

Fire-related cues break seed dormancy of six legumes of tropical eucalypt savannas in north-eastern Australia

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Abstract This paper describes an assessment of the effect of exposure to fire-related cues (heat shock, smoke and nitrate) and the interactions between the cues on seed dormancy release of tropical savanna legumes in north-eastern Australia. Ten legume species were tested, comprising both native and exotic species. The ten species responded variously to the treatments. Brief exposure to temperatures between 80 and 100°C was found to break the seed dormancy of the native ephemeral herbs *Chamaecrista mimosoides*, *Crotalaria calycina*, *Crotalaria montana*, *Indigofera hirsuta* and *Tephrosia juncea*, as well as the exotic ephemeral herb *Crotalaria lanceolata*. Exposure to 80°C combined with treatment with a nitrate solution produced an additive effect on the germination of *Chamaecrista mimosoides* and *Crotalaria lanceolata*. However, the four species with the heaviest seeds, two exotic ephemeral herbs (*Chamaecrista absus* and *Crotalaria pallida*) and two native perennials (*Galactia tenuiflora* and *Glycine tomentella*) displayed no significant increase in germination with exposure to fire-related cues. Exposure to 120°C for 5 min produced seed mortality in all species tested. Two of the largest seeded species, *Crotalaria pallida* and *Galactia tenuiflora*, displayed the lowest tolerance to heat shock, with seed mortality after exposure to 100°C for 5 min. These data indicate that fire can promote the germination of some tropical savanna legumes. As a proportion of seeds of each species displayed no innate dormancy, some germination may occur in the absence of fire, especially of exotic species.

Key words: heat shock, legumes, seed dormancy, seed germination, tropical savanna.

INTRODUCTION

Seed dormancy can increase the chance of seedling establishment by delaying germination time until climatic and microsite conditions are most favourable, and by spreading the germination of a seed bank across several rainfall events (Harper 1977; Bell 1999). Although innate dormancy is absent from some Australian tropical savanna species, such as *Eucalyptus miniata* (Setterfield 1997) and the perennial grass *Alloteropsis semialata* (Crowley & Garnett 2001), seed dormancy has been documented in a number of tropical species. Dormancy in some grasses is related to an after-ripening requirement in the seed embryo that lapses during the dry season, linking germination with the onset of the wet season (Bell 1999). This after-ripening requirement has been detected in both annual and perennial tropical grasses, including *Chrysopogon fallax*, *Heteropogon contortus*, *Sorghum* spp. and *Themeda triandra* (Mott 1978; Andrew & Mott 1983; Mott & Andrew 1985; McIvor & Howden 2000).

The brief exposure of seeds to elevated temperatures ('heat shock'; Bell *et al.* 1993) typically breaks a physical barrier in the seed coat that inhibits moisture uptake by the seed. The physical barrier is broken either by cracking the cuticular layer or opening a strophilar plug in the seed coat (Bell *et al.* 1993; Bell 1999). Heat shock may also influence physiological processes within the embryo (Bell & Williams 1998). The high soil surface temperatures that are experienced in tropical savannas during the late dry season (30–60°C) have been shown to increase seed germination in some tropical savanna grasses (Mott 1978). There has been limited research on the effect of heat shock on tropical savanna species. However, the arid zone shrubs *Acacia aneura* and *Senna nemophila*, which extend into tropical savannas, show increased germination after brief exposure to temperatures between 40 and 70°C (Hodgkinson & Oxley 1990).

The stimulatory effects of fire-related chemical cues on the germination of Australian tropical savanna species have also received limited attention. In other habitats, however, fire-related chemicals that break seed dormancy include: (i) nitrates (the availability of which can increase in the soil with the first rain

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Accepted for publication March 2003.

following fire (Thanos & Rundel 1995; Bell *et al.* 1999); (ii) compounds present in smoke (Dixon *et al.* 1995; Keith 1997); and (iii) charcoal (Bell *et al.* 1987). Positive smoke responses have been shown in the germination of the tropical savanna grasses *Heteropogon contortus* and *Themeda triandra*, and the fire-killed tree *Callitris intratropica* (Baxter *et al.* 1994; Campbell *et al.* 1996; Roche *et al.* 1997). Multiple cues, specifically exposure to both heat shock and smoke, have also been shown to provide an additive effect in promoting germination of the seeds of temperate species (Keith 1997; Gilmour *et al.* 2000; Kenny 2000; Morris 2000).

In the present paper we aimed to answer the following questions:

1. Does the percentage germination of a number of representative legumes of Australian tropical savannas increase with exposure to heat shock?
2. Does the percentage germination of legumes increase with exposure to chemicals related to the passage of fire, specifically compounds found in smoke and nitrate?
3. Is the percentage germination of legumes enhanced by exposure to both heat shock and chemicals?

METHODS

Test species and treatments

Ten legume species were chosen to represent both native and exotic species and ephemeral and perennial species that are commonly found in the savannas of northern-eastern Australia (Table 1). Seeds were collected between March and June 1999 from 20–50

separate individuals of each species, in eucalypt savanna at Cape Cleveland, approximately 25 km east of Townsville (147°02'30''E, 19°16'30''S). Seeds of each species were pooled and stored in paper bags in the dark at room temperature for several months prior to the germination experiment, which ran from September to December 1999.

A pilot study of three of the test species, *Chamaecrista mimosoides*, *Crotalaria lanceolata* and *C. pallida* (taxonomy follows Henderson 2002), indicated that an incubation temperature between 25 and 30°C was most suitable for germination. This is consistent with the results of Andrew and Mott's (1983) study, which demonstrated that incubation temperatures of between 25 and 35°C were best for the germination of Northern Territory grasses.

Three replicates of 30 seeds were used for each treatment in the experiment. Seed weights were determined for each species by weighing three replicates of 30 seeds. Controls and up to 11 different treatments were used to examine the seed dormancy of each species (Table 1). A subset of treatments was implemented for several species where seed availability was limited. A 5-min exposure was used for most heat treatments because it is a realistic residence time for the peak elevated temperatures in the topsoil during the passage of fire (Bradstock & Auld 1995; Smith *et al.* 2000). One longer, 45-min, exposure to 85°C was also used. For the heat treatment, the three replicates for each treatment were placed in a preheated oven separately, with ovens cooled and reheated between treatments, as recommended by Morrison and Morris (2000) to produce true replication. A further heat treatment involved a 5-min exposure of seeds to water heated to 80°C, because Martin and Cushwa (1966) and Martin *et al.* (1975) considered heating seeds in

Table 1. Species and fire-related treatments in the laboratory experiment

Species	N	80°C W, 5 min	85°C, 45 min	100°C, 5 min	120°C, 5 min	S + 80°C 5 min	N + 80°C 5 min
<i>Chamaecrista absus</i> *				×			
<i>Chamaecrista mimosoides</i>	×	×	×	×	×	×	×
<i>Crotalaria calycina</i>	×	×	×	×	×	×	×
<i>Crotalaria lanceolata</i> *	×	×	×	×	×	×	×
<i>Crotalaria montana</i>	×	×	×	×	×	×	×
<i>Crotalaria pallida</i> *	×	×	×	×	×	×	×
<i>Galactia tenuiflora</i>				×	×		
<i>Glycine tomentella</i>							
<i>Indigofera hirsuta</i>	×	×	×	×	×	×	×
<i>Tephrosia juncea</i>			×	×	×		

×, species exposed to specific treatments: N, initially watered with 5 mL 1 g L⁻¹ potassium nitrate solution; 80°C W 5 min, exposure to 80°C water for 5 min; 85°C 45 min, exposure in the oven at 85°C for 45 min; 100°C (or 120°C) 5 min, exposure in the oven at 100°C (or 120°C) for 5 min. All 10 species were also exposed to no pretreatment, i.e. control (C); ambient temperature smoke for 90 min (S); and oven heating at 40, 60 and 80°C for 5 min (40°C 5 min, etc.). *, exotic species; *Galactia tenuiflora* and *Glycine tomentella* are perennial species capable of sprouting following fire. The remaining species are ephemerals that complete their life cycle within a single year, with plants occasionally living 2 years, and are killed by fire.

hot water may more accurately depict conditions in the soil seed bank during fire than oven heating.

The smoke treatment followed the method described in Dixon *et al.* (1995). Smoke was produced in a 20-L metal drum filled with smouldering grass and litter collected from the Cape Cleveland seed collection site. The smoke was pumped through a 3-m length of flexible metal tubing, which allowed the smoke to cool before entering a plastic tent, in which the seeds were placed. Smoke was pumped into the tent for 90 min before seeds were removed for incubation in the laboratory.

Replicates subjected to the nitrate treatment were watered with 5 mL of a 1 g L⁻¹ solution of potassium nitrate, which promotes the germination of several Western Australian species (Bell *et al.* 1999). The smoke and nitrate treatments were applied simultaneously to all pertinent replicates, although it is acknowledged that three separate applications would have produced a more appropriate replication of these treatments (Morrison & Morris 2000).

An assessment was also made of multiple cues by examining the interactions between exposure to chemicals and heat shock. In these two treatments, seeds were exposed to 80°C for 5 min, then exposed to either smoke or watered with nitrate solution.

After treatment, seeds were placed onto filter paper in Petri dishes, sprayed with a 2 g L⁻¹ solution of fungicide (Thiram) and, for all but the nitrate treatments, watered with 5 mL of distilled water. Petri dishes were placed randomly within a controlled temperature room set at 27.5°C with a 12-h diurnal light regime. In many eucalypt woodland species from south-eastern Australia, this light regime has been shown to enhance germination significantly (Clarke *et al.* 2000). Germination was defined by radicle emergence, and germinants were removed. Petri dishes were sprayed with distilled water as required, and sprayed periodically with fungicide.

Germination was assessed daily for 12 weeks. At the end of this period, all ungerminated seeds in the control treatment were assessed for viability using a tetrazolium test (Moore 1985). A slit was made in seeds, which were subsequently soaked in a 1% tetrazolium solution in the dark for 48 h. Seeds were then dissected under a microscope and assessed for presence of the pink colouration that indicates a viable embryo. The number of viable ungerminated seeds was added to the number of germinants to give a total number of viable seeds for each replicate of the control treatment. The means were used to estimate the percentage viability for each species. A tetrazolium test was also performed on *Crotalaria pallida* seeds exposed to 120°C, to assess whether the absence of germination after exposure to this temperature was due to seed mortality.

Statistical analyses

Data analysed were percentage germination of viable seeds for each replicate. A one-factor ANOVA was used to assess the effects of differences among all single treatments. Scheffe's post-hoc test was used to determine significant differences among treatments and a Cochran's test was used to assess homogeneity of variance (Underwood 1997). Germination data for *Glycine tomentella* required arcsine transformation. Two-factor ANOVA were used to assess interactions between the factors smoke (or nitrate) and exposure to 80°C. Variance heterogeneity for the two-factor ANOVA for *Crotalaria montana* could not be resolved by transformations. Therefore separate non-parametric Kruskal-Wallis ANOVA by ranks were performed for the individual factors smoke and 80°C, and nitrate and 80°C (Zar 1999).

The significance of the differences in mean seed weight between the three exotic species (*Chamaecrista absus*, *Crotalaria lanceolata* and *Crotalaria pallida*) and

Table 2. Mean (standard error) seed mass, percentage viability and size ranking of each species examined in the laboratory experiment

Species	Size ranking	Mean (SE) weight (g) per 30 seeds ($n = 3$)	Mean individual seed weight (mg)	Mean (SE) viability (%)
<i>Chamaecrista absus</i>	10	0.433 (0.008)	14.4	96 (1)
<i>Chamaecrista mimosoides</i>	1	0.018 (0.005)	0.6	93 (2)
<i>Crotalaria calycina</i>	5	0.111 (0.002)	3.7	98 (2)
<i>Crotalaria lanceolata</i>	4	0.079 (0.002)	2.6	99 (1)
<i>Crotalaria montana</i>	2	0.051 (0.001)	1.7	90 (3)
<i>Crotalaria pallida</i>	8	0.159 (0.005)	5.3	96 (3)
<i>Galactia tenuiflora</i>	9	0.298 (0.021)	9.9	100 (0)
<i>Glycine tomentella</i>	7	0.118 (0.003)	3.9	94 (2)
<i>Indigofera hirsuta</i>	3	0.070 (0.003)	2.3	82 (10)
<i>Tephrosia juncea</i>	6	0.116 (0.002)	3.9	92 (3)

Size ranking is from 1 (lightest) to 10 (heaviest).

the other seven species; and the two perennial species (*Galactia tenuiflora* and *Glycine tomentella*) and the eight ephemeral species, was tested using independent *t*-tests (Zar 1999). The proportions of non-dormant seed, estimated by the percentage germination of seeds in control treatments, of the three exotic species were contrasted with those of the seven native species. A Mann–Whitney *U*-test was used to test the significance of this comparison, because the homogeneity of vari-

ance assumptions of a *t*-test (Zar 1999) were not met, even after data transformations.

RESULTS

The mean seed weight per species ranged from 0.6 to 14.4 mg (Table 2). Mean seed weight of the three exotic species (7.4 mg, SE = 3.6 mg) was not signifi-

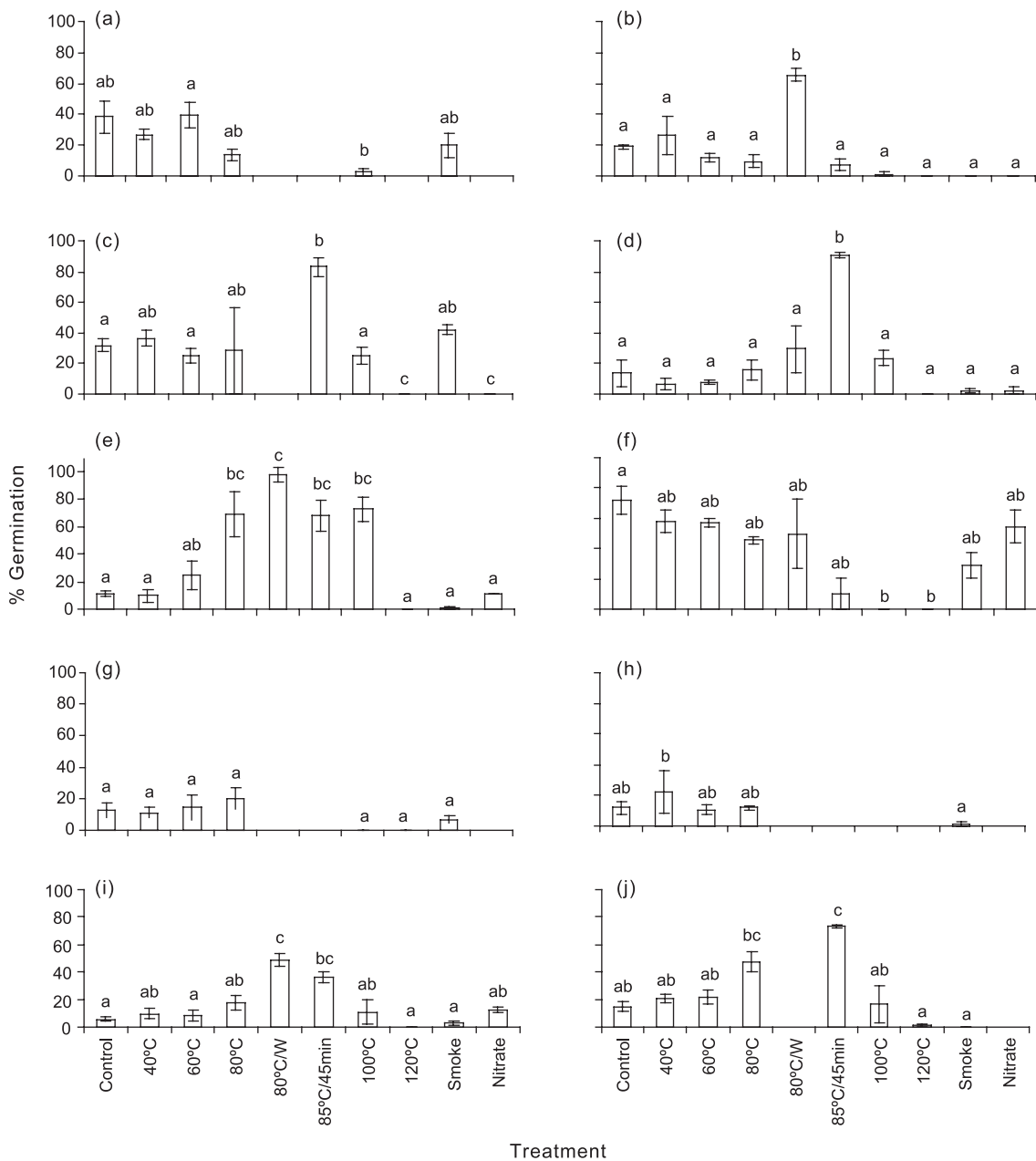


Fig. 1. Mean (\pm SE) percentage germination of viable seed after exposure to various levels of heat shock, as well as smoke and nitrate. Columns in each graph with the same lower-case letter are not significantly different at $P > 0.05$. All temperature exposures are for 5min, except the 45min duration of 85°C 45 min. 80°C/W, exposure to 80°C water for 5 min. (a) *Chamaecrista absus*; (b) *Chamaecrista mimosoides*; (c) *Crotalaria calycina*; (d) *Crotalaria lanceolata*; (e) *Crotalaria montana*; (f) *Crotalaria pallida*; (g) *Galactia tenuiflora*; (h) *Glycine tomentella*; (i) *Indigofera hirsuta*; (j) *Tephrosia juncea*.

cantly greater than that of the seven native species (3.7 mg, SE = 1.1 mg; $t = 1.33$, $P < 0.219$). The mean seed weight of the two perennial species (6.9 mg, SE = 3.0) was also not significantly greater than that of the eight ephemeral species (4.3 mg, SE = 1.5 mg; $t = 0.759$, $P < 0.470$).

Mean percentage viability for the 10 species was high, ranging from 82 to 100% (Table 2). The mean percentage germination of viable seed varied between species, with the highest germination by a species ranging from 98% in the ephemeral *Crotalaria montana*

to 20% for the perennial *Galactia tenuiflora* (Fig. 1). Exposure to elevated temperatures between 80 and 100°C significantly increased the germination of six of the 10 species: *Chamaecrista mimosoides*, *Crotalaria calycina*, *Crotalaria lanceolata*, *Crotalaria montana*, *Indigofera hirsuta* and *Tephrosia juncea* (Fig. 1, Table 3). The treatments that produced the highest germination overall were exposure to 80°C water for 5 min and 85°C dry heat for 45 min. The four species with no enhancement of germination by heat shock, *Chamaecrista absus*, *Crotalaria pallida*, *Galactia tenuiflora* and

Table 3. Statistical results of one- and two-factor ANOVAs for seed germination of 10 legume species

Species	Treatment	One-factor ANOVA		Two-factor ANOVA (Heat × Smoke)			Two-factor ANOVA (Heat × Nitrate)	
		Heat (80°C) $F_{1,8}$	Smoke $F_{1,8}$	Heat × Smoke $F_{1,8}$	$F_{1,8}$ Heat (80°C)	Nitrate $F_{1,8}$	Heat × Nitrate $F_{1,8}$	
<i>Chamaecrista absus</i>	$F_{5,12} = 4.512^*$			8.909*	956.0000	4.481	16.333**	
<i>Chamaecrista mimosoides</i>	$F_{9,20} = 19.151^{***}$	0.182	11.636**	2.647	2.223	31.711***	3.943	
<i>Crotalaria calycina</i>	$F_{8,18} = 62.370^{***}$	5.188	0.1059	3.330	12.082**	2.219	9.890*	
<i>Crotalaria lanceolata</i>	$F_{9,20} = 13.806^{***}$	4.433	0.177	12.149**	6.203*	$H_{1,8} = 6.203^*$		
<i>Crotalaria montana</i>	$F_{9,20} = 19.883^{***}$	12.149**	73.644***	2.375	4.840	1.284	0.751	
<i>Crotalaria pallida</i>	$F_{9,20} = 6.824^{***}$	4.796	19.901**	0.048				
<i>Galactia tenuiflora</i>	$F_{6,14} = 2.757$	1.734	1.735					
<i>Glycine tomentella</i>	$F_{4,10} = 4.432^*$			2.579	19.862**	8.828*	1.241	
<i>Indigofera hirsuta</i>	$F_{9,20} = 13.087^{***}$	6.368*	6.368*					
<i>Tephrosia juncea</i>	$F_{7,16} = 16.744^{***}$							

Because of variation in seed supply, two-factor ANOVA were not performed for all species. Non-parametric Kruskal–Wallis ANOVA by ranks was used in place of the two-factor ANOVA for assessing the effect of heat and nitrate for *Crotalaria montana*. $F_{5,12}$ indicates F -value, denominator d.f., numerator d.f.; F - or H -values without an asterisk (*) are not significantly different at $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

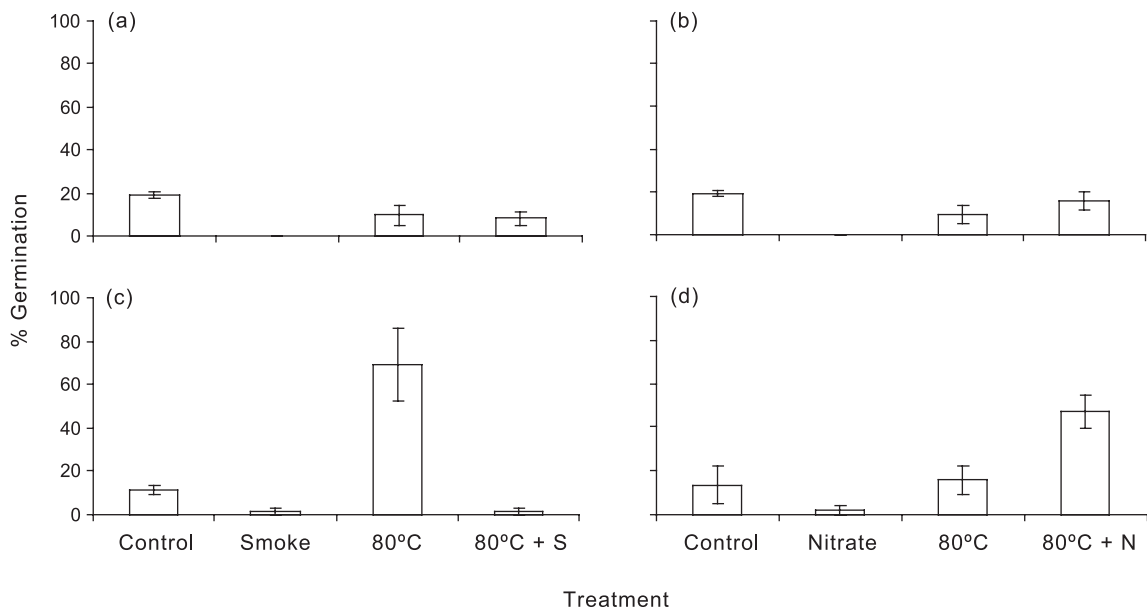


Fig. 2. Mean (\pm SE) percentage germination of viable seed after exposure to heat shock and smoke (S), and heat shock and nitrate, for species with significant interactions. (a) *Chamaecrista mimosoides* (Heat × Smoke); (b) *Chamaecrista mimosoides* (Heat × Nitrate); (c) *Crotalaria montana* (Heat × Smoke); (d) *Crotalaria lanceolata* (Heat × Nitrate).

Glycine tomentella, were the four heaviest-seeded species (Tables 2 and 3).

The percentage germination of viable seeds in the control treatments (i.e. non-dormant seeds), averaged 23% across the 10 species and ranged from 72% in the exotic *Crotalaria pallida* to 5% in the native *Indigofera hirsuta*. The three exotic species, as a group, had a significantly higher percentage of non-dormant seeds (mean = 41%, SE = 10; $U = 43.00$; $P < 0.02$) compared with the seven native species (mean = 15%, SE = 2).

Seeds of seven of the eight species exposed to 120°C did not germinate (Fig. 1). The only species to germinate after exposure to 120°C was *Tephrosia juncea*, with just 1% germination. A tetrazolium test of the *Crotalaria pallida* seeds exposed to 120°C for 5 min showed that none were viable, indicating that exposure to this temperature is lethal to the embryos.

Exposure to smoke or nitrate in isolation did not significantly promote germination in any species (Fig. 1). Exposure to smoke and nitrate significantly inhibited the germination of *Crotalaria calycina*.

A significant interaction was detected from the combined exposure to smoke and 80°C for 5 min for *Chamaecrista mimosoides* and *Crotalaria montana*, with exposure to both heat shock and smoke producing less germination of *C. montana* than heat shock alone (Fig. 2, Table 3). A significant interaction was also detected with the combined exposure to nitrate and 80°C for 5 min for *Chamaecrista mimosoides* and *Crotalaria lanceolata*, with the combined exposure to heat shock and nitrate producing a higher percentage germination than exposure to each treatment separately (Fig. 2, Table 3).

DISCUSSION

Evidence was found that fire-related factors break the seed dormancy of six of the 10 species examined. Significantly greater germination occurred after exposure to temperatures between 80 and 100°C, which is consistent with the germination requirements of many legumes of southern Australia (Floyd 1976; Shea *et al.* 1979; Auld & O'Connell 1991; Bell *et al.* 1993; Jhurree *et al.* 1998). Exposures to temperatures as low as 40°C can significantly enhance the germination of some legumes in south-eastern Australia (Auld & O'Connell 1991). This was not found in the current study, perhaps because of inadequate exposure time or because higher ambient temperatures in the tropics may have lead to the development of higher minimum levels to elicit a heat shock response.

The 80°C water treatment, which produced significantly more germination than the 5 min exposure to 80°C air temperature for *Chamaecrista mimosoides* and *Indigofera hirsuta*, may be a more accurate reflection of

soil seed bank conditions during fire, when moisture is present in the topsoil, than oven heating (Martin & Cushwa 1966; Martin *et al.* 1975). The 85°C air temperature for 45 min produced significantly greater germination than the 80°C air temperature for 5 min in *Crotalaria lanceolata*. This may have been due to the slightly higher temperature 5°C or the longer duration of heating, or both. After the passage of fire, although soil temperatures may decline rapidly from the maximum, temperatures can remain elevated for 20 min or more (Bradstock & Auld 1995). Therefore, the increased germination with elevated temperatures of 45 min duration may have some ecological significance.

Mean seed weights varied considerably between species; however, no significant relationships were found between seed weight and the ecological syndrome of species (i.e. exotic *vs* natives, and ephemerals *vs* perennials). The four species with the largest mass displayed no significant increase in germination with exposure to elevated temperatures, but survived exposure to at least 80°C. This suggests an ability to tolerate the passage of fire, but provides no evidence of fire-promoted germination in those species. Exposure to 120°C for 5 min was lethal to most seeds in this experiment, which is consistent with reports from other studies (Auld & O'Connell 1991). The second and third largest seeded species, *Galactia tenuiflora* and *Crotalaria pallida*, displayed the lowest tolerance to heat shock, with apparent mortality at 100°C. This contrasts with African acacias, where larger seeded species possess a greater tolerance of heat shock than those with smaller seeds (Midgley & Bond 2001), although no correlation between seed size and thermal tolerance is apparent for legumes of south-western Australia (Bell & Williams 1998).

The two native species that did not respond significantly to heat shock, *Galactia tenuiflora* and *Glycine tomentella*, were the only perennial species examined, and each is capable of sprouting after fire (P. R. Williams *et al.*, pers. obs. 1999). Sprouting species may require fewer seedlings to maintain population density than annual or ephemeral species, and therefore the requirements to break seed dormancy may differ with life history and fire response (Bell 2001). However, the germination of *Galactia tenuiflora* and *Glycine tomentella* was low (< 25%) in all treatments, including the control. This may have resulted from suboptimal incubation conditions, an after-ripening requirement not satisfied by the few months of storage, and/or the lack of a heat shock or chemical treatment that would have produced greater germination. Further examination of the dormancy requirements of these species is required.

Although germination in the laboratory without pretreatment does not necessarily indicate the absence of seed dormancy (Whelan 1995), the germination in control treatments suggests fire-related stimuli are not

obligatory. The mean percentage of 'non-dormant' seeds (i.e. those lacking an innate dormancy related to fire cues) for the seven native species in the present study (15%) is similar to averages reported for legumes of south-eastern Australia (11–15%; Auld & O'Connell 1991; Morrison *et al.* 1992; Clarke *et al.* 2000) and south-western Australia (11–18%; Shea *et al.* 1979; Bell *et al.* 1993). However, the exotic species examined in the present study had a significantly higher mean percentage of non-dormant seeds (41%) compared with the natives. This suggests that some exotic legumes possess a greater capacity for recruitment in the absence of fire than native legumes in the savannas of north-eastern Australia. Indeed, several other exotic pasture legumes used in the region, including *Macroptilium atropurpureum* and *Stylosanthes humilis*, establish successfully in the absence of fire (McIvor *et al.* 1993).

Neither smoke nor nitrate in isolation significantly promoted seed germination, and the germination of *Crotalaria calycina* was inhibited by both. The significant interaction produced by exposure to heat shock followed by smoke, or nitrate, suggests that multiple components of fire operate to affect germination. The combination of heat shock and smoke produced less germination of *Chamaecrista mimosoides* and *Crotalaria montana* than heat shock alone. This may have resulted from the use of the 90 min exposure to smoke; Roche *et al.* (1997) demonstrated that a duration of more than 60 min can inhibit seed germination of other, non-legume, species. Roche *et al.* (1997) also found that the legume *Hovea chorizemifolia* was inhibited by the application of smoke directly onto seeds, but was promoted by smoke application after seeds were incorporated into the soil.

The synergistic effect of smoke and heat shock has recently been reported for several shrubs of fire prone regions in south-eastern Australia (Keith 1997; Gilmour *et al.* 2000; Kenny 2000; Morris 2000). Nitrate interacts with light regime to increase the germination of several Western Australian species (Bell *et al.* 1999), but we are not aware of previous reports of the additive effect of nitrate and heat shock. The greatest change in soil nitrate levels can occur with the first rains after fire (Bell 1999). The enhanced response to nitrate and heat shock may therefore be particularly useful in timing recruitment with the first rain following fire, thus allowing seedlings of these ephemeral species to take advantage of the full wet season to grow and produce seeds. Multiple fire cues are also beneficial for ensuring increased germination after fire when elevation of temperature in the topsoil is insufficient to break seed dormancy (Kenny 2000).

The results of the present study suggest that the post-fire pulse in the abundance of grasses and forbs, documented in a eucalypt savanna in north-eastern Australia (Williams *et al.* 2003) may in part be due to the release of some seeds from a state of dormancy

by the temperature elevation and enhanced nitrate concentrations in the topsoil as a result of fire.

ACKNOWLEDGEMENTS

We thank Eleanor Collins for her assistance with maintaining the laboratory experiment, Mike Lloyd for advice on the design of the smoke-producing apparatus and Brett Galloway for welding together the smoke-producing apparatus. We are also grateful to Mike Steele and Bob Mayer for their expert statistical advice. This paper was improved through comments on an earlier draft by Michael Bull, David Bell and an anonymous referee.

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