

# Soil temperature and depth of legume germination during early and late dry season fires in a tropical eucalypt savanna of north-eastern Australia

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**Abstract** Temperatures that significantly increase seed germination of some tropical legumes (i.e. 80–100°C) were documented in the topsoil during the passage of early (May) and late (October) dry season fires in a tropical eucalypt savanna of north-eastern Australia. Elevated temperatures penetrated at least 30 mm into the soil during the higher-intensity, late dry season fires, but were only detected at 10 mm during the early dry season fires. The depth from which germination of two native legume forbs *Galactia tenuiflora* and *Indigofera hirsuta* occurred was positively related to the temperature elevation in the topsoil and was greater after late compared with early dry season fires. A broader range in germination depth, resulting in higher seedling densities, was recorded for *I. hirsuta* after late dry season fires. These results suggest that seedling emergence of native leguminous forbs is likely to occur at a greater density after late rather than early dry season fires in tropical eucalypt savannas of north-eastern Australia. Therefore, the season of burning, as a result of its relationship to fire intensity, can influence species composition through its effect on seed germination.

**Key words:** fire regime, northern Australia, savanna, seed germination, soil temperature.

## INTRODUCTION

Brief exposure to elevated temperatures (known as heat shock) has been demonstrated to release the seeds of many legume species from innate dormancy (Floyd 1976; Shea *et al.* 1979; Hodgkinson & Oxley 1990; Auld & O'Connell 1991; Moreno & Oechel 1991; Bradstock & Auld 1995; Smith *et al.* 2000). A direct relationship has been shown between heat penetration into the topsoil during the passage of fire and the depth of germination of temperate legume species (Bradstock & Auld 1995; Auld & Tozer 1999). Heat penetration into the topsoil varies between fires, influenced by soil characteristics and the quantity of fine ground fuel consumed during fire (Bradstock & Auld 1995; Whelan 1995). During southern Australian fires that consume sufficient fine fuel, the top few centimetres of soil can reach temperatures that break seed dormancy in legumes (Floyd 1976; Bradstock & Auld 1995; Smith *et al.* 2000). Greater temperature penetration into the topsoil occurs in fires during autumn (i.e. late

dry season) than spring (i.e. early dry season) in southern Western Australia (Grant *et al.* 1997).

In Australian tropical savannas, fire intensity is also highest during the late dry season (i.e. September–November; Gill *et al.* 1990; Williams *et al.* 1999) and differences in soil temperatures between seasons will be strongly linked to the relationship between season and fire intensity. If temperature elevation in the topsoil is highest during the higher-intensity, late dry season fires, then the season of burning would be expected to affect seed germination of species with seed dormancy broken by heat shock, and therefore species composition following fire.

Exposure to temperatures between 80 and 100°C has been shown to break the seed dormancy of several legumes of eucalypt savannas in north-eastern Australia, but temperatures greater than 100–120°C are lethal to seeds of these species (Williams *et al.* 2003a). The present paper assesses whether (i) the range of temperatures that break seed dormancy occur in the topsoil during the passage of early and late dry season fires and (ii) the depth of seed germination of species with seed dormancy released by heat shock increases with greater heat penetration into the topsoil.

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## METHODS

### Study site

Temperature elevation in the topsoil during the passage of early (May) and late (October) dry season fires, and the depth of seed germination were documented in a tropical eucalypt savanna at Cape Cleveland, approximately 25 km east of Townsville, north-eastern Australia (19°16'30''S, 147°02'30''E). The site is dominated by *Corymbia clarksoniana*, *Corymbia tessellaris* and *Eucalyptus platyphylla*, with a dense *Heteropogon triticeus*, *Heteropogon contortus* and *Themeda triandra* ground layer. Townsville experiences summer wet seasons, with 78% of the 1143 mm mean annual rain falling between December and March.

The site was burnt in July 1997 and then split into nine parallel blocks, each approximately 1 ha in area (80 m × 130 m), by slashing 4-m-wide fire lines. Three fire treatments were implemented in 1999: unburnt control, or burnt either early (May) or late (October) in the dry season of 1999 (Williams *et al.* 2003b). Each fire treatment was imposed on three of the nine 1-ha blocks and the blocks were allocated to treatments using a randomized block design.

### Soil temperatures

Fine fuel loads prior to the 1999 fires averaged 8.9 tonnes ha<sup>-1</sup> in the early dry season burnt blocks and 11.7 tonnes ha<sup>-1</sup> in the late dry season burnt blocks (Williams *et al.* 2003b). Fire intensities averaged 1534 kW m<sup>-1</sup> during the early dry season fires and 5511 kW m<sup>-1</sup> during the late dry season fires (Williams *et al.* 2003b).

Topsoil temperatures during the early and late dry season fires were measured at 10 points in each of the three replicate blocks per treatment. Each measurement point was adjacent to a corner of a 100-m<sup>2</sup> floristic survey plot within the block (Williams *et al.* 2003b). To assess microsite variation in temperatures between grass tussocks and gaps, five of the 10 points in each block were located at the base of a grass tussock. The remaining five per block were located in a gap with at least 30 cm to the nearest grass tussock.

Topsoil temperatures during the passage of fire were measured using Therman temperature strips. These strips contain segments that turn black when a designated temperature is reached. The strips recorded temperatures ranging from 37 to 182°C, providing increments of 3–5°C. Strips were placed at four soil depths at each of the temperature measurement points (surface, 3 mm, 10 mm and 30 mm). To ensure as little disturbance to the topsoil as possible, a small hole with a vertical wall was dug at each point. A knife was used

to create slits at depths of 10 mm and 30 mm in the wall, parallel to the soil surface. The temperature strips were pushed into these slits and the hole re-filled. The temperature at 3 mm was recorded directly above the 10 mm and 30 mm measurements by scraping away approximately 3 mm of topsoil, which was then replaced over the top of the temperature strip. The soil surface measurement was made by placing strips on the soil surface, adjacent to the strips at 3 mm, and replacing leaf litter over the top.

### Depth of seed germination

The depth of seed germination was assessed in relation to the temperatures recorded during the passage of fires for two common legume species *Galactia tenuiflora* (Spreng.) Willd. ex Wight & Arn. and *Indigofera hirsuta* L. A laboratory experiment found temperatures between 80 and 100°C enhanced the seed germination of *I. hirsuta* but not of *G. tenuiflora* (Williams *et al.* 2003a). The depth of germination of each of these species was measured by digging around recently germinated seedlings, following rain in early December 1999. The depth of germination was measured to the junction between radicle and hypocotyl (Bradstock & Auld 1995). The two temperature measurement points with the highest and the two with the lowest temperatures in each of the early and late dry season fires (i.e. a total of four points in each fire treatment) were assessed to cover the range of temperatures experienced during the fires. All seedlings within a 1-m radius of these points were assessed for depth of germination, and seedling density was recorded. There was almost no germination of these species in the unburnt control blocks, precluding the assessment of seed germination depth in undisturbed savanna. Therefore, seedlings over a 30-m length of a 4-m wide unburnt, slashed fire line were measured. The slashed savanna was used to compare germination depth in the absence of fire with that in the early and late burnt savanna, although it is acknowledged that the removal of the grass layer is likely to have elevated the temperatures of the topsoil to some degree (Auld & Bradstock 1996).

### Statistical analyses

#### *Soil temperatures*

Temperature elevation in the topsoil was compared between early and late dry season fires using separate non-parametric Mann–Whitney *U*-tests at each of the four soil depths (surface, 3 mm, 10 mm and 30 mm) and between temperatures recorded at the base of grass tussocks and in tussock gaps. The Bonferroni method of adjustment of  $\alpha$  was made to compensate for the

multiple comparisons by the *U*-tests (Sokal & Rohlf 1995).

A non-parametric Spearman's rank correlation was used to determine the relationship between temperature and soil depth for both early and late dry season fires. Where elevated temperatures were not detected (e.g. at 30-mm depths), the ambient atmospheric temperature recorded on the day of each fire (Williams *et al.* 2003b) was used in the analysis. Modal values have been presented in the results, rather than means, because of the incremental nature of temperature records, and as the upper temperature records were capped at 182°C, precluding the calculation of a true mean.

#### Depth of seed germination

The relationship between the temperatures recorded in the topsoil and depth of seed germination of *G. tenuiflora* and *I. hirsuta* was examined using Spearman's rank correlation (Sokal & Rohlf 1995). Ambient atmospheric temperatures, recorded at the time of the fires, were used in the calculations where elevated soil

**Table 1.** Statistical results of non-parametric Mann-Whitney *U*-tests of soil temperatures at the base of grass tussocks compared with tussock gaps during early and late dry season fires in eucalypt savanna at Cape Cleveland, Queensland

Depth	<i>U</i> statistic	<i>P</i> -value*
Early dry season fires		
Surface	106.000	>0.787
3 mm	83.000	>0.221
10 mm	112.500	1.000
30 mm	105.000	>0.756
Late dry season fires		
Surface	112.500	1.000
3 mm	103.000	>0.694
10 mm	112.000	>0.983
30 mm	83.000	>0.221

\*Significance level after Bonferroni adjustment for multiple comparisons is  $P < 0.013$ .

**Table 2.** Statistical results of non-parametric Mann-Whitney *U*-tests comparing soil temperatures during early and late dry season fires in eucalypt savanna at Cape Cleveland, Queensland

Depth	<i>U</i> Statistic	<i>P</i> -value*
Surface	0.000	<0.001
3 mm	15.000	<0.001
10 mm	65.000	<0.001
30 mm	17.000	<0.001

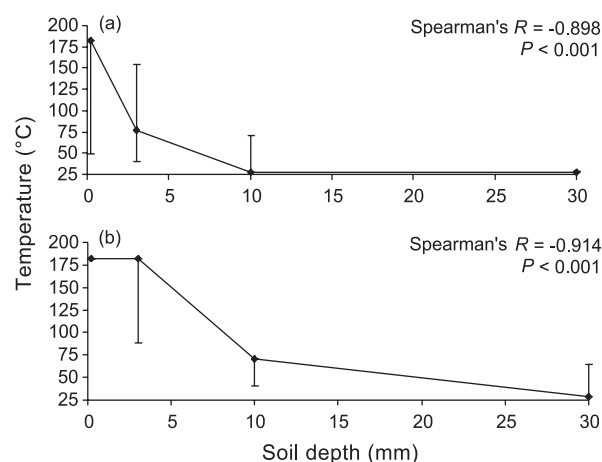
\*Significance level after Bonferroni adjustment for multiple comparisons is  $P < 0.013$ .

temperatures were not detected, including along the slashed fire break. Differences in the depth of germination between the slashed track, early and late burnt sites were compared using a one-factor ANOVA for both species. Seedling density around the temperature measurement points in the early and late dry season burnt sites was compared using a *t*-test for each species. As seedling assessment along the slashed fire break was not restricted to a precise area, seedling density could not be calculated, and therefore germination along the slashed track was not included in this analysis.

## RESULTS

### Temperature elevation in the topsoil during the passage of fire

There were no statistically significant differences between temperatures recorded at the base of grass clumps and in gaps of at least 30 cm for any soil depth during either early or late dry season fires (Table 1). A significant negative correlation was detected between soil temperature and soil depth for both early and late dry season fires, indicating the decline in temperature with soil depth (Fig. 1). Temperatures were significantly higher at all depths during the higher-intensity, late dry season fires compared with early dry season fires (Table 2; Fig. 1). Although maximum temperatures at the surface during the early season fires ranged from 49°C to at least 182°C, all surface measurements and most recordings at 3 mm were at least 182°C during the late season fires (Fig. 1). No elevated temperatures were recorded at 30 mm during



**Fig. 1.** Modal temperatures recorded at four depths in the topsoil during (a) early and (b) late dry season fires in eucalypt savanna at Cape Cleveland, Queensland, during 1999 ( $n = 30$  measurements). Error bars represent upper and lower temperatures recorded (maximum  $\geq 182^\circ\text{C}$ , minimum  $37^\circ\text{C}$ ). Results of Spearman's rank correlation coefficient of temperature with soil depth are provided.

early dry season fires, whereas temperatures of up to 65°C were recorded at that depth during late season fires.

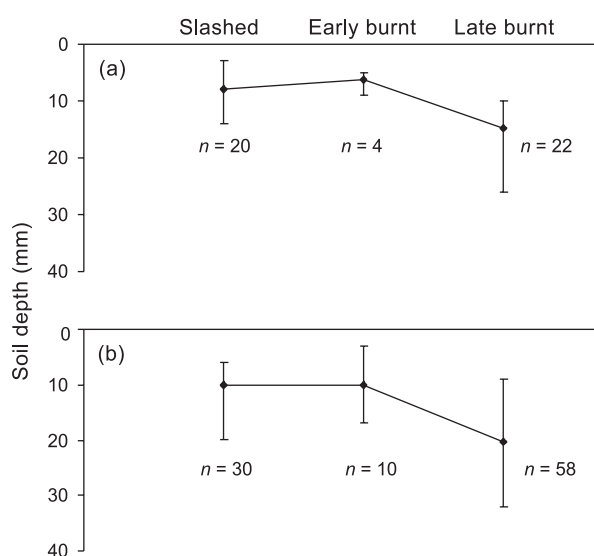
### Depth of seed germination

The depth of seed germination of both *G. tenuiflora* and *I. hirsuta* was significantly correlated to temperatures recorded in the upper 30 mm of soil (Table 3). The mean and deepest germination depths were greater after late dry season fires than either early dry season fires or along the slashed fire break for both *G. tenuiflora* ( $F_{2,43} = 24.75$ ;  $P < 0.001$ ) and *I. hirsuta* ( $F_{2,95} = 59.30$ ;  $P < 0.0001$ ; Fig. 2). The broader range in germination depth after late rather than early dry season fires resulted in significantly greater seedling density in the late dry season burnt sites for *I. hirsuta* ( $t_6 = 5.041$ ;  $P < 0.002$ ), but not for *G. tenuiflora* ( $t_6 = 2.141$ ;  $P > 0.05$ ; Fig. 3).

## DISCUSSION

### Soil temperatures

Early and late dry season fires elevated topsoil temperature, but the degree of elevation declined rapidly with increasing soil depth. No differences in temperature were detected between tussock gaps and the base of grass tussocks, suggesting uniformity in heating at the scale of tens of centimetres. Elevated temperatures were recorded down to at least 30 mm during high-



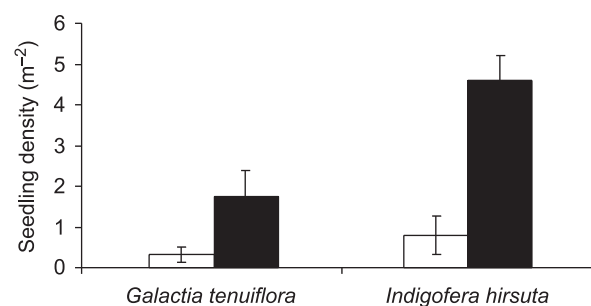
**Fig. 2.** Depth of seed germination in eucalypt savanna that has been slashed or burnt early or late in the dry season for (a) *Galactia tenuiflora* and (b) *Indigofera hirsuta*. Dots represent mean depth of germination. Error bars display the upper and lower germination depths recorded.

intensity, late dry season fires, but did not penetrate as deep during lower-intensity, early dry season fires. Temperatures of 80–100°C, which significantly increase seed germination of some tropical legumes, were documented at the surface and at 3-mm depth during early dry season fires. During late dry season fires, surface temperatures always exceeded 120°C, the lethal temperature for most seeds (Williams *et al.* 2003a), whereas temperatures between 80 and 100°C were recorded only at a depth of 3 mm.

The temperature elevation in the topsoil recorded during these fires at Cape Cleveland was consistent with temperatures recorded during fires in other eucalypt communities (Shea *et al.* 1979; Bradstock & Auld 1995; Bebawi & Campbell 2000; Smith *et al.* 2000). These data highlight the insulating capacity of soil that protects seeds from lethal temperatures during fires, while exposing a narrow band of the soil seed bank to temperatures capable of breaking dormancy. Bradstock and Auld (1995) demonstrated the importance of fine fuel combustion in determining soil temperatures during fires. In the current study, the greatest temperature elevation was recorded during the late dry season fires, which completely consumed fine fuels, whereas some fuel, such as grass stalks, remained unconsumed after early fires (Williams *et al.* 2003b). The seasonal variation was also consistent with the

**Table 3.** Results of Spearman's rank correlation coefficient analysis of differences in seed germination depth with temperatures recorded at four separate soil depths

Soil depth	R statistic	P-value
<i>Galactia tenuiflora</i> (n = 46 seedlings)		
Surface	0.590	<0.001
3 mm	0.719	<0.001
10 mm	0.647	<0.001
30 mm	0.505	<0.001
<i>Indigofera hirsuta</i> (n = 98 seedlings)		
Surface	0.675	<0.001
3 mm	0.747	<0.001
10 mm	0.675	<0.001
30 mm	0.332	<0.001



**Fig. 3.** Mean seedling density ( $\pm 1$  standard error) of *Galactia tenuiflora* and *Indigofera hirsuta* at four temperature measurement points in early (□) and late (■) dry season burnt eucalypt savanna at Cape Cleveland, Queensland.

findings of Grant *et al.* (1997), who documented higher temperature penetration into the topsoil during fires in autumn (i.e. late dry season) than during fires in spring (i.e. early dry season) in southern Western Australia.

### Depth of seed germination

The depth of seed germination in *G. tenuiflora* and *I. hirsuta* was positively related to the temperature elevation in the topsoil during fires and was recorded at greater depths after late dry season fires. This suggests that greater depths of both seed mortality and dormancy release occurred during the higher-intensity, late dry season fires, which is consistent with results from a laboratory experiment that indicated exposure to 100°C is lethal to *G. tenuiflora* and exposure to 120°C is lethal to *I. hirsuta* seeds (Williams *et al.* 2003a).

Mean germination depths of *G. tenuiflora* and *I. hirsuta* are consistent with those recorded for the New South Wales legume *Acacia suaveolens*, although the latter also germinates from greater depths (Bradstock & Auld 1995). It has been suggested that larger seeded species could benefit the most from increased temperature penetration into the topsoil, because their larger starch reserves might allow survival of germinants from greater depths in the topsoil (Midgley & Bond 2001). However, in this instance, the smaller-seeded *I. hirsuta* germinated from greater depths, even though the larger-seeded *G. tenuiflora* displayed a greater percentage of non-dormant seeds in the laboratory experiment (Williams *et al.* 2003a).

The depth of seed germination of *G. tenuiflora* correlated to temperature penetration even though no significant heat shock cue was demonstrated in a laboratory experiment (Williams *et al.* 2003a). *Indigofera hirsuta* germinated from a depth of 32 mm, where the highest temperature recorded was 65°C during the late fires, and from 17 mm after early fires, where maximum temperatures at 10 mm were 40°C. The field germination therefore suggested seed dormancy of *G. tenuiflora* can be broken by heat shock and that germination of *I. hirsuta* can be promoted by lower temperatures than indicated in a laboratory experiment (80–100°C; Williams *et al.* 2003a). This suggests that exposure of seeds to 40–60°C using hot water, heated soil, or an extended duration in heated air, could produce significantly enhanced germination following heat shock by temperatures less than 80°C in a laboratory experiment.

There was a greater density of *I. hirsuta* seedlings recorded within the 1-m radius of temperature measurement points after late rather than after early dry season fires. This reflects the greater range in depth of germination after late fires and therefore the greater

proportion of the soil seed bank from which germination is triggered.

In conclusion, the present study demonstrates that temperatures that break seed dormancy of several tropical legumes (i.e. 80–100°C) occur in the topsoil during the passage of both early and late dry season fires. Greater penetration of elevated temperatures was recorded during the higher-intensity fires that occurred in the late dry season. However, higher temperatures that are lethal to seeds also occurred near the soil surface in this season. The depth of germination of two native legumes confirms that temperatures experienced during fires can trigger germination in the topsoil. The data also suggest that temperatures as low as 40°C can increase germination of these species. A greater range in germination depth, resulting in higher seedling densities, was recorded after late dry season fires, suggesting more abundant seedling emergence may occur after late rather than after early dry season fires. Therefore, fire season, as a result of its relationship with fire intensity, can influence species composition in the vegetation emerging following fire through its effect on seed germination.

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