil seed banks that otherwise would persist ungerminated after fire. Persistent seed banks play a fundamental role minimising the risk of decline or local extinction in plants for the cases where the fire-free intervals are less than the primary juvenile periods of the species (Auld and Denham 2006).

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