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## Germination and dormancy of grassy woodland and forest species: effects of smoke, heat, darkness and cold

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**Abstract.** The germination requirements of a broad spectrum of common species found in grassy woodlands and forests in the New England region of northern New South Wales were tested in a series of replicated growth-cabinet experiments. The effects of dark/diurnal light and smoke/no smoke were measured on 65 species in an orthogonal experiment, 21 of which were retested after storage for 12 months. The effect of storage for several years was also assessed under a diurnal light regime. In addition, the effects of preimbibition heat (80°C), and chilling on germination were also measured. A single temperature regime (15°C night/25°C day) was used in all treatments for comparative purposes. Most species had high viability and germinability under a diurnal light regime. Small shrub species included, however, a large proportion of species with entrenched dormancy. Light enhanced germination of 21 species significantly, whereas dark stimulated germination of only eight species. Heat and cold treatments also stimulated some germination but more often inhibited germination or produced no effect. Smoke stimulated germination, relative to other cues, in only one species (*Ajuga australis*) and more often inhibited germination or produced no effect. The relationship between variation in germination (stimulation, no effect or inhibition) of species in six growth-form classes was tested by using contingency tables for each treatment. No significant relationship between growth form and the effects of light, smoke or chilling was detected. Preimbibition heat effects were, however, significantly different among growth forms. Subshrubs showed a higher than expected proportion of species with a heat stimuli while herbaceous species showed a higher than expected proportion of species inhibited by preimbibition heat. Germinability generally increased in herbaceous species when stored at ambient temperatures while it remained relatively constant in woody species. Conversely, viability decreased in herbaceous species but remained relatively more constant in woody species. The effects of seed storage and high germinability suggest that most perennial herbaceous species have transient or short-term persistent seed banks. Germinability, with and without cues, was also negatively correlated with increasing seed size and larger growth forms. These traits might be related to the need for woody species, with soil-stored seed banks, to spread establishment risks in an environment where herbaceous competition and herbivory are likely to be important selection factors.

### Introduction

Germination, or lack of it, is a major control on the flux of seeds from the soil seed bank to seedlings. This essential link in the population dynamics of plants is one of a number of life history transitions that is important for understanding how populations and whole communities of plants are maintained. The dormancy and germination cues of plant species in Australian temperate grass-dominated communities are poorly understood in a comparative sense (see reviews by Trémont and McIntyre 1994; Yates and Hobbs 1997; Bell 1999; Clarke 2000) and attempts at relating plant attributes to ecological function have not been fruitful (Morgan 1998).

Germination studies of herbaceous species found in temperate communities have examined the effect of temperature (Willis and Groves 1991; Gilfedder and Kirkpatrick 1994),

the effects of varying temperature and light (McIntyre 1990; Morgan and Lunt 1994) and darkness (Morgan 1998). A number of native perennial grasses have also been examined for dormancy and germination cues in relation to light and storage (e.g. Hagon 1976; Lodge and Whalley 1981; Maze *et al.* 1993). In comparison with the herbaceous layer, relatively little is known about the germination of shrubs in grass-dominated temperate systems (Clarke 2000).

Fire-related effects on breaking seed dormancy are well known for many plant species in fire-prone vegetation in Australia (e.g. Auld and O'Connell 1991; Keith 1996; Bell 1999). In particular, there has been a recent surge in interest on the effects of smoke as a germination cue of Australian taxa. This has been demonstrated extensively in the flora of south-western Western Australia (Dixon *et al.* 1995; Roche

*et al.* 1997, 1998), and for a range of sclerophyllous species in eastern Australia (Enright *et al.* 1997; Keith 1997; Morris 1999) and some temperate grass species (Read and Bellairs 1999). However, the interactive effects of smoke and light on the dormancy and germination on tree, shrub and herbaceous species that occur in temperate grassy systems are not well understood.

The aims of our study were to test the germination requirement of a broad spectrum of common species found in grassy woodlands and forests in the New England bioregion of northern New South Wales. In particular, we examined the effects of smoke, darkness, extreme heat and chilling on the germination of a wide range of species with different growth forms. We then examined the relationship between variation in germination (stimulation, no effect or inhibition) across treatments, time and growth forms. The relationship between dormancy and growth form was also examined as a step toward the development of a functional group analysis on the basis of phylogenetic independence (Silvertown *et al.* 1997).

## Methods

### Seed collections

Seeds of 65 species of commonly occurring tableland species were collected from wild populations of plants on the New England bioregion during 1995–1996 (Appendix 1). Seed collections were treated for insects by purging with CO<sub>2</sub> and stored in paper bags at room temperature before use. Voucher specimens for each species were collected and lodged in the Beadle Herbarium New England. Species nomenclature follows Harden (1991–1993) except for recent changes recognised by the NSW Herbarium. A list of species used, their plant families, growth form, life-form, fire response and seed weights are given in Appendix 1. Seed weights were determined from a random subsample of 100 seeds.

### Germination

Germination of seed was tested by placing between 10 and 25 seeds on a germination pad placed over a moisture retaining sponge in a square germination dish. Four replicate dishes were randomly placed in each of two replicate Thermocline germination cabinets set to a diurnal cycle of 12 h of light and 12 h of dark, with a corresponding temperature cycle of 25 and 15°C, respectively. Seed was collected 3–6 months before germination tests as after-ripening is known to break dormancy in some species (Lodge and Whalley 1981). Mature dispersal units of grasses were collected and processed to remove the enclosing structures around the caryopses just before germination tests as these are known to inhibit germination (Lodge and Whalley 1981). Germinations were assessed at weekly intervals for up to 4 weeks, then for selected species at 8 weeks. Dark treatments were inspected after 2 weeks as this was the median time taken for germination in a range of temperate grassland species (Morgan 1998).

### Germination treatments

The effects of smoke water and light on germination of 65 species were assessed in a multifactorial experiment (Appendix 1). The smoke treatment consisted of applying freshly made smoke water to seed lots. Smoke fuel was collected from ground litter in a grassy woodland. Smoke water was made by drawing smoke through 5 L of distilled water for 30 min. This water was then diluted 1 : 10 before application to seeds on germination pads. Dark treatments consisted of wrapping half the germination trays in foil to exclude light in the germination cabinet.

Light was provided by fluorescent tubes emitting an intensity of 35  $\mu\text{E m}^{-2} \text{s}^{-1}$  over a diurnal cycle. Thus, there were four treatments consisting of two levels of smoke  $\times$  two levels of light. In addition, 21 species were retested after storage of seed at ambient temperature for about 1 year (Appendix 1). In these cases, there were two levels of smoke  $\times$  two levels of light  $\times$  2 years. Fifty-three species were also tested for germination and viability under diurnal light regime after storage between 29 and 54 months (Appendix 1).

The preimbibition effects of heat (80°C for 15 min) and chilling (5°C imbibed for 1 week) were also assessed on replicate seed samples of selected species under conditions of diurnal cycle of 12 h of light and 12 h of dark with a corresponding temperature cycle of 25 and 15°C. Fifty-six species were assessed for heat effects and 54 species were assessed for chilling (Appendix 1). The germination attribute measured was percentage germination of viable seeds after 14 days. Post-hoc statistical comparisons were made with the diurnal light treated seeds.

Any seeds that did not germinate, and looked viable, after about 6–8 weeks were initially tested for viability by using the tetrazolium test. Subsequent assessments were based on a visual inspection of ungerminated seeds. The overall viability of seed was estimated by using the highest germination percentage and adding any seeds that remained dormant but viable.

Analyses of treatment effects were made by ANOVA. Means were compared using a post-hoc Scheffé's test. Germination data were expressed as a percentage of viable seed. All data were arcsine transformed before analysis and tested for heterogeneity of variance using Cochran's test. Germination cabinet effects were pooled with replicates to increase power as no cabinet effects were detected.

### Comparison of treatments and growth forms

The viability response to storage (decreased or no change) was compared for 45 species across two-growth form classes (woody or herbaceous) by chi-squared statistic. Germinability, in diurnal light, response to storage (significantly increased, no change, or significantly decreased) was also compared for 52 species across two growth-form classes (woody or herbaceous) by chi-squared statistic.

The germination response (stimulated, no effect, or inhibited) was compared across treatments and growth-form groups by chi-squared statistic. Dormancy classes (strongly dormant, <50% germination) by treatments and weak dormancy, >50% germination by treatments) were compared across growth-form groups by chi-squared statistic. When significant independence was detected, with expected values less than five, a permutation test was used to verify the significance. Log seed size and dormant fraction of seeds under diurnal light was also compared using regression analysis.

## Results

### Viability, dormancy and seed germination

The initial viability of seeds tested ranged from as low as 12 to 100% (Appendix 2), with a median viability of 99%. No significant difference in the viability of seeds from different growth forms was initially detected ( $F_{7,50} = 0.5$ ,  $P > 0.1$ ). Most species (44) began to germinate in the first week of initial experiments and only a few species had germination delayed more than 3 weeks. Low germination percentages (<50% of viable seeds) were, however, detected in 28 species across a wide range of plant groups and growth forms (Appendices 2, 3). Eleven of these species showed little or no response to a germination cue (Appendix 3). The rest of these species showed enhanced germination when one or more of the treatments were applied (Appendix 3). Nine species did

not germinate in any of the treatments after 2 weeks and indicate some level of innate dormancy as seeds were viable. All dormant species were retained on germination pads under diurnal temperature and light conditions for several months and at the end of this period three epacrid species (*Leucopogon muticus*, *Lissanthe strigosa* and *Melichrus urceolatus*) failed to germinate.

#### Effects of storage

The effect of storing seeds at ambient room temperature and humidity for approximately one year on germinability was assessed for 21 species (Appendix 2). Three species showed a decrease in germination while one grass increased germination after storage. After a further period of storage (24–54 months) at ambient room temperature and humidity, seeds of 25 species showed a marked decrease in viability while 20 showed no change (Appendix 2). In general, viability decreased more prominently and across a wider range of herbaceous species than woody species (Appendix 2, Table 1). Conversely, germinability of herbaceous species often increased with storage but seeds of woody species did not, in general, increase in germinability (Table 1).

#### Effects of light

The effects of light treatments on germination was prominent on 29 of the 65 species tested (Table 2, Appendix 3). Twenty one species showed significant enhancement of initial germination in the presence of alternating light treatment relative to total

darkness; conversely eight species showed some suppression of germination in the presence of a diurnal light cycle (Table 2, Appendix 3). These effects are mostly consistent in seed stored for 1 year and where interactive effects were detected, storage appeared to enhance the inhibition of germination by darkness in three species of Asteraceae (Appendix 3).

#### Effects of smoke

Of the 64 tested one species, *Ajuga australis* (Lamiaceae), showed a strong enhancement of germination when exposed to smoke water in comparison with other treatments (Appendix 3). One other species, *Daviesia genistifolia*, also had a significant smoke effect after 5 weeks but this was a small enhancement relative to heat effects (Appendix 3). *Hibbertia obtusifolia* (Dilleniaceae) also had enhanced germination in one replicate in the presence of smoke. Most species tested showed no enhancement or suppression of germination in the presence of smoke either in darkness or in the presence of alternating light and dark. Ten species across a broad range of plant groups had significant reductions in germination after smoke water was applied (Table 2). In these instances, germination was suppressed but after prolonged observations most species attained similar germination percentages to those seed not treated with smoke water. Seed viability of ungerminated seed was also checked and found to be similar to those seeds not exposed to smoke water.

**Table 1. Contingency table of number of species in germination (increase, no change, decrease) and viability response (decrease, no change) classes versus woodiness after dry storage**

Expected values are given in parentheses based on the null hypothesis of independence. Germination response:  $\chi^2 = 18.67$ ,  $P < 0.01$ ; viability response:  $\chi^2 = 5.51$ ,  $P < 0.05$

	Germination response class			Viability response class	
	Increase	No change	Decrease	Decrease	No change
Woody	2 (7.8)	23 (15.6)	4 (5.6)	10 (13.9)	15 (11.1)
Herbaceous	12 (6.2)	5 (12.4)	6 (4.4)	15 (11.1)	5 (8.9)

**Table 2. Summary effects of treatment on numbers of species in growth-form groups**

Prom., significantly promoted germination; None, no significant effect; Inhib., significantly inhibited germination. Note that some treatments of cold and heat were not performed on all species in groups

	Light			Smoke			Cold			Heat		
	Prom.	None	Inhib.	Prom.	None	Inhib.	Prom.	None	Inhib.	Prom.	None	Inhib.
Trees	2	5	1	0	7	1	0	7	0	1	6	1
Shrubs	6	4	2	0	11	1	1	4	3	2	6	0
Subshrubs and climbers	3	7	0	1	7	2	0	4	4	4	1	3
Forbs	6	7	1	1	10	3	2	9	3	1	7	6
Forbs with woody base	2	4	1	0	7	0	0	4	1	2	1	2
Grasses and graminoids	2	9	3	0	10	3	3	6	4	1	4	8
Total	21	36	8	2	52	10	6	34	15	11	25	20

### Effects of temperature

The effects of dry heat enhanced germination in 11 species, 10 of which were in the family Fabaceae (Appendix 3). In several other plant groups heat appeared to enhance germination although low numbers of replicates precluded the detection of significant effects (Appendix 3). Twenty species showed reduced germination after application of dry heat (Table 2). Unlike light and smoke treatments, the effects of heat were often absolute over the period of the germination trials. Those species with dormant seed broken by a heat treatment remained dormant in the absence of heat over the 8 weeks of the germination trial. Similarly, several grass and forb species where germination was suppressed by heat remained suppressed throughout the experiments. In part, this was the result of seed becoming non-viable but some seeds of these species appeared to have induced dormancy. Chilling only significantly enhanced germination of six species, while chilling suppressed germination of 15 species across a range of growth forms (Table 2).

### Comparisons among treatments and plant traits

Germination comparisons of growth forms should be interpreted cautiously because the species used were not selected on the basis of phylogenetic independence (see Silvertown *et al.* 1997). Nevertheless, comparisons between woody and herbaceous groups have a wide range of phylogeny represented.

The overall germination response of species (inhibition, no effect, and stimulation) was independent across the four treatments and was consistent among both woody and herbaceous species (Tables 3, 4). The extreme heat response was the most varied, followed by cold, light and then smoke (Tables 3, 4).

The germination characteristics of species with different growth forms showed lack of independence for effects of light, smoke and cold (Table 5). In other words, the effects of these treatments did not vary significantly across growth forms. The only trend apparent was that woody species with canopy-held seed often showed enhanced germination in the presence of alternating light treatment relative to total darkness. Heat effects were, however, significantly different among growth forms (Table 5). Woody species tended to have enhanced or

neutral effects of heat whereas herbaceous species tended to have germination inhibited by heat pretreatment.

The dormancy characteristics of species showed some independence with growth form (Table 6, Fig. 1). The subshrubs show a marked characteristic of having dormant seeds, with only a small number of species that readily germinate despite being viable (Fig. 1). Both the woody based forbs and shrubs >1m tall had some species that showed dormancy, while the trees, forbs and grasses had few species with innate dormancy (Fig. 1). Over all species, there was a positive correlation between increasing seed mass and dormant fraction ( $r=0.14$ ,  $P < 0.05$ ). In part this relates to the fact that diaspores from woody species were significantly heavier (5.37 mg) than those from herbaceous species (1.99 mg) ( $F_{1,60} = 5.1$ ,  $P < 0.05$ ).

### Discussion

Our research into the germination cues of a wide range of grassy woodland species revealed that most species produce highly viable seeds and have a large non-dormant fraction that is available for germination. The germination cues for species that showed innate dormancy were, in order of importance, light, heat and cold. We have also demonstrated that what may be a cue for one species can suppress germination in another. The response to cues and inhibitors is not uniform across plant growth forms and suggest functional groupings independent of phylogeny. However, for this issue to be advanced the selection of species for contrasts needs to be made on the basis of independent phylogeny. In the following discussion we propose explanations for these patterns and highlight critical issues yet to be resolved.

**Table 3. Contingency table of number of species in germination response classes versus treatments**

Expected values are given in parentheses based on the null hypothesis of independence.  $\chi^2 = 33.9$ ,  $n = 6$ ,  $P < 0.001$

Treatment	Germination response class		
	Stimulated	No effect	Inhibited
Light/dark	21 (11.02)	36 (39.94)	8 (14.05)
Smoke	2 (10.68)	52 (38.71)	10 (13.61)
Cold	6 (8.98)	34 (32.56)	15 (11.45)
Heat	11 (9.32)	25 (33.79)	20 (11.89)

**Table 4. Contingency table of number of herbaceous and woody species in response classes versus treatments**

Expected values are given in parentheses based on the null hypothesis of independence. Herbaceous plants:  $\chi^2 = 22.4$ ,  $n = 6$ ,  $P < 0.01$ ; woody plants:  $\chi^2 = 17.8$ ,  $n = 6$ ,  $P < 0.01$

Treatment	Response class of herbaceous species			Response class of woody species		
	Stimulated	No effect	Inhibited	Stimulated	No effect	Inhibited
Light/dark	10 (5.26)	20 (20.53)	5 (9.21)	11 (5.67)	16 (19.53)	3 (4.81)
Smoke	1 (5.11)	27 (19.94)	6 (8.95)	1 (5.66)	25 (19.53)	4 (4.81)
Cold	5 (4.81)	19 (18.77)	8 (8.42)	1 (4.15)	15 (14.32)	6 (3.53)
Heat	4 (4.81)	12 (18.77)	16 (8.42)	7 (4.52)	13 (15.63)	4 (3.85)

**Table 5.** Summary of contingency table analyses for growth form (trees, shrubs, subshrubs, forbs, woody rootstock forbs, grasses and graminoids) and woodiness (woody and non-woody) versus germination response (stimulated, no effect, inhibited) across each treatment  
Values are  $\chi^2$ ; \*,  $P < 0.05$ ; n.s., not significant

	Light	Smoke	Cold	Heat
Growth form	7.7n.s.	6.8n.s.	10.9n.s.	20.4*
Woodiness	0.0n.s.	5.4n.s.	1.6n.s.	7.0*

**Table 6.** Summary of contingency table analyses for growth forms (trees, shrubs, subshrubs, forbs, woody rootstock forbs, grasses and graminoids) and woodiness (woody, non-woody) versus dormancy classes (strong dormancy, weak dormancy)

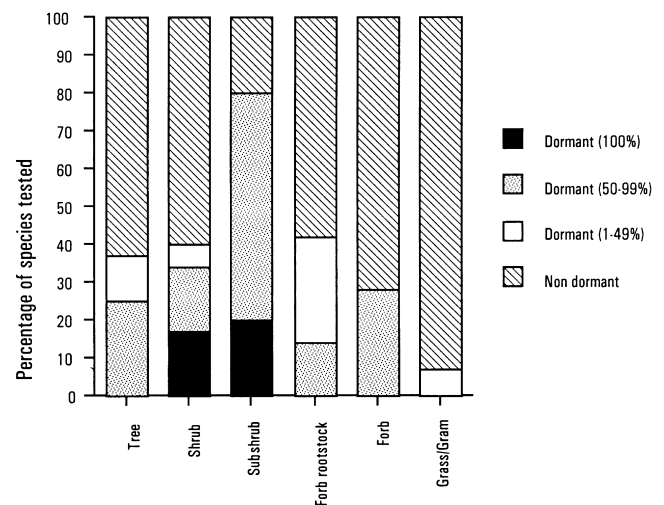
Expected values are given in parentheses based on the null hypothesis of independence. Growth forms:  $\chi^2 = 17.5$ ,  $n = 5$ ,  $P < 0.01$ ; woodiness:  $\chi^2 = 8.57$ ,  $n = 1$ ,  $P < 0.01$

	Strong dormancy	Weak dormancy
Growth forms		
Trees	2 (3.2)	6 (4.8)
Shrubs	5 (4.8)	7 (7.2)
Subshrubs	9 (4.0)	1 (6.0)
Forbs (woody rootstock)	7 (5.6)	7 (8.4)
Forbs	1 (2.8)	6 (4.2)
Grasses and graminoids	2 (5.6)	12 (8.4)
Woodiness		
Woody	23 (17.6)	21 (8.4)
Herbaceous	3 (26.4)	18 (12.6)

### Darkness and diurnal light

The range of germination responses to light treatments was similar across all growth forms. Relatively few species had a dark requirement for germination (eight spp.), but a larger proportion showed either no significant effect (36 spp.) or inhibition of germination by darkness (21 spp.). Lack of a dark germination effect for forbs and grasses has been a common syndrome in Australian temperate grasslands (Lodge and Whalley 1981; Morgan 1998; McIntyre 1990). In contrast, dark germination has been reported in the shrub component of species in Mediterranean-type climates (Bell 1994; Bell *et al.* 1995). Our results show no trend in relation to enhanced germination of shrubs under dark conditions. Similarly the suggestion that myrmecochorous seeds might be able to germinate in the dark is not supported by our results.

Light-stimulated germination was common in 10 of the 25 herbaceous species. This is consistent with the overall trends found in previous studies of temperate grassland forbs (McIntyre 1990; Morgan and Lunt 1994; Morgan 1998; Bell 1999). Buried seeds of forbs appear to need ground disturbance for light exposure, similarly surface seed appear to require light gaps to stimulate germination (Thompson and Grime 1983; Trémont and McIntyre 1994; Morgan 1998).



**Fig. 1.** The relative proportion of species with entrenched dormancy (100% of viable seeds tested not germinable), strong dormancy (50–99% of viable seeds tested not germinable), partial dormancy (1–45% of viable seeds not germinable), and no dormancy (all viable seeds germinable) across the main growth forms tested.

A strong interaction of light and storage time was detected for three species of Asteraceae, suggesting that after-ripening promotes dark-dormancy. Light-stimulated germination was equally prominent among the woody species tested. In particular, pronounced dark-dormancy was common in serotinous shrub species as is often reported in shrubby communities (e.g. Bell 1994; Williams and Clarke 1997). These results suggest that components of all growth forms in temperate grassy systems respond to light gaps created by disturbance and have at least some soil-surface germination.

Despite the indication that light is an important factor stimulating germination of a wide range of growth forms, 36 of the 65 species tested showed no significant inhibitory effect of continuous darkness. Both Morgan (1998) and our study showed that more than half the number of forbs tested (11 in both studies) could germinate equally well in the dark as in diurnal light conditions. In both studies, however, temperature fluctuations may have allowed germination in the dark that might not otherwise occur when seed is buried (Thompson and Grime 1983).

The complexity of the effects of light should not be underestimated in relation to ecological generalisations. Thompson and Grime (1983) suggest that dormancy might be induced when temperature fluctuations are dampened, as is the case when seeds are buried deeply. The relationship between dark-dormancy and temperature also requires investigation as far-red reversion of germination has been shown to be temperature mediated (Pons 1991). Both induction and reversibility of dormancy by light and light quality requires better understanding in temperate grassy systems.

Intra-specific variation in germination response and cues also place limits on our ability to generalise about light

effects (McIntyre 1990; Willis and Groves 1991; Gilfedder and Kirkpatrick 1994; Morgan 1998). A summary of the range of results from other studies and ours highlight these inconsistencies (see Table 7) and may be a result of a range of, methods, seed ages, genotypes, and environmental conditions at the time of harvesting.

### Smoke

Surprisingly, the effects of smoke were less varied than other treatments across all growth forms. Several studies have shown that cool smoke produced by burning native vegetation can stimulate germination of seeds in the laboratory (Dixon *et al.* 1995; Keith 1997; Roche *et al.* 1997; Morris 1999; Read and Bellairs 1999). Smoking of seed-banks (Read *et al.* 1997; Marsden-Smedley *et al.* 1997) has also been able to germinate species that are otherwise difficult to germinate. The effects of smoke water on germination of the species tested in the present study were to either have no effect or to significantly inhibit germination of six species of forbs and grasses. Only two species *Ajuga australis* (Lamiaceae) and *Daviesia genistifolia* (Fabaceae) showed a significant enhancement in germination with the application of cool smoke. Several genera that have been reported to respond to smoke treatment did not show any pronounced effects; these include the monocot genera *Austrostipa*, *Arthropodium*, *Dichanthium*, *Lomandra*, and *Themeda* and the dicot genera *Clematis*, *Hakea*, *Hibbertia*, *Hovea*, *Leucopogon*, *Leptospermum*, *Petrophile*, *Pimelea*, *Stylidium* and *Velleia*. Conversely, the reported inhibitory effect of smoke on *Bursaria spinosa* (Roche *et al.* 1997) was not shown in our experiments. Contrasting dormancy and germination in relation to smoke have also been reported for *Burchardia umbellata* (Bell *et al.* 1987; Dixon *et al.* 1995 cf. Morgan 1998) and *Themeda triandra* (Baxter *et al.* 1994 cf. Marsden-Smedley *et al.* 1997). The lack of any strong smoke germination cue led us to question the method and concentrations of smoke being used in our study. However, tests on other shrub species, with strong innate dormancy, show strong smoke-mediated germination using the same smoke methods (Clarke and Fulloon, unpubl. data).

Cool smoke inhibited the germination of several forb species but did not affect viability, suggesting smoke-induced dormancy. Smoke inhibition effects have also been reported in the South African forb, *Helichrysum aureonitens*, (Afolyan *et al.* 1997). This inhibition was unexpected as Read *et al.* (1997) and Marsden-Smedley (1997) have shown that emergence of herbaceous species from eucalypt forest and grassy woodland seed banks were partially enhanced by smoke. A range of smoke effects on emergence from seed banks on the New England tablelands have recently been reported by Grant (unpubl. data), most species were indifferent to smoke, four were promoted and six were inhibited. Read and Bellairs (1999) have recently shown pronounced smoke enhanced germination in four species of temperate grasses, some of which were used in our experiment, and

inhibition in one species. Most species, however, showed little or no effect, despite the title of their paper. Their results are consistent with ours in that *Austrostipa scabra*, *Dichanthium sericeum* and *Themeda australis* showed a trend of increased germination with added smoke that may have been resolved with greater seed numbers.

The suggestion that smoke inhibits germination and induces dormancy in forb species in grassy communities is important because burning grasslands and grassy woodlands has been proposed as a management option to open up grass tussocks to allow recruitment gaps for forbs (Trémont and McIntyre 1994). Critical to this issue is how long this dormancy remains in place and if it is beneficial in allowing delayed germination in the post-fire environment.

### Temperature extremes

The effects of temperature extremes on germination were more varied than either light or smoke effects with extreme heat producing the most varied response in terms of inhibition and stimulation. The effects of dry heat in breaking dormancy are well known for those species with hard seed coats (e.g. Auld and O'Connell 1991; Bell *et al.* 1993; Bell 1998; Bell 1999). All but one of the legume species tested in our study showed that dormancy was broken by exposure to dry heat. Nevertheless, some germination occurred in nearly all legumes without heat pretreatment that is similar to the results of Morgan (1998) and Bell (1998). The woody-fruited members of the Epacridaceae did not show any response to either heat or smoke or a combination of treatments (cf. Keith 1997). The heat effects on seeds of the serotinous species, with the exception of *Petrophile canescens*, were generally not affected by a short duration of heat at 80°C. In particular, the eucalypt species showed a trend of increased germination after heat pretreatment. Several studies of heat on serotinous species at temperature of 100°C have shown that their seeds are vulnerable to heat shock (Judd 1993; Bell *et al.* 1995). Such temperatures, however, would be moderated by the woody fruits (Judd 1993; Bradstock *et al.* 1994; Whelan and Brown 1998).

The effects of temperature extremes on grassy woodland herbaceous species, without a hard seed coat, were varied. About half of the species, across a range of families and growth forms, showed little adverse effects on exposure to a temperature that could be expected 1–2 cm below the soil surface during an intense fire (Bradstock and Auld 1995). The after-ripening period of grass and some forb species has been shown to decrease with dry heat pretreatment (Lodge and Whalley 1981; Willis and Groves 1991; Bell *et al.* 1993; Maze *et al.* 1993; Bell 1999). These effects were not prominent in the herbaceous species we tested and generally they were the converse i.e. many showed dry heat induced dormancy. Similarly to the smoke-induced dormancy it is not clear if these effects are reversible and further experiments are required to test this. If dormancy is reversible then this

may point to a mechanism where herbaceous species avoid germination at times of high summer temperatures.

Chilling enhanced the germination of six species and inhibited germination of 15 species. Promotion effects of cold on two species of Asteraceae used in our experiments were inconsistent with the results of Willis and Groves (1991) (Table 7). Again, this may reflect ecotypic variation or other sources of variation that require standardisation before comparison can be drawn.

#### Seed bank implications

Differences in viability, germinability and germination cues in the species tested provide a preliminary indication of the potential for native seed banks to accumulate in the grassy woodlands and forests of the New England Tablelands. Viability of seeds generally decreased for herbaceous species while germinability increased through time. This trend is supported by the results of Morgan (1998) who found consistently higher germination for 10–12-month stored seed compared with initial 1–3-month stored seed for the same species as in our study. Short-term storage of seed has also been shown to increase germination in eight tableland forbs tested by McIntyre (1990). This suggests that the dormant fraction of herbaceous species would rapidly decrease for those species not inhibited by darkness. The apparent lack of innate dormancy across most herbaceous species tested suggests that seed banks are unlikely to accumulate when soil moisture conditions are able to imbibe seeds and when temperatures reach a diurnal summer range of 15–25°C or when soil temperatures are raised by fires. Our results are similar to those of Morgan (1998) who found high and rapid germination in 24 of 28 species of forbs under conditions that surface-dispersed seeds would experience. This is also supported by seed burial studies of forbs (Lunt 1995; Morgan 1995). Our results suggest that not only forbs but perennial native grasses also have, at best, short-term seed banks.

In contrast to many herbaceous species, woody plants show relatively stable levels of viability and germinability through time. High innate dormancy is prominent in the shrub component dominated by the Fabaceae and Epacridaceae. Soil seed bank accumulations for serotinous species are unlikely although some short-term persistence may be induced by deep burial and low soil water potentials. Nevertheless, the potential for long-term canopy-stored seed banks is shown in the high viability and germinability of species after several years of dry storage.

The contrasting dormancy patterns between herbaceous species and woody species may be related, in terms of selection, to the risk involved in recruitment (Rees 1997). Many woody species appear to have the ability to remain dormant while many of the forbs and grasses have less dormancy. This suggests some selection for 'risk-spreading' in woody species relating to the need to establish and grow in the absence of herbaceous competition or herbivores. Such conditions

**Table 7. Comparison of significant germination effects of light and cold on grassland herbaceous species for the same or related taxa from different sources**

+, germination enhancement; o, no effect; –, inhibition; ?, no germination

Species	Factor	Source	Germination effect
<i>Aristida ramosa</i>	Light	This study	o
		Lodge and Whalley 1981	o
<i>Bothriochloa macra</i>	Light	This study	o
		Lodge and Whalley 1981	o
<i>Bulbine bulbosa</i>	Light	This study	+
		Morgan 1998	+
	Cold	Willis and Groves 1991	o
		Willis and Groves 1991	?
<i>Dichanthium sericeum</i>	Light	This study	+
		Lodge and Whalley 1981	+
<i>Leucochrysum albicans</i>	Light	This study	+
		Morgan 1998	+
	Cold	Willis and Groves 1991	o
		This study	–
<i>Podolepis jaceoides</i>	Light	Willis and Groves 1991	+
		This study	+
<i>Stylidium graminifolium</i>	Light	Morgan 1998	+
		This study	+
		Willis and Groves 1991	o
<i>Vittadinia muelleri</i>	Light	Hitchmough <i>et al.</i> 1989	+
		This study	+
	Cold	Willis and Groves 1991	+
		This study	o
		Willis and Groves 1991	+

probably occur at infrequent intervals after intense fires or ground disturbance. Perennial herbaceous species may, on the other hand, be able to exploit smaller but more frequent events that allow recruitment. These generalisations are tentative and require more rigorous testing with more species from different phylogenies.

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**Appendix 1. Attributes and germination treatments of common grassy woodland species of the northern tablelands of New South Wales**

Growth form: C, climber or scrambler; F, forb; Fw, forb with woody rootstock; G, graminoid; Gr, grass; S, shrub; Ss, subshrub; T, tree. Life form: Ch, chamaephyte; Cr, cryptophyte; He, hemicryptophyte; Ge, geophyte; P, phanerophyte; Th, therophyte. Fire response: S, seeder—killed by fire; R, resprouter. Treatments: L×S, light and smoke; L×S×Y, light and smoke and storage time 1 year; H, heat; S, smoke; C, chilling. \*, multi-ovule drupaceous fruits. n.d., not determined

Taxon	Growth form/life form	Fire response	Diaspore weight (mg)	Germination treatment
<b>Monocotyledonae</b>				
Anthericaceae				
<i>Arthropodium milleflorum</i>	F/Ge	R	1.248	L×S, H, C
Asphodelaceae				
<i>Bulbine bulbosa</i>	F/Ge	R	4.442	L×S, H, C
Cyperaceae				
<i>Carex inversa</i>	G/Cr	R	0.697	L×S×Y, H, C
Dasypogonaceae				
<i>Lomandra longifolia</i>	G/Cr	R	12.275	L×S×Y, H, C
Poaceae				
<i>Austrostipa scabra</i> ssp. <i>scabra</i>	Gr/He	R	n.d.	L×S×Y, H, C
<i>Aristida ramosa</i>	Gr/He [C4]	R	2.330	L×S, H, C
<i>Bothriochloa macra</i>	Gr/He [C4]	R	1.370	L×S, H, C
<i>Notodanthonia racemosa</i>	Gr/He	R	0.364	L×S, H, C
<i>Notodanthonia racemosa</i> (naked)	Gr/He	R	0.820	L×S
<i>Dichanthium sericeum</i>	Gr/He [C4]	R	0.590	L×S, H, C
<i>D. setosum</i>	Gr/He [C4]	R	1.060	L×S, H, C
<i>Microlaena stipoides</i>	Gr/He	R	0.345	L×S, H, C
<i>Poa sieberiana</i>	Gr/He	R	0.330	L×S, H, C
<i>Sorghum leiocladum</i>	Gr/He [C4]	R	3.00	L×S, H, C
<i>Themeda triandra</i>	Gr/He [C4]	R	n.d.	L×S×Y, H, C
Xanthorrhoeaceae				
<i>Xanthorrhoea johnsonii</i>	Gr/Ph	R	18.050	L×S×Y
<b>Dicotyledonae</b>				
Asteraceae				
<i>Ammobium alatum</i>	F/Th	S	0.497	L×S×Y, H, C
<i>Bracteantha bracteata</i>	F/Th	S	0.395	L×S×Y, H, C
<i>Cassinia quinquefaria</i>	S/Ph	R	0.068	L×S×Y, H, C
<i>Leucochrysum albicans</i> ssp. <i>albicans</i>	Fw/He	S	0.312	L×S, H, C
<i>Microseris lanceolata</i>	F/Ge	R	3.532	L×S, H, C
<i>Olearia</i> sp. aff. <i>elliptica</i>	S/Ph	R	0.453	L×S
<i>Podolepis jaceoides</i>	F/He	S	1.060	L×S, H, C
<i>Vittadinia muelleri</i>	Fw/He	R	0.565	L×S×Y, H, C
Boraginaceae				
<i>Cynoglossum australe</i>	F/He	R	3.117	L×S, H, C
Campanulaceae				
<i>Wahlenbergia planifolia</i>	Fw/H	R	0.012	L×S
Casuarinaceae				
<i>Allocasuarina littoralis</i>	T/Ph	S	2.590	L×S, H, C,
Dilleniaceae				
<i>Hibbertia obtusifolia</i>	Ss/Ch	R	—	L×S
Epacridaceae				
<i>Leucopogon muticus</i>	S/Ch	R	1.495*	L×S
<i>Lissanthe strigosa</i> ssp. <i>subulata</i>	S/Ch	R	8.965*	L×S
<i>Melichrus urceolatus</i>	Ss/Ch	R	4.520	L×S
Euphorbiaceae				
<i>Phyllanthus virgatus</i>	Fw/He	R	—	L×S, C
Goodeniaceae				
<i>Velleia paradoxa</i>	F/He	R	3.744	L×S, H, C
Fabaceae				
<i>Acacia dealbata</i>	T/Ph	R	13.830	L×S×Y, H, C
<i>Daviesia genistifolia</i>	Ss/Ph	R	5.837	L×S, H, C
<i>Desmodium varians</i>	Fw/He	R	2.080	L×S×Y, H, C

## Appendix 1. (continued)

Taxon	Growth form/life form	Fire response	Diaspore weight (mg)	Germination treatment
<i>Glycine tomentella</i>	Fw/He	R	3.770	L × S, H, C
<i>Hovea linearis</i>	Ss/Ch	R	6.445	L × S, H, C
<i>Hardenbergia violacea</i>	C/Ch	R	39.640	L × S × Y, H, C
<i>Indigofera australis</i>	S/Ch	R	6.136	L × S × Y, H, C
<i>Jacksonia scoparia</i>	S/Ch	R	2.580	L × S, H, C
<i>Lezpedeza juncea</i> ssp. <i>juncea</i>	Fw/He	R	2.345	L × S × Y, H, C
<i>Lotus australis</i>	F/He	R	1.995	L × S, H, C
<i>Pultanea microphylla</i>	Ss/Ch	R	1.960	L × S, H
<i>Cullen tenax</i>	Fw/He	R	5.045	L × S, H
Lamiaceae				
<i>Ajuga australis</i>	F/He	R	0.250	L × S, H, C
<i>Mentha saturooides</i>	F/He	R	0.185	L × S × Y, H, C
Myrtaceae				
<i>Eucalyptus blakelyi</i>	T/Ph	R	0.123	L × S × Y, H, C
<i>E. dalrympleana</i> ssp. <i>heptantha</i>	T/Ph	R	0.540	L × S, H, C
<i>E. melliodora</i>	T/Ph	R	0.278	L × S × Y, H, C
<i>E. pauciflora</i>	T/Ph	R	1.364	L × S × Y, H, C
<i>E. viminalis</i>	T/Ph	R	1.062	L × S × Y, H, C
<i>E. youmannii</i>	T/Ph	R	2.230	L × S × Y, H, C
<i>Leptospermum polygalifolium</i> ssp. <i>tansmontanum</i>	S/Ph	R	0.156	L × S × Y, H, C
Pittosporaceae				
<i>Bursaria spinosa</i> ssp. <i>spinosa</i>	S/Ch	R	1.024	L × S, H, C
Proteaceae				
<i>Hakea eriantha</i>	S/Ch	R	18.254	L × S, H, C
<i>Hakea microcarpa</i>	S/Ch	R	5.207	L × S, H, C
<i>Lomatia fraseri</i>	S/Ch	R	n.d	L × S
<i>Petrophile canescens</i>	Ss/Ch	R	2.823	L × S × Y, H, C
Polygonaceae				
<i>Rumex brownii</i>	F/He	R	1.113	L × S, H, C
Ranunculaceae				
<i>Clematis glycinoides</i>	C/Ch	R	2.786	L × S, H, C
Rosaceae				
<i>Acaena ovina</i>	F/He	R	4.900	L × S, H, C
Sapindaceae				
<i>Dodonaea viscosa</i>	S/Ph	R	4.752	L × S, H, C
Stylidiaceae				
<i>Stylidium graminifolium</i>	F/Cr	R	0.200	L × S, H, C
Thymeliaceae				
<i>Pimelea linifolia</i> ssp. <i>linifolia</i>	Ss/Ch	R	0.002	L × S, H, C

**Appendix 2. The mean percentage germination and viability of common species in grassy woodlands on the New England Tableland after dry storage**

G1, germination in diurnal light 3–6 months after seed collected; G2, germination in diurnal light 15–18 months after seed collected; G3, germination in diurnal light 29–54 months after seed collected; V1, viability 3–6 months after seed collected; V3, viability 29–54 months after seed collected. G3–V3, age of seed for final viability and germination tests. n.s., not significant; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; #, seeds scarified

Taxon	Germinability (% viable seed)					Non-viable (% total seed)		
	G3/V3 (months)	G1	G2	G3	Significance	V1	V3	Significance
<b>Monocotyledonae</b>								
Anthericaceae								
<i>Arthropodium milleflorum</i>	42	1.4	—	44.0	**	—	11.3	—
Asphodelaceae								
<i>Bulbine bulbosa</i>	40	14.2	—	31.3	**	4.8	3.8	n.s.
Cyperaceae								
<i>Carex inversa</i>	—	49.7	58.3	—	—	0.0	—	—
Dasygongonaceae								
<i>Lomandra longifolia</i>	55	0.0	0.0	50.8	**	0.4	33.8	**
Poaceae								
<i>Austrostipa scabra</i> ssp. <i>scabra</i>	55	28.8	26.5	83.7	**	—	23.8	—
<i>Aristida ramosa</i>	54	93.7	—	100.0	*	0.0	36.3	**
<i>Bothriochloa macra</i>	29	79.7	—	92.5	**	13.0	51.3	**
<i>Notodanthonia racemosa</i>	55	70.0	95.0	47.6	**	1.4	30.0	**
<i>Notodanthonia racemosa</i> (naked)	—	92.5	—	—	—	—	—	—
<i>N. richardsonii</i>	55	100.0	—	86.2	*	0.0	50.0	**
<i>Dichanthium sericeum</i>	24	67.2	—	93.7	*	2.0	27.5	**
<i>D. setosum</i>	—	97.2	—	—	—	—	—	—
<i>Microlaena stipoides</i>	—	100.0	—	—	—	—	—	—
<i>Poa sieberiana</i>	30	94.2	—	84.3	*	—	43.8	—
<i>Sorghum leiocladum</i>	—	26.5	—	—	—	8.3	—	—
<i>Themeda triandra</i>	—	36.0	47.0	—	—	2.7	—	—
Xanthorrhoeaceae								
<i>Xanthorrhoea johnsonii</i>	47	20.0	—	24.3	n.s.	0.0	11.3	**
<b>Dicotyledonae</b>								
Asteraceae								
<i>Ammobium alatum</i>	—	93.8	96.2	—	—	1.0	—	—
<i>Bracteantha bracteata</i>	54	53.8	23.8	0.0	**	—	96.3	—
<i>Cassinia quinquefaria</i>	43	63.2	77.5	89.8	**	0.0	47.5	**
<i>Leucochrysum albicans</i> ssp. <i>albicans</i>	54	77.2	—	100.0	**	5.4	86.3	**
<i>Microseris lanceolata</i>	43	47.5	—	89.0	*	0.0	10.0	**
<i>Olearia</i> sp. aff. <i>elliptica</i>	53	41.0	—	0.0	*	—	93.8	—
<i>Podolepis jaceoides</i>	30	38.7	—	25.0	n.s.	0.8	98.8	**
<i>Vittadinia muelleri</i>	53	55.0	30.0	50.0	n.s.	0.0	82.5	**
Boraginaceae								
<i>Cynoglossum australe</i>	42	97.4	—	98.7	n.s.	1.0	3.8	*
Campanulaceae								
<i>Wahlenbergia planifolia</i>	53	60.5	—	12.8	**	0.0	2.5	*
Casuarinaceae								
<i>Allocasuarina littoralis</i>	49	82.0	—	91.0	n.s.	15.2	13.8	n.s.
Dilleniaceae								
<i>Hibbertia obtusifolia</i>	—	0.0	—	—	—	56.7	—	—
Epacridaceae								
<i>Leucopogon muticus</i>	54	0.0	—	0.0	n.s.	—	93.8	—
<i>Lissanthe strigosa</i> ssp. <i>subulata</i>	54	0.0	—	0.0	n.s.	—	60.6	—
<i>Melichrus urceolatus</i>	—	0.0	—	—	—	—	—	—
Euphorbiaceae								
<i>Phyllanthus virgatus</i>	—	12.5	—	—	—	88.2	—	—
Goodeniaceae								
<i>Velleia paradoxa</i>	51	39.3	—	53.8	n.s.	16.3	46.3	**
Fabaceae								
<i>Acacia dealbata</i>	54	4.1	3.8	#93.8	n.s.	0.0	17.5	**
<i>Daviesia genistifolia</i>	—	0.0	—	—	—	—	—	—
<i>Desmodium varians</i>	53	37.9	32.0	#98.8	n.s.	0.5	1.3	n.s.
<i>Glycine tomentella</i>	> 60	15.5	—	#97.5	n.s.	1.9	1.3	n.s.
<i>Hovea linearis</i>	—	2.5 a	—	—	—	—	—	—

## Appendix 2. (continued)

Taxon	Germinability (% viable seed)					Non-viable (% total seed)		
	G3–V3 (months)	G1	G2	G3	Significance	V1	V3	Significance
<i>Hardenbergia violacea</i>	42	0.0	—	#100.0	n.s.	0.0	10.0	*
<i>Indigofera australis</i>	52	17.5	7.5	#74.9	n.s.	0.0	16.3	*
<i>Jacksonia scoparia</i>	30	76.0	—	#94.4	n.s.	40.3	35.0	n.s.
<i>Lezpedeza juncea</i> ssp. <i>juncea</i>	51	2.5	1.3	#33.8	n.s.	0.0	0.0	n.s.
<i>Lotus australis</i>	53	2.5	—	#49.9	**	1.9	11.3	*
<i>Cullen tenax</i>	52	5.0	—	#97.2	n.s.	0.0	7.5	**
<i>Pultanaea microphylla</i>	—	13.3	—	—	—	—	—	—
Lamiaceae								
<i>Ajuga australis</i>	25	18.8	—	26.3	n.s.	35.0	31.3	n.s.
<i>Mentha saturoides</i>	50	51.2	64.7	75.0	**	22.0	18.8	n.s.
Myrtaceae								
<i>Eucalyptus blakelyi</i>	50	99.3	98.7	100.0	n.s.	0.0	0.0	n.s.
<i>E. dalrympleana</i> ssp. <i>heptantha</i>	47	95.5	—	100.0	n.s.	0.0	0.0	n.s.
<i>E. melliodora</i>	50	86.8	92.5	91.0	n.s.	0.0	3.8	n.s.
<i>E. pauciflora</i>	50	3.9	3.8	25.3	*	47.6	52.5	n.s.
<i>E. viminalis</i>	52	96.1	93.7	100.0	n.s.	0.0	0.0	n.s.
<i>E. youmannii</i>	48	22.9	33.8	85.6	**	22.5	36.3	n.s.
<i>Leptospermum polygalifolium</i> ssp. <i>transmontanum</i>	49	100.0	100.0	0.0	**	52.0	100.0	**
Pittosporaceae								
<i>Bursaria spinosa</i> ssp. <i>spinosa</i>	48	57.7	—	12.8	**	55.0	70.0	*
Proteaceae								
<i>Hakea eriantha</i>	49	67.5	—	81.3	n.s.	0.0	0.0	n.s.
<i>Hakea microcarpa</i>	52	46.2	—	50.9	n.s.	0.0	8.8	*
<i>Lomatia fraseri</i>	—	88.7	—	—	—	—	—	—
<i>Petrophile canescens</i>	42	43.3	42.5	60.7	n.s.	0.0	41.3	**
Polygonaceae								
<i>Rumex brownii</i>	53	75.5	—	80.9	n.s.	11.1	11.3	n.s.
Ranunculaceae								
<i>Clematis glycinoides</i>	42	81.0	—	0.0	**	12.7	8.8	n.s.
Rosaceae								
<i>Acaena ovina</i>	51	18.8	—	59.0	**	12.7	58.8	**
Sapindaceae								
<i>Dodonaea viscosa</i>	44	2.5	—	4.0	n.s.	0.0	3.8	n.s.
Stylidiaceae								
<i>Stylidium graminifolium</i>	53	6.5	—	3.3	n.s.	28.0	16.3	n.s.
Thymeliaceae								
<i>Pimelea linifolia</i> ssp. <i>linifolia</i>	44	5.0	—	0.0	**	—	6.3	—

**Appendix 3. The mean percentage germination of viable seed for treatment effects of light, smoke, chilling and heat on seed germination of common species in grassy woodlands on the New England Tableland**

Means followed by different letters are significantly different (\*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ ; n.s. not significant) by Sheffe's test. Is, interaction light  $\times$  smoke; It, interaction light  $\times$  time, in all cases time enhanced the effect of light

Taxon	Significance	Diurnal	Dark	Smoke	Chilling	Heat
<b>Monocotyledonae</b>						
Anthericaceae						
<i>Arthropodium milleflorum</i>	**	1.4a	9.3b	3.0a	13.5b	0.0a
Asphodelaceae						
<i>Bulbine bulbosa</i>	n.s.	14.2a	5.5a	15.0a	5.5a	6.5a
Cyperaceae						
<i>Carex inversa</i>	***	49.7c	10.0b	43.4c	77.5d	0.0a
Dasyopogonaceae						
<i>Lomandra longifolia</i>	*	0.0a	3.7b	0.0a	0.0a	0.0a
Poaceae						
<i>Austrostipa scabra</i> ssp. <i>scabra</i>	**	28.8a	30.4a	30.6a	28.0a	0.0b
<i>Aristida ramosa</i>	***	93.7c	93.7c	72.5b	93.0c	22.5a
<i>Bothriochloa macra</i>	*	79.7a	79.0a	88.7a	96.9b	93.5b
<i>Notoanthonia racemosa</i>	*	70.0a	63.7a	59.4a	92.4b	100.0c
<i>Notodanthonia racemosa</i> (naked)	n.s.	92.5a	88.7a	92.5a	—	—
<i>N. richardsonii</i>	**	100.0b	100.0b	100.0b	75.0a	60.0a
<i>Dichanthium sericeum</i>	*	67.2a	29.7b	89.7a	90.0a	87.5a
<i>D. setosum</i>	*	97.2b	90.1b	97.5b	93.9b	70.0a
<i>Microlaena stipoides</i>	***	100.0b	100.0b	100.0b	100.0b	0.0a
<i>Poa sieberiana</i>	n.s.	94.2a	100.0a	98.5a	85.0b	87.5b
<i>Sorghum leiocladum</i>	*	26.5a	61.5b	54.5b	42.5b	65.0b
<i>Themeda triandra</i>	*	36.0a	34.1a	42.0a	64.0b	33.0a
Xanthorrhoeaceae						
<i>Xanthorrhoea johnsonii</i>	**	20.0a	53.7b	37.5a	—	—
<b>Dicotyledonae</b>						
Asteraceae						
<i>Ammobium alatum</i>	** It	93.8b	72.4a	94.7b	97.5b	87.5b
<i>Bracteantha bracteata</i>	** It	53.8c	37.1b	50.2c	17.5b	0.0a
<i>Cassinia quinquefaria</i>	*	63.2b	33.0a	67.2b	40.0a	61.0b
<i>Leucochrysum albicans</i> ssp. <i>albicans</i>	*	77.2c	43.7b	72.0c	72.0c	15.0a
<i>Microseris lanceolata</i>	**	47.5b	34.5b	41.2b	49.0b	0.0a
<i>Olearia</i> sp. aff. <i>elliptica</i>	*	41.0b	24.5a	52.0b	—	—
<i>Podolepis jaceoides</i>	** Is	38.7b	2.5a	3.8a	17.5b	5.0a
<i>Vittadinia muelleri</i>	*** It	55.0b	9.4a	42.5b	35.0b	33.5b
Boraginaceae						
<i>Cynoglossum australe</i>	*	97.4b	58.2a	92.5b	97.5b	100.0b
Campanulaceae						
<i>Wahlenbergia planifolia</i>	**	60.5b	58.7b	28.0a	—	—
Casuarinaceae						
<i>Allocasuarina littoralis</i>	*	82.0b	62.7a	88.9b	92.0b	96.0b
Dilleniaceae						
<i>Hibbertia obtusifolia</i>	n.s.	0.0	0.0	0.0	—	—
Epacridaceae						
<i>Leucopogon muticus</i>	n.s.	0.0	0.0	0.0	—	—
<i>Lissanthe strigosa</i> ssp. <i>subulata</i>	n.s.	0.0	0.0	0.0	—	—
<i>Melichrus urceolatus</i>	n.s.	0.0	0.0	0.0	—	—
Euphorbiaceae						
<i>Phyllanthus virgatus</i>	*	12.5b	68.7c	8.3b	0.0a	—
Goodeniaceae						
<i>Velleia paradoxa</i>	*	39.3b	5.0a	24.2b	30.5b	27.0b
Fabaceae						
<i>Acacia dealbata</i>	***	4.1a	2.6a	1.5a	0.0a	16.5b
<i>Daviesia genistifolia</i>	**	0.0a	1.3a	5.0a	0.0a	21.0b
<i>Desmodium varians</i>	*	37.9a	36.8a	21.6a	20.0a	62.0b
<i>Glycine tomentella</i>	**	15.5a	22.5a	17.5a	21.5a	67.2b
<i>Hovea linearis</i>	** I	2.5a	2.5a	8.7a	5.0a	23.5b
<i>Hardenbergia violacea</i>	**	0.0a	0.0a	0.0a	0.0a	61.2b
<i>Indigofera australis</i>	*	17.5a	6.9a	12.5a	0.0b	45.0c

## Appendix 3. (continued)

Taxon	Significance	Diurnal	Dark	Smoke	Chilling	Heat
<i>Jacksonia scoparia</i>	**	76.0b	76.7b	74.2b	36.5a	72.5b
<i>Lezpedeza juncea</i> ssp. <i>juncea</i>	*	2.5b	0.0a	1.7b	0.0a	5.0b
<i>Lotus australis</i>	**	2.5a	22.5b	5.0a	5.0a	30.3b
<i>Cullen tenax</i>	**	5.0a	6.0a	3.5a	—	27.5b
<i>Pultanaea microphylla</i>	**	13.3b	5.5a	7.0a	—	25.0c
Lamiaceae						
<i>Ajuga australis</i>	* I	18.8b	8.3b	59.2d	21.0c	0.0a
<i>Mentha saturooides</i>	***	51.2c	3.1a	32.4b	79.5d	0.0a
Myrtaceae						
<i>Eucalyptus blakelyi</i>	*** It	99.3c	46.1a	59.5a	100.0c	85.0b
<i>E. dalrympleana</i> ssp. <i>heptantha</i>	n.s.	95.5a	94.5a	96.5a	100.0a	100.0a
<i>E. melliodora</i>	n.s.It	86.8a	90.7a	77.7a	100.0a	72.5a
<i>E. pauciflora</i>	n.s.	3.9a	9.0a	7.1a	7.0a	8.0a
<i>E. viminalis</i>	n.s.	96.1a	95.5a	95.5a	100.0a	100.0a
<i>E. youmannii</i>	*	22.9a	55.1b	19.0a	17.5a	38.5a
<i>Leptospermum polygalifolium</i> ssp. <i>tansmontanum</i>	***	100.0b	15.4a	97.1b	100.0b	100.0b
Pittosporaceae						
<i>Bursaria spinosa</i> ssp. <i>spinosa</i>	*	57.7a	89.2b	75.2b	67.0b	27.5a
Proteaceae						
<i>Hakea eriantha</i>	*	67.5b	17.5a	31.2a	82.5b	68.5b
<i>Hakea microcarpa</i>	**	46.2b	5.0a	45.0b	80.0c	40.5b
<i>Lomatia fraseri</i>	n.s.	88.7a	80.0a	92.5a	—	—
<i>Petrophile canescens</i>	**	43.3b	5.8a	17.2a	40.0b	4.2a
Polygonaceae						
<i>Rumex brownii</i>	*	75.5b	82.7b	67.5b	88.5b	37.0a
Ranunculaceae						
<i>Clematis glycinoides</i>	**	81.0b	68.2b	73.7b	6.0a	0.0a
Rosaceae						
<i>Acaena ovina</i>	n.s.	18.8a	18.5a	31.5a	2.5a	25.0a
Sapindaceae						
<i>Dodonaea viscosa</i>	**	2.5a	5.0a	1.3a	0.0a	37.0b
Stylidiaceae						
<i>Stylidium graminifolium</i>	*	6.5b	2.5b	0.0a	0.0a	0.0a
Thymeliaceae						
<i>Pimelea linifolia</i> ssp. <i>linifolia</i>	n.s.	5.0a	2.5a	0.0a	0.0a	0.0a