

Effect of season of burning and removal of herbaceous cover on seedling emergence in a eucalypt savanna of north-eastern Australia

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Abstract Seedling emergence in a eucalypt savanna of north-eastern Australia was documented over a 12-month period, between May 1999 and May 2000. Seedling emergence for grasses, forbs and subshrubs was found to mainly occur in a brief pulse at the start of the wet season following fire or the removal of grass biomass. Only a minor number of tree and shrub seedlings were detected overall. Burning, or cutting away the grass layer in unburnt savanna, in both the early (i.e. May) and the late (i.e. October) dry seasons significantly increased seedling emergence over undisturbed savanna that had been unburnt for 3 years. Removing the grass layer in unburnt savanna, during either the early or the late dry season, triggered similar seedling densities to savanna burnt in the early dry season. Late dry season fires promoted the greatest seedling density. We attribute this to the higher intensity, late dry season fires releasing a greater proportion of seed from dormancy, coupled with the higher density of soil seed reserves present in the late dry season.

Key words: fire regime, northern Australia, savanna, seed dormancy, seedling emergence, soil seed bank.

INTRODUCTION

Seedling emergence depends on the availability of seeds and safe sites, which provide a moisture, light and temperature regime appropriate for germination (Harper 1977). In Australian tropical savannas, seedling emergence of many annual grasses, such as *Schizachyrium* spp. and *Sorghum* spp., is linked to seasonal cycles in rainfall, with abundant recruitment occurring at the start of each wet season, irrespective of disturbance (Andrew & Mott 1983; Crowley & Garnett 1999). Seedling emergence of tropical savanna trees, such as eucalypts and *Melaleuca viridiflora*, is irregular and may primarily occur in years with above average rainfall (Lacey 1974; Gill *et al.* 1990; Fensham 1992; Crowley & Garnett 1998).

Fire can influence seed production and mortality, release seed from dormancy, reduce competitive inhibition from overstorey and grass layers and often enhance soil nutrient availability (Whelan 1995; Bond & van Wilgen 1996). Seedling emergence in many fire-prone communities occurs primarily in the first wet season following fire. This has been documented for

species of Californian chaparral (Keeley & Bond 1997), South African fynbos (Pierce & Cowling 1991), heaths of south-eastern (Bradstock 1991) and south-western Australia (Bell *et al.* 1987), and temperate eucalypt forests (Ashton 1979) and woodlands (Purdie & Slatyer 1976). In tropical savannas, fire is known to enhance seedling emergence of some perennial grasses, such as *Heteropogon contortus* (Shaw 1957; Tothill 1969).

The duration of fire intervals can influence seedling recruitment by affecting seed bank size and fire intensity (Whelan 1995). Fire intensity influences seed mortality and the proportion of seeds that are released from dormancy (Keith 1996). Fire season can affect seedling recruitment through the coincidence of fire with seasonal fluctuations in seed bank size and post-fire rainfall, and its influence on fire intensity (Whelan 1995; Bond & van Wilgen 1996).

The abundance of some savanna species in north-eastern Australia increases in the year following fire (Williams *et al.* 2003a) and may result from increased vegetative reproduction and/or seedling emergence. Fire has been demonstrated to break seed dormancy of several forb and grass species of this community, with a greater proportion of legume seeds released from dormancy by late rather than early dry season fires (Williams *et al.* 2003b, 2004; 2005). Germinable

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soil seed bank size, suggesting the density of seed available to be influenced by fire, is also larger in the late dry season than the early dry season (Williams *et al.* 2005).

This article examines the patterns of seedling emergence in a eucalypt savanna near Townsville, north-eastern Australia. It assesses seedling emergence after fires in different seasons and in the absence of fire. The experimental removal of the herbaceous layer in unburnt savanna is also examined to help understand the effect of fire on seedling emergence. Specific questions addressed are: (i) Does seedling emergence occur at similar densities in recently burnt compared to savanna unburnt for 3 years? (ii) What are the effects of fire season on seedling emergence? (iii) What level of seedling emergence is promoted by the removal of herbaceous cover? and (iv) What is the total density of seedlings that emerge over a year?

METHODS

Study site

Seedling emergence was examined 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 (taxonomy follows Henderson 2002). 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 of approximately 1 ha in area (80 m width by 130 m length), by slashing 4 m wide fire lines. Three fire treatments were implemented in 1999: unburnt control, or burnt in either the early (May) or the late dry season (October) of 1999 (Williams *et al.* 2003a). 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 (Williams *et al.* 2003a).

Sampling methods

Seedling emergence was recorded within permanent 1 m² plots fortnightly, or occasionally every 3 weeks, between May 1999 and May 2000, prior to and following early and late dry season fires in 1999. The effect on seedling emergence of removing the herbaceous layer was also examined to help understand fire effects, by isolating the release from competition by herbaceous cover from the heat and chemical attributes of fire.

The treatments examined were:

1. Undisturbed – savanna that was last burnt in July 1997 and remained undisturbed.
2. Early burnt – savanna burnt in July 1997 and in the early dry season (i.e. May) 1999.
3. Late burnt – savanna burnt in July 1997 and in the late dry season (i.e. October) 1999.
4. Early cut – herbaceous layer cut and removed (including leaf litter) from unburnt plots at the time of early dry season fires, in savanna that was last burnt in July 1997. The herbaceous layer was allowed to regrow following the initial treatment, to simulate post-fire regrowth.
5. Late cut – herbaceous layer (grasses and forbs) cut and removed (including leaf litter) from unburnt plots at the time of late dry season fires, in savanna that was last burnt in July 1997. The herbaceous layer was allowed to regrow following the initial treatment, to simulate post-fire regrowth.

The undisturbed, early cut and late cut treatments were established in the three 1-ha control blocks last burnt in July 1997 (Williams *et al.* 2003a). The early burnt and late burnt treatments were established in the respective early and late burnt 1-ha blocks, which were all burnt in July 1997 and in either May 1999 or October 1999 (Williams *et al.* 2003a). Each of the five treatments were represented by ten 1-m² plots in each of three 1-ha blocks at Cape Cleveland, providing a total of 30 1-m² plots per treatment. To facilitate relocation, each 1-m² plot was randomly allocated to a corner of one of the four 100-m² plots used in the floristic surveys (Williams *et al.* 2003a). Plots for the cut treatment were established on the outside of the allotted corner and the herbaceous layer was removed from an area of 1.5 m radius to reduce shading effects on the 1-m² plots. Seedling emergence was documented at each plot over the study period by placing fencing wire in the soil, 2–3 cm from the base of recently emerged seedlings. The top of the wire was bent into various shapes to represent different common species.

Statistical analyses

The statistical significance of differences in the seedling emergence among treatments was assessed for total seedling emergence, species richness and for each of the most common species (that comprised at least 1% of the total seedling emergence). For each treatment, seedling densities were averaged for the 10 1-m² plots in each 1-ha block, providing three replicates per treatment. A one-factor ANOVA was used to detect differences among the five treatments. Where significant differences were detected, a two-factor ANOVA assessed the effect of disturbance (burnt or cut) and season of disturbance (early or late dry season).

RESULTS

The majority of seedlings emerged from the permanent 1-m² plots following rains at the start of the 1999 wet season, which began in early November 1999 (Fig. 1; Table 1). The highest rate of seedling emergence occurred in late burnt plots in the first fortnight of November 1999, when an average of 55 new seedlings per square metre were recorded. A minor germination event also occurred in September in the early burnt and early cut sites after some rain in late August 1999 (Fig. 1).

Total seedling emergence between May 1999 and May 2000 was significantly enhanced by both burning and cutting (Table 2). Burning in the early dry season promoted similar seedling densities to cutting in either season. Burning during the late dry season promoted the highest seedling densities. The species richness of seedlings was equally enhanced by burning and cutting in both seasons.

Burning in both the early and the late dry seasons significantly enhanced seedling density of the dominant grass, *H. triticeus*, compared with undisturbed and cut treatments (Table 2). The greatest seedling density of *H. triticeus* followed late season fires. Late

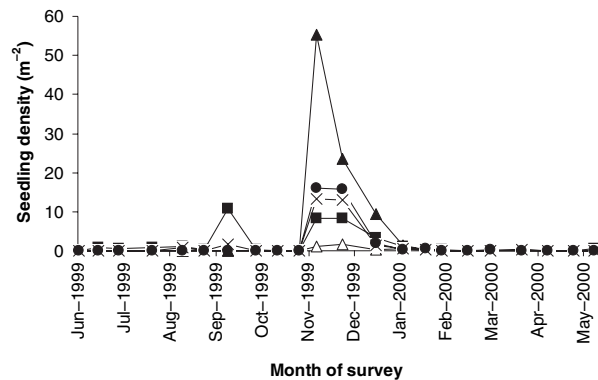


Fig. 1. Mean rate of seedling emergence in eucalypt savanna at Cape Cleveland in savanna undisturbed since burning July 1997 (Δ); savanna burnt early dry season (May) 1999 (\blacksquare); savanna burnt late dry season (October) 1999 (\blacktriangle); savanna unburnt since July 1997, with herbaceous layer cut and removed in May 1999 (\times); savanna unburnt since July 1997 with herbaceous layer cut and removed in October 1999 (\bullet).

dry season burning also promoted the highest seedling densities of the ephemeral legume, *Indigofera hirsuta* (Table 2). The exotic twiner, *Passiflora foetida*, was promoted by burning or cutting in the late dry season.

Significant disturbance type and season effects, and their interactions, were found for total seedling density, *H. triticeus*, *I. hirsuta* (Table 3). A seasonal effect was documented for *P. foetida*.

DISCUSSION

Seedling emergence within eucalypt savanna at Cape Cleveland occurred primarily at the onset of the wet season, in the first year after fire. Burning and cutting in both the early and the late dry seasons significantly promoted seedling emergence over undisturbed savanna, with late dry season fires promoting the highest seedling density. The dominance of seedlings of herbaceous species reflects the dominance of herbs in the germinable soil seed bank at Cape Cleveland (Williams *et al.* 2005).

The removal of the herbaceous layer has been demonstrated to increase seedling emergence significantly in this savanna. Therefore, multiple fire-related cues promote germination in the eucalypt savanna at Cape Cleveland, including exposure to heat shock, smoke, enhanced nitrate levels (Williams *et al.* 2003b, 2004; 2005), and the removal of competition from the herbaceous layer. Shaw (1957) found similar results in that cutting and removing the grass layer produced a seedling density of *H. contortus* that was intermediate between that of burnt and undisturbed treatments. Inhibition of germination may be due to competition for light, or be linked to soil temperatures, which can increase after the removal of grass cover (Shaw 1957; Tothill 1969).

The pulse of seedling emergence at the start of the wet season is consistent with reports of other northern Australian forbs (Torrsell & McKeon 1976; McIvor & Gardener 1991). The fire-promoted germination of herbaceous species at Cape Cleveland concurs with many species in temperate eucalypt forests (e.g. Purdie & Slatyer 1976; Bell *et al.* 1993; Benwell 1998) but contrasts with that of some annual grasses and trees (*Acacia oncinocarpa* and *Eucalyptus miniata*) of Cape York and the Northern Territory. Seedling emergence

Table 1. Monthly rainfall (mm) for 1999 and 2000, recorded by the Australian Bureau of Meteorology 10 km from the study site at Cape Cleveland

Year	Annual total	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1999	1111.0	160.6	238.6	102.8	111.0	14.4	0.0	8.0	31.2	4.6	1.6	233.4	204.8
2000	2716.6	79.4	937.6	184.4	442.0	132.6	35.2	0.0	1.2	0.0	46.8	437.2	418.4

Seedling emergence was documented between May 1999 and May 2000.

Table 2. Mean (standard error) seedling density (per square metre) and one-factor ANOVA results in undisturbed, early burnt, late burnt, early cut and late cut plots at Cape Cleveland

Species and groups	Undisturbed (<i>n</i> = 30)	Early burnt (<i>n</i> = 30)	Late burnt (<i>n</i> = 30)	Early cut (<i>n</i> = 30)	Late cut (<i>n</i> = 30)	ANOVA (d.f. = 4)
Total seedlings (<i>n</i> = 49 spp.)	1.60 ^a (0.61)	37.00 ^b (3.53)	90.23 ^c (11.41)	31.57 ^b (3.31)	35.10 ^b (4.09)	<i>F</i> = 139.532 <i>P</i> < 0.001
Species richness	1.77 ^a (0.24)	7.83 ^b (0.54)	8.63 ^b (0.36)	6.30 ^b (0.45)	6.87 ^b (0.32)	<i>F</i> = 15.989 <i>P</i> < 0.001
<i>Commelina</i> spp.	0.77 ^a (0.20)	4.07 ^a (1.09)	8.70 ^a (2.21)	7.90 ^a (2.24)	9.53 ^a (2.37)	<i>F</i> = 2.259 <i>P</i> < 0.135
<i>Crotalaria pallida</i>	0.00 ^a (0.00)	1.00 ^a (0.49)	1.40 ^a (0.60)	0.10 ^a (0.07)	0.40 ^a (0.21)	<i>F</i> = 1.422 <i>P</i> = 0.296
<i>Galactia tenuiflora</i>	0.27 ^a (0.12)	4.53 ^a (1.34)	2.37 ^a (0.63)	0.93 ^a (0.30)	1.10 ^a (0.34)	<i>F</i> = 1.677 <i>P</i> < 0.231
<i>Glycine tomentella</i>	0.00 ^a (0.00)	1.70 ^a (0.50)	5.17 ^a (2.78)	0.50 ^a (0.21)	1.13 ^a (0.36)	<i>F</i> = 2.726 <i>P</i> < 0.090
<i>Heteropogon contortus</i>	0.00 ^a (0.00)	0.03 ^a (0.03)	17.00 ^a (10.18)	1.27 ^a (1.27)	0.07 ^a (0.05)	<i>F</i> = 1.375 <i>P</i> < 0.311
<i>Heteropogon triticeus</i>	0.23 ^a (0.20)	11.07 ^b (1.72)	27.43 ^c (3.13)	7.40 ^a (1.77)	4.97 ^a (0.94)	<i>F</i> = 25.784 <i>P</i> < 0.001
<i>Hybanthus</i> spp.	0.10 ^a (0.07)	3.30 ^a (1.51)	1.63 ^a (0.73)	0.90 ^a (0.40)	1.40 ^a (0.48)	<i>F</i> = 1.742 <i>P</i> < 0.217
<i>Indigofera hirsuta</i>	0.03 ^a (0.03)	1.70 ^a (0.44)	8.37 ^b (1.93)	1.00 ^a (0.28)	1.23 ^a (0.54)	<i>F</i> = 12.091 <i>P</i> < 0.001
<i>Macroptilium atropurpureum</i>	0.27 ^a (0.10)	0.27 ^a (0.11)	0.27 ^a (0.13)	0.40 ^a (0.22)	0.67 ^a (0.26)	<i>F</i> = 0.663 <i>P</i> < 0.631
<i>Passiflora foetida</i>	0.73 ^a (0.27)	2.20 ^a (0.56)	6.73 ^b (1.08)	3.30 ^{a,b} (0.69)	6.83 ^b (1.29)	<i>F</i> = 11.950 <i>P</i> = 0.001
<i>Pycnospora lutescens</i>	0.10 ^a (0.07)	0.77 ^a (0.39)	1.77 ^a (0.77)	2.13 ^a (0.96)	3.17 ^a (1.18)	<i>F</i> = 1.148 <i>P</i> = 0.389
<i>Spermacoce brachystema</i>	0.03 ^a (0.03)	0.17 ^a (0.84)	2.50 ^a (1.55)	0.60 ^a (0.33)	1.07 ^a (0.69)	<i>F</i> = 1.760 <i>P</i> < 0.213
<i>Tephrosia juncea</i>	0.03 ^a (0.03)	1.23 ^a (0.43)	1.83 ^a (0.84)	0.13 ^a (0.08)	0.03 ^a (0.03)	<i>F</i> = 2.432 <i>P</i> < 0.116
<i>Triumfetta rhomboidea</i>	0.63 ^a (0.41)	0.73 ^a (0.63)	1.37 ^a (0.49)	2.17 ^a (0.58)	1.80 ^a (0.52)	<i>F</i> = 2.158 <i>P</i> < 0.148

Total seedling density includes the sum of seedling emergence documented between May 1999 to May 2000 in undisturbed, early burnt and early cut plots; and between October 1999 and May 2000 in late burnt and late cut plots. Means across each row with the same superscript are not significantly different at *P* < 0.05. Significant *P* values are in bold.

Table 3. Results of a two-factor ANOVA of the effect of disturbance type (burnt or cut) and season of disturbance (early or late dry season) on seedling emergence in eucalypt savanna at Cape Cleveland

Species	Disturbance	Season	Disturbance × season
Total seedlings	<i>F</i> _{1,8} = 25.597***	<i>F</i> _{1,8} = 22.486**	<i>F</i> _{1,8} = 17.236**
Species richness	<i>F</i> _{1,8} = 4.891	<i>F</i> _{1,8} = 0.839	<i>F</i> _{1,8} = 0.024
<i>Heteropogon triticeus</i>	<i>F</i> _{1,8} = 32.672***	<i>F</i> _{1,8} = 9.287*	<i>F</i> _{1,8} = 16.908**
<i>Indigofera hirsuta</i>	<i>F</i> _{1,8} = 11.063*	<i>F</i> _{1,8} = 6.833*	<i>F</i> _{1,8} = 5.407*
<i>Passiflora foetida</i>	<i>F</i> _{1,8} = 0.499	<i>F</i> _{1,8} = 22.551**	<i>F</i> _{1,8} = 0.347

*F*_{1,8} indicates *F*-value, denominator d.f., numerator d.f.; *F*-values without an asterisk (*) are not significantly different at *P* > 0.05; **P* < 0.05; ***P* < 0.01; ****P* < 0.001.

of many annual grasses tends to occur each wet season irrespective of fire (Andrew & Mott 1983; Crowley & Garnett 1999). Seedling recruitment of both *A. oncinocarpa* and *E. miniata* is inhibited by regular fire, due to reduced seed supply and microsite availability (Setterfield 2002). However the effects of fire

on savanna trees may differ between species, communities and fire events, as seedling emergence of *C. clarksoniana*, a dominant tree in north-eastern Queensland with only episodic germination, can be most dense where seed falls onto recently burnt ground (Williams 2002).

Seedling density at Cape Cleveland, with an average maximum in 1 year of 90 seedlings per square metre, is higher than that recorded by Purdie and Slatyer (1976) in a temperate eucalypt woodland in south-eastern Australia, where total seedling emergence levels ranged from 7.5 to 25 per square metre. However, it is lower than that recorded in some fire-prone communities. For instance, the fire-killed shrub *Beaufortia elegans* in south-western Australia, can produce an average of 235 seedlings per square metre after autumn fires (Bell *et al.* 1987). Annual grasses of tropical savannas can also recruit seedlings at higher densities than recorded in this study of a perennial grass-dominated savanna. For example, the annual grass *Schizachyrium fragile* can produce 2560 seedlings per square metre (Crowley & Garnett 1999), and *Sorghum intrans* 253 per square metre (Andrew & Mott 1983).

Late dry season fires promoted greater seedling density than early dry season fires. This is consistent with reports from other fire-prone communities that high intensity, late dry season fires promote the emergence of more seedlings than early dry season fires (Tohill 1969; Bell *et al.* 1987; Hobbs & Atkins 1990), or than low intensity fires in general for regions with a poor distinction between wet and dry seasons (Clark 1988; Bradstock & Auld 1995). The greater seedling density after late, rather than early, dry season fires at Cape Cleveland accounts for the larger increase in species abundance after late dry season fires, documented in the floristic surveys (Williams *et al.* 2003a).

Bond and van Wilgen (1996) proposed that differences in seedling recruitment after fires of different seasons may be due to variation in either the size of the seed bank, or the heat of fire in causing seed mortality and dormancy release. Williams *et al.* (2004) demonstrated that late dry season fires produce greater heat penetration into the top soil and can release a greater proportion of seed from dormancy than do early dry season fires. Germinable soil seed banks at Cape Cleveland are also larger during the late rather than early dry season (Williams *et al.* 2005), which suggests that a greater density of seed is available to be affected by fire in the late dry season. Therefore, both the greater dormancy-release stimuli of late dry season fires, and the higher seed bank density in the late dry season, combine to promote the greatest seedling emergence. Further experimental work involving the manipulation of seed bank density and fire stimuli is required to elucidate the relative contributions of each factor.

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