

Germinable soil seed banks in a tropical savanna: seasonal dynamics and effects of fire

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Abstract The germinable soil seed bank of a tropical eucalypt savanna of north-eastern Australia was found to be dominated by grasses and forbs, with seed bank density ranging from 58 to 792 seeds per square metre, from a total of 53 species. Late dry season fires and the fire-related cues, heat shock and smoke, broke the seed dormancy of a range of tropical savanna species. Heat shock promoted the germination of the species groups natives, exotics, subshrubs, ephemeral and twining perennial forbs, and the common species *Indigofera hirsuta*, *Pycnospora lutescens* and *Triumfetta rhomboidea*. Exposure to smoke at ambient temperature promoted germination from the soil seed bank of the species groups combined natives, upright perennial forbs and grasses, as well as the common grasses *Digitaria breviglumis* and *Heteropogon triticeus*. The germinable soil seed bank varied seasonally, increasing from the mid west season (February) and early dry season (May) to a maximum in the late dry season (October). The effect of recent fire history on soil seed bank dynamics was limited to the immediate release of some seed from dormancy; a reduction in seed densities of subshrubs and monocots, other than grasses, in recently burnt savanna; and enhanced seed density of the ephemeral *I. hirsuta* in the year following fire. The seed banks of most savanna species were replenished in the year following burning.

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

INTRODUCTION

Seed banks bridge the temporal gap between seed production and seed germination. They provide a mechanism for population persistence through harsh seasons and supply propagules for re-establishment after disturbance (Lunt 1997; Auld *et al.* 2000). Seed banks are stored in either the canopy (bradyspory) or the soil, the latter being most common in northern Australia (Andrew & Mott 1983; McIvor 1987; Williams *et al.* 1999).

The period of time that seeds remain viable in the seed bank varies among species. Many dominant grasses of tropical savannas, including annual *Sorghum* spp. and *Themeda triandra*, produce a transient soil seed bank. Their seed is stored through the dry season and either germinates or dies during the wet season, so that further seed input is required to ensure a seed bank for the following year (Andrew & Mott 1983; McIvor 1987). For many of these grasses, storage

through the dry season is made possible by an after-ripening seed dormancy mechanism (McIvor & Howden 2000).

The survival of populations of short-lived or fire-killed species may require seeds that remain viable for more than 1 year (Thompson & Grime 1979; Bond & van Wilgen 1996). These persistent seed banks contain both dormant and non-dormant seeds (Bell 1999; Auld *et al.* 2000; Thompson *et al.* 2003).

In many fire-prone communities, seedlings primarily recruit from the local seed bank rather than from seed dispersed from outside the immediate area (Whelan 1986). Therefore seed bank density and germination response to fire-related cues are important factors influencing post-fire seedling emergence (Auld *et al.* 2000). Soil seed banks are dynamic, with seasonal and annual fluctuations in composition and abundance resulting from variations in seed production, seed fall, seed mortality, release of seeds from dormancy and seed germination (Thompson & Grime 1979). All of these processes can be influenced by fire, which can enhance or restrict seed production, affect seed dispersal agents, cause seed mortality, and break seed dormancy to allow germination (Keith 1996; Whelan

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et al. 2002). The effect of fire on seed dormancy can be indirectly assessed through experimental treatment of soil seed banks, exposing them to heat shock and smoke (Enright *et al.* 1997; Read *et al.* 2000; Hill & French 2003).

As fire can influence seed bank processes, variations in fire regime may be expected to have a considerable effect on seed bank dynamics. The season of fire can influence seed bank dynamics by interacting with reproductive phenology, and fires that are synchronized with seasonal peaks in seed bank density will influence the survival and germination of a greater number of seeds. Post-fire climatic conditions also influence seed germination, and therefore seed bank dynamics (Whelan 1995).

Most soil seed bank research in Australian tropical savannas has concentrated on a few dominant grasses, many of which produce seed banks lasting from several weeks to 1 year (Andrew & Mott 1983; Andrew 1986; McIvor 1987; Crowley & Garnett 2001). Details of the seasonal variation of seed banks of a broad range of savanna species will improve our understanding of the regenerative ecology of this widespread vegetation, including reasons for differential germination following fires of different seasons. The abundance of the standing vegetation in tropical savannas of north-eastern Australia has been demonstrated to be influenced by fire regime (Williams *et al.* 2003a). This paper asks: (i) how does fire regime influence the germinable soil seed bank dynamics?; (ii) how do the fire-related cues, heat shock and smoke, affect seed germination from the soil seed bank?; and (iii) what seasonal fluctuations in composition and density occur in the germinable seed bank?

METHODS

Study site

Soil seed bank dynamics were 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). The site was grazed by a low density of free ranging cattle from the early 1900s to the 1970s, after which all cattle were removed from the area (C. Adams, pers. comm., 1997). Townsville experiences summer wet seasons, with 78% of the 1143 mm mean annual rain falling between December and March. The site was burnt in December 1990, December 1994 and July 1997. Following the 1997 fire, the site was 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 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 randomised block design (Williams *et al.* 2003a).

Sampling methods

Soil samples were collected from across each of the nine 1 ha blocks at Cape Cleveland during the early

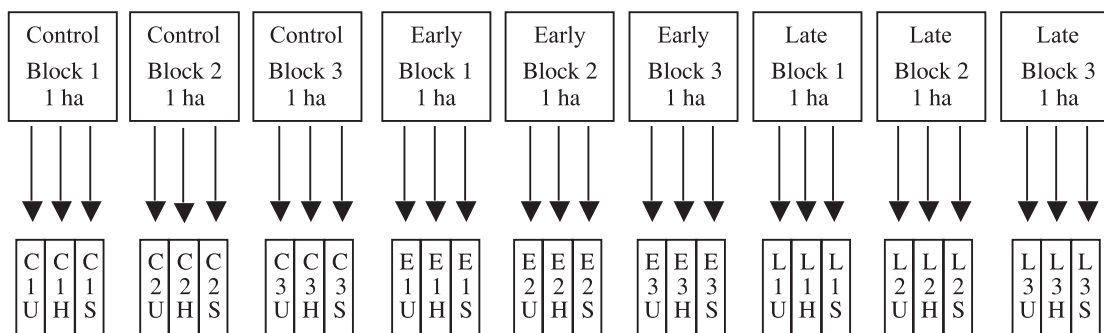


Fig. 1. Schematic diagram of the sampling design used in the soil seed bank study of eucalypt savanna at Cape Cleveland, Australia, between May 1999 and October 2000. A complete set of soil seed bank samples was collected in each of the early dry season, i.e. May; mid dry season, i.e. July; and late dry season, i.e. October, in 1999 and 2000, and wet season, i.e. February. The top row of boxes represent the nine 1 ha blocks at Cape Cleveland: Control blocks 1–3, last burnt in July 1997; Early blocks 1–3, burnt in July 1997 and May 1999; Late blocks 1–3, burnt July 1997 and October 1999. The lower row of boxes represent soil samples collected in each of early, mid and later dry season of 2000. Each soil sample contained 4000 cm³ of soil, combined from 32, 125 cm³ subsamples. Each subsample of 125 cm³ was collected from a soil mass of 73 440 cm³, dug to a depth of 5 cm. C, Control block; E, Early burnt; L, late burnt; U, untreated soil; H, soil heated in oven at 85°C for 45 min; S, soil exposed to smoke at ambient temperature for 30 min; numbers 1–3 represent replicate soil samples. Note that only heated and untreated soil treatments were undertaken between May 1999 and February 2000.

(May), mid (July) and late (October) dry seasons of 1999 and the wet season (February), and early (May), mid (July) and late (October) dry seasons of 2000. The 1999 early dry season soil collection was taken 1 week prior to the early dry season fire, the late dry season soil collected in 1999 was taken 1 week after the late dry season fire. The early dry season of 2000 coincided with the start of seed fall in most plants following the 1999 fires.

During each season of collection, soil samples were taken from 32 points, to a depth of 5 cm, across each of the nine 1 ha blocks. Sampling involved walking in a zig-zag pattern through each 1 ha block and stopping approximately every five paces. At each point a spadeful of soil was dug to 5 cm, providing a volume of 2295 cm³. The soil was mixed and then two 125 cm³ subsamples were collected from each point, in the May 1999 to February 2000 collections. Three subsamples were collected from each point in May to October 2000 to allow for an additional soil treatment (smoke). The two (three in 2000) subsamples collected at each point were kept separate, so that the 32 points sampled in each 1 ha block provided two soil collections (three in 2000), each containing a pooled set of 32 soil subsamples. This provided two (three in 2000) soil collections of 4000 cm³ in total, subsampled from a total of 73 440 cm³ of soil, for each 1 ha block (Fig. 1).

Soil treatment and storage

Seed bank composition and abundance were assessed were assessed through seedling emergence, and therefore this study examines the 'germinable' soil seed bank. Soil samples were either heated, exposed to aerosol smoke or remained untreated, with the combination of these treatments improving the ability to detect germinable seeds.

One of the samples collected from each 1 ha block in each season remained untreated and was placed into a shadehouse covered with 50% shade cloth. The samples were watered daily from overhead sprinklers, which provided approximately 21 mm of water per day. Seedlings were recorded regularly and removed once large enough to be identified. Each collection was put into the shadehouse on the first or second day following collection, and observed for 6 months. By observing for 6 months, all soil samples were exposed to a period of mild and warm temperatures, irrespective of the season of collection. This exposure, coupled with daily watering, should have minimized any seasonal storage effects.

A second soil sample from each 1 ha block in each season was spread across two aluminium trays and placed in an oven at 85°C for 45 min, and then placed into a seedling tray in the shadehouse. This pre-

treatment was used to assess the effect of heat shock on seed dormancy of species present in the soil seed bank. It also allowed detection of a wider range of species from the germinable soil seed bank. A temperature of 85°C occurs at topsoil depths of less than 10 mm during the passage of fire at Cape Cleveland (Williams *et al.* 2004). This is consistent with temperatures documented during fires in other eucalypt communities (Shea *et al.* 1979; Bradstock & Auld 1995; Bebawi & Campbell 2000; Smith *et al.* 2000). Brief exposure to temperatures around 85°C have been shown to release seeds of many species from dormancy (Shea *et al.* 1979; Auld & O'Connell 1991), including species at Cape Cleveland (Williams *et al.* 2003b). The 45 min duration is longer than the period that temperatures remain elevated in the topsoil during the passage of a fire (Bradstock & Auld 1995), but thermometer readings of the soil whilst in the oven indicated that 45 min was required to allow temperatures of approximately 80°C to penetrate into the centre of the soil mass. Each soil sample was mixed after 20 min in the oven to aid heat penetration through the soil and to spread the heating effect through the seed bank. Similar soil heating durations have been shown to promote seed germination from soil seed banks in tropical Australia (Hopkins & Graham 1984; Skull 1992; Williams 2000).

The third soil samples collected from each 1 ha block over the dry season of 2000 were exposed to smoke at ambient temperature for a duration of 30 min. Smoke was produced following the method described in Dixon *et al.* (1995), in a 20 L metal drum filled with smoldering grass and litter collected from the Cape Cleveland site. The smoke was pumped through a 3 m length of flexible metal tubing which allowed the cooling of smoke prior to entry into a plastic tent, in which soil samples were placed. Smoke was pumped into the tent for 30 min before samples were removed for incubation in the shadehouse. Collections from replicate blocks for each of the control, early and late burnt treatments were exposed to smoke separately, as recommended by Morrison and Morris (2000).

Statistical analyses

Early, mid and late dry seasons and wet season 1999 (before and after fire)

The soil seed bank was examined immediately before and after the implementation of fire season treatments between May 1999 and February 2000. A three-factor ANOVA was used to examine differences among fire treatments, with three levels (unburnt, early and late dry season burnt); between soil treatments, with two levels (untreated and heated); and among seasons of soil collection, which was a repeated measures factor,

with four levels (early, mid and late dry season 1999 and wet season 2000).

An assessment was also made of the effect of the 1999 fires on the untreated soil samples from the unburnt and burnt blocks. Independent *t*-tests were performed on the control and early burnt untreated soil seed bank collected in July 1999 (the first collection after the early dry season fire) and to compare the control and late burnt untreated soil seed bank collected in October 1999 (the first collection after the late dry season fire).

Separate analyses were performed on species richness, total soil seed bank, native and exotic species, growth form groups (defined in Williams *et al.* 2003a), and individual species which contributed at least 5% of the total germinable seed bank density. Due to the large overall number of analyses undertaken on the soil seed bank data, the significance value was set at $P < 0.01$, to reduce the possibility of inappropriately assigning a significant conclusion (type 1 error; Zar 1999).

Variance heterogeneity was checked using a Cochran's test (Underwood 1997). The non-parametric Mann-Whitney *U*-tests were performed

for *Glycine tomentella* and *Indigofera hirsuta*, due to their non-normally distributed data.

Early, mid and late dry seasons 2000 (the year after fire)

Analyses were made of the effects of recent fire history, exposure to heat shock and smoke, and the season of soil collection, on the composition and abundance of the soil seed bank. The data were analysed using a three-factor ANOVA with the factors fire treatment with three levels (unburnt in 1999; burnt in the early dry season of 1999 or burnt in the late dry season of 1999); soil treatment possessing three levels (untreated, heated and smoked soil); and season of soil collection, as a repeated measures factor with three levels (early, mid and late dry season).

Homogeneity of variances was tested using Cochran's test (Underwood 1997). A Scheffe's post-hoc test was used to determine differences within treatments. Where the data were non-normally distributed, a Kruskal-Wallis ANOVA by rank was performed separately for the two factors, soil and fire treatments (Zar 1999). Where the Kruskal-Wallis ANOVA detected significant differences, Mann-Whitney *U*-tests were

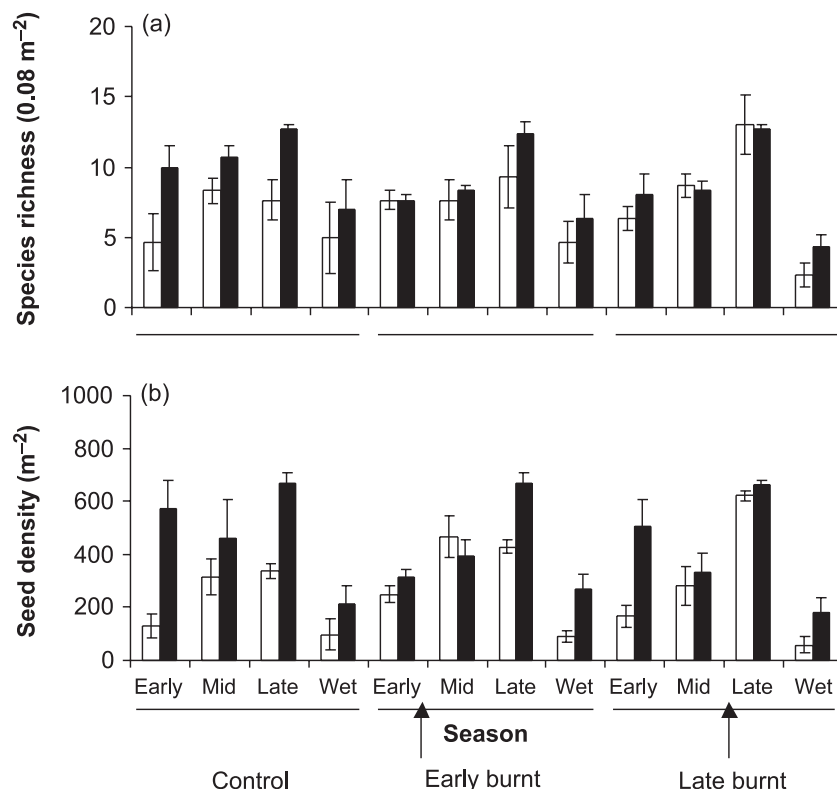


Fig. 2. Mean (± 1 standard error) (a) species richness and (b) total seed density of germinable soil seed bank, collected in eucalypt savanna at Cape Cleveland, between May 1999 and February 2000. Soil samples remained untreated (\square); or were heated in an oven at 85°C for 45 min (\blacksquare). Arrows indicate timing of early and late dry season fires in relation to soil sample collections. Early, early dry season, i.e. May 1999; Mid, mid dry season, i.e. July 1999; Late, late dry season, i.e. October 1999; Wet, mid wet season, i.e. February 2000. Control, sites last burnt in July 1997; Early burnt, sites burnt July 1997 and May 1999; Late burnt, sites burnt July 1997 and October 1999.

Table 1. ANOVA of the statistical significance of differences between fire treatment, soil treatment and season of soil seed bank collection, before and after the 1999 fire season treatments in eucalypt savanna at Cape Cleveland, Australia

Species group	Fire	Soil treatment	Season	Fire × soil treatment	Fire × season	Soil treatment × season	Fire × soil treatment × season
Species richness	$F_{2,12} = 0.107$	$F_{1,12} = 11.814^{**}$ H > U	$F_{3,36} = 22.381^{**}$ M & L > W; L > E	$F_{2,12} = 2.553$	$F_{6,36} = 1.602$	$F_{3,36} = 0.439$	$F_{6,36} = 0.628$
All species ($n = 39$)	$F_{2,12} = 0.036$	$F_{1,12} = 24.340^{**}$ H > U	$F_{3,36} = 53.822^{**}$ E, M & L > W; L > E	$F_{2,12} = 2.028$	$F_{6,36} = 2.332$	$F_{3,36} = 4.928^{*}$	$F_{6,36} = 2.436$
Native species ($n = 31$)	$F_{2,12} = 0.569$	$F_{1,12} = 21.539^{**}$ H > U	$F_{3,36} = 64.940^{**}$ E, M & L > W; L > E & M	$F_{2,12} = 0.897$	$F_{6,36} = 4.083^{*}$	$F_{3,36} = 7.236^{**}$	$F_{6,36} = 2.048$
Exotic species ($n = 8$)	$F_{2,12} = 5.730$	$F_{1,12} = 1.600$	$F_{3,36} = 2.197$	$F_{2,12} = 4.202$	$F_{6,36} = 1.167$	$F_{3,36} = 0.753$	$F_{6,36} = 1.480$
Subshrubs ($n = 5$)	$F_{2,12} = 5.122$	$F_{1,12} = 6.814$	$F_{2,24} = 3.485$	$F_{2,12} = 6.817$	$F_{4,24} = 0.357$	$F_{2,24} = 0.126$	$F_{4,24} = 1.345$
<i>Early, Mid & Late</i>							
Upright perennial forbs ($n = 6$)	$F_{2,12} = 3.214$	$F_{1,12} = 0.624$	$F_{2,24} = 12.538^{*}$ L > W	$F_{2,12} = 0.225$	$F_{4,24} = 2.809$	$F_{2,24} = 6.585^{*}$	$F_{6,36} = 0.710$
<i>Mid, Late & Wét</i>							
Twining perennial forbs ($n = 10$)	$F_{2,12} = 1.283$	$F_{1,12} = 11.019^{*}$ H > U	$F_{3,36} = 9.823^{**}$ E & L > W	$F_{2,12} = 0.322$	$F_{6,36} = 1.100$	$F_{3,36} = 0.879$	$F_{4,24} = 1.539$
<i>Log</i>							
<i>Glycine tomentella</i>	$F_{2,12} = 0.232$	$F_{1,12} = 3.889$	$F_{3,36} = 0.627$	$F_{2,12} = 0.022$	$F_{6,36} = 1.205$	$F_{3,36} = 0.795$	$F_{6,36} = 0.556$
<i>Pycnospora lutescens</i>	$F_{2,12} = 2.858$	$F_{1,12} = 44.555^{**}$ H > U	$F_{1,12} = 1.561$	$F_{2,12} = 0.682$	$F_{2,12} = 1.162$	$F_{1,12} = 1.763$	$F_{2,12} = 0.981$
<i>Early, Late</i>							
Ephemeral forbs ($n = 9$)	$F_{2,12} = 3.263$	$F_{1,12} = 64.001^{**}$ H > U	$F_{2,24} = 1.583$	$F_{2,12} = 2.559$	$F_{4,24} = 0.726$	$F_{2,24} = 1.819$	$F_{4,24} = 0.913$
<i>Mid, Late & Wét</i>							
<i>Indigofera hirsuta</i>	$F_{2,12} = 1.441$	$F_{1,12} = 93.866^{**}$ H > U	$F_{2,24} = 0.112$	$F_{2,12} = 0.408$	$F_{4,24} = 1.840$	$F_{2,24} = 5.559^{*}$	$F_{4,24} = 3.761$
<i>Log; Early, Mid & Late</i>							
Grasses ($n = 6$)	$F_{2,12} = 2.054$	$F_{1,12} = 6.091$	$F_{3,36} = 52.607^{**}$ M & L > W; L > M	$F_{2,12} = 1.714$	$F_{6,36} = 2.822$	$F_{3,36} = 4.457^{*}$	$F_{6,36} = 1.739$
<i>Digitaria breviglumis</i>	$F_{2,12} = 1.687$	$F_{1,12} = 4.529$	$F_{3,36} = 13.395^{**}$ L > W & E	$F_{2,12} = 1.534$	$F_{6,36} = 5.652^{**}$	$F_{3,36} = 2.658$	$F_{6,36} = 1.428$
<i>Heteropogon triticeus</i>	$F_{2,12} = 1.820$	$F_{1,12} = 4.934$	$F_{2,24} = 32.653^{**}$ M & L > E; L > M	$F_{2,12} = 0.908$	$F_{4,24} = 0.560$	$F_{2,24} = 2.472$	$F_{4,24} = 1.339$
<i>Early, Mid & Late</i>							
Non-grass monocots ($n = 3$)	$F_{2,12} = 0.418$	$F_{1,12} = 0.268$	$F_{2,24} = 47.042^{**}$ M & L > W; L > M	$F_{2,12} = 2.527$	$F_{4,24} = 1.654$	$F_{2,24} = 0.217$	$F_{4,24} = 2.073$
<i>Mid, Late & Wét</i>							

log indicates $\log(x + 1)$ transformation was used to rectify heterogeneity of variances; $F_{2,12}$ indicates F -value, denominator d.f., numerator d.f.; F -values without an asterisk are not significantly different at $P > 0.01$; $*P < 0.01$; $**P < 0.001$; *Early & Late*, indicate the subset of seasons of collection used in analysis where data transformation did not resolve variance heterogeneity for other seasons. Results presented from a Scheffé's post-hoc test for soil treatment, fire and season of collection differences. E, early dry season; H, soil heated in oven at 85°C for 45 min; L, late dry season; M, mid dry season; U, untreated soil; W, wet season.

used to detect differences within treatments, with a Bonferroni adjustment of significance values used for multiple comparisons (Sokal & Rohlf 1995).

Where significant variance heterogeneity of one of the seasons of soil collection could not be resolved with data transformations, the repeated measures ANOVA was undertaken using the remaining two seasons. Where the data of more than one season were non-normally distributed and could not be resolved by data transformations, a Friedman ANOVA by ranks was used to analyse seasonal fluctuations. In that instance, a Wilcoxon matched pair test was used to detect differences within treatments, with a Bonferroni adjustment of significance values for multiple comparisons (Sokal & Rohlf 1995).

RESULTS

Early, mid and late dry seasons and wet season 1999 (before and after fire)

The germinable seed bank collected between May 1999 and February 2000 contained 39 species and the total seed bank ranged from 58 to 670 seeds per square metre. Soil heating significantly increased the species richness of seedlings germinating from the seed bank (Fig. 2a; Table 1). Species richness was highest in seed banks collected in the mid and late dry seasons compared to the wet season, and in the late dry season compared to the early dry season. Total density of seedlings germinating from the seed bank was signifi-

cantly increased by soil heating (Fig. 2b; Table 1). There was a significantly higher total seed bank density detected in the early, mid and late dry seasons compared to the wet season, and in the late dry season compared to the early dry season. A significant interaction between soil treatment and season of collection was also demonstrated. The fire treatments had no significant impact on either species richness or density of the germinable seed bank.

The germination of native species, twining perennial forbs, the common twiner *Pycnospora lutescens*, ephemeral forbs, and the common ephemeral *Indigofera hirsuta*, was significantly increased by soil heating (Table 1). Significant interactions between fire and season of soil collection were detected for natives as a group and for the common grass *Digitaria breviflumis*, indicating seed bank density increased following early and late dry season fires (Table 1).

The seed bank density of native species was higher in the mid and late dry seasons than the wet season, and in the late rather than early dry season (Table 1). The seed bank of upright perennial forbs was more abundant in the late dry season rather than the wet season, and that of twining perennial forbs was greater in the early and late dry seasons than the wet season (Table 1). Seed bank density of grasses and non-grass monocots was higher in the mid and late dry seasons than in the wet season, and in the late rather than mid dry season (Table 1). The seed bank of the common grass *D. breviflumis* was more abundant in the late dry season than the wet and early dry seasons, while that of *Heteropogon triticeus* was greater in the late rather than mid dry season, in the mid dry season compared with

Table 2. Results of an independent *t*-test of untreated germinable soil seed bank after early dry season fire (control vs early burnt of July 1999 soil collection) and late dry season fire (control vs late burnt of October 1999 soil collection) at Cape Cleveland, Australia

Species and groups (<i>n</i> = number of species in mid/late)	Mid dry season (d.f. = 4)		Late dry season (d.f. = 4)	
	<i>t</i> -value	<i>P</i> -value	<i>t</i> -value	<i>P</i> -value
Species richness	0.392	NS	2.101	NS
All species (<i>n</i> = 23/20)	1.449	NS	8.308	< 0.001
Native species (<i>n</i> = 18/17)	2.020	NS	6.508	< 0.003
Exotic species (<i>n</i> = 5/3)	0.686	NS	0.134	NS
Subshrubs (<i>n</i> = 1/3)	1.000	NS	1.581	NS
Upright perennial forbs (<i>n</i> = 4/3)	0.898	NS	5.00	< 0.007
Twining perennial forbs (d.f. = 6/6)	1.857	NS	0.585	NS
<i>Glycine tomentella</i>	<i>U</i> = 3.000	NS	0.171	NS
<i>Pycnospora lutescens</i>	1.732	NS	1.067	NS
Ephemeral forbs (<i>n</i> = 5/4)	0.625	NS	1.868	NS
<i>Indigofera hirsuta</i>	<i>U</i> = 3.000	NS	0.179	NS
Grasses (<i>n</i> = 5/2)	2.051	NS	1.743	NS
<i>Digitaria breviflumis</i>	1.600	NS	2.528	NS
<i>Heteropogon triticeus</i>	1.337	NS	0.171	NS
Non-grass monocots (<i>n</i> = 2/2)	0.822	NS	2.530	NS

NS, not significant at *P* > 0.01; *U*, Mann–Whitney *U*-test used for *Indigofera hirsuta* and *Glycine tomentella* July 1999 collected soil seed bank, due to variance heterogeneity.

the early dry season. A significant interaction was detected between soil treatment and season of collection for the seed banks of native species, upright perennial forbs, grasses and *Indigofera hirsuta* (Table 1).

Analyses of the untreated seed bank immediately following the early dry season fire indicated that neither total seed density nor species richness significantly differed between the unburnt control and early dry season burnt blocks (Table 2). However, the late dry season fire significantly increased the total untreated seed bank and that of native species and upright perennial forbs (Table 2), indicating that the late dry season fire released seed from dormancy.

Early, mid and late dry seasons 2000 (the year after fire)

In the samples collected in 2000, the germinable soil seed bank density ranged from 129 to 792 seeds per square metre, with a total of 53 species detected (Fig. 3). The highest germinable seed bank densities documented for individual species were of the native

perennial grasses *Digitaria breviglumis* (350 m⁻² in late burnt, smoked soil collected in the mid dry season) and *Heteropogon triticeus* (142 m⁻², in unburnt, smoked soil collected in the mid dry season); and the native ephemeral forb *Indigofera hirsuta* (192 m⁻², in late burnt, heated soil collected in the late dry season).

The germinable seed bank of subshrubs as a group was significantly higher in the unburnt blocks than blocks burnt in either the early or late dry season of year prior to soil collection (Table 3). Seed bank density of non-grass monocots was significantly higher in control blocks than in those burnt in the late dry season. *Indigofera hirsuta* was the only species with greater germinable seed bank density in soil collected from savanna burnt in the early dry season than in the control blocks, which had remained unburnt for 3 years.

Heat shock significantly increased species richness of germinants, total density of seedlings from the seed bank, and the density of native species, exotic species, subshrubs, ephemeral and twining perennial forbs, and *Indigofera hirsuta*, *Pycnospora lutescens* and *Triumfetta rhomboidea* seed banks (Fig. 3; Table 3). The density of germinants of grasses as a group, and the common

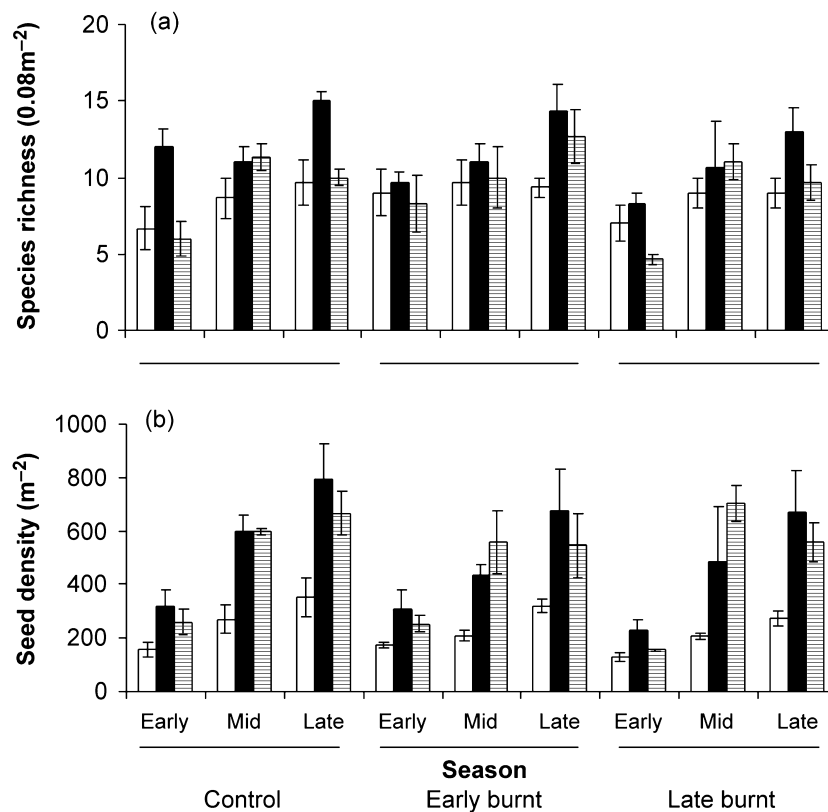


Fig. 3. Mean (± 1 standard error) (a) species richness and (b) total seed density of germinable soil seed bank, collected in eucalypt savanna at Cape Cleveland, between May and October 2000. Soil samples remained untreated (\square); or were heated in an oven at 85°C for 45 min (\blacksquare); or exposed to smoke at ambient temperature for 30 min (\square with diagonal lines). Early, soil collected in the early dry season, i.e. May; Mid, soil collected in the mid dry season, i.e. July; Late, soil collected in the late dry season, i.e. October. Control, sites last burnt in July 1997; Early burnt, sites burnt July 1997 and May 1999; Late burnt, sites burnt July 1997 and October 1999.

Table 3. ANOVA results of fire treatment, soil treatment, and seasonal of collection in germinable soil seed bank collected in the year following fire, between May and October 2000, at Cape Cleveland

Species Group	Fire	Soil treatment	Season	Fire × soil treatment	Fire × season	Soil treatment × season	Fire × soil treatment × season
Species richness	$F_{2,18} = 1.452$	$F_{2,18} = 8.267^*$ H > U	$F_{2,36} = 20.171^{**}$ L > E	$F_{4,18} = 0.514$	$F_{4,36} = 0.786$	$F_{4,36} = 3.250$	$F_{8,36} = 0.765$
All species ($n = 53$) <i>Early & Late</i>	$F_{2,18} = 1.458$	$F_{2,18} = 213.734^{**}$ H > U	$F_{1,18} = 95.182^{**}$ L > E	$F_{4,18} = 0.082$	$F_{2,18} = 0.643$	$F_{2,18} = 6.021^{**}$	$F_{4,18} = 0.098$
Native species ($n = 40$) <i>Early & Late</i>	$F_{2,18} = 0.546$	$F_{2,18} = 10.255^{**}$ H & S > U	$F_{1,18} = 86.145^{**}$ L > E	$F_{4,18} = 0.091$	$F_{2,18} = 0.018$	$F_{2,18} = 4.873$	$F_{4,18} = 0.374$
Exotic species ($n = 13$) <i>log</i>	$F_{2,18} = 3.224$	$F_{2,18} = 7.922^*$ H > U	$F_{2,36} = 13.215^{**}$ M & L > E	$F_{4,18} = 1.234$	$F_{4,36} = 9.083^{**}$	$F_{4,36} = 4.082^*$	$F_{8,36} = 1.986$
Subshrubs ($n = 5$) <i>Early & Late</i>	$F_{2,18} = 28.357^{**}$ U > E & L	$F_{2,18} = 61.928^{**}$ H > U & S	$F_{1,18} = 3.539$	$F_{4,18} = 27.179^{**}$	$F_{2,18} = 8.539^*$	$F_{2,18} = 3.657$	$F_{4,18} = 7.377^{**}$
<i>Triunfetta rhomboidea</i>	$H_{2,18} = 2.498$	$H_{2,18} = 41.822^{**}$ H > U & S	$\chi^2_{2,36} = 21.500^{**}$ L > E				
<i>Non-parametric</i>							
Uprightperennial forbs ($n = 6$)	$F_{2,18} = 0.866$	$F_{2,18} = 9.085^*$ S > U & H	$F_{2,36} = 6.302^*$ L > E	$F_{4,18} = 0.338$	$F_{4,36} = 0.721$	$F_{4,36} = 1.266$	$F_{8,36} = 0.337$
<i>Spermacoe brachystema</i>	$F_{2,18} = 2.496$	$F_{2,18} = 3.751$	$F_{2,36} = 2.800$	$F_{4,18} = 0.751$	$F_{4,36} = 1.798$	$F_{4,36} = 0.494$	$F_{8,36} = 1.531$
Twinning perennial forbs ($n = 12$), <i>log</i>	$F_{2,18} = 2.305$	$F_{2,18} = 15.887^{**}$ H > U & S	$F_{2,36} = 2.760$	$F_{4,18} = 2.374$	$F_{4,36} = 0.451$	$F_{4,36} = 0.453$	$F_{8,36} = 0.318$
<i>Pycnospora lutescens</i>	$F_{2,18} = 0.390$	$F_{2,18} = 9.197^*$ H > U & S	$F_{1,18} = 0.000$	$F_{4,18} = 0.396$	$F_{2,18} = 0.733$	$F_{2,18} = 0.419$	$F_{8,36} = 0.262$
<i>Early & Late</i>							
Ephemeral forbs ($n = 12$) <i>log</i>	$F_{2,18} = 3.512$	$F_{2,18} = 31.243^{**}$ H > U & S	$F_{2,36} = 5.912^*$ L > E	$F_{4,18} = 0.489$	$F_{4,36} = 0.950$	$F_{4,36} = 0.060$	$F_{8,36} = 0.480$
<i>Indigofera hirsuta</i>	$F_{2,18} = 7.161^*$	$F_{2,18} = 55.135^{**}$ H > U & S	$F_{2,36} = 0.619$	$F_{4,18} = 0.632$	$F_{2,18} = 5.484$	$F_{4,36} = 0.136$	$F_{8,36} = 1.879$
<i>Log, Mid & Late</i>	$E > U$						
Grasses ($n = 10$) <i>Early & Late</i>	$F_{2,18} = 0.143$	$F_{2,18} = 16.749^{**}$ S > U & H	$F_{2,36} = 36.856^{**}$ L > E	$F_{4,18} = 0.460$	$F_{2,18} = 3.304$	$F_{4,36} = 5.312$	$F_{8,36} = 0.771$
<i>Digitaria breviglumis</i>	$H_{2,18} = 1.057$	$H_{2,18} = 36.878^{**}$ S > U & H	$\chi^2_{2,36} = 6.433$				
<i>Non-parametric</i>							
Heteropogon contortus	$H_{2,18} = 4.175$	$H_{2,18} = 8.622$	$\chi^2_{2,36} = 6.433$				
<i>Non-parametric</i>							
<i>Heteropogon triticeus</i>	$F_{2,18} = 1.939$	$F_{2,18} = 15.506^{**}$ S > U & H	$F_{2,36} = 6.321^*$ M > L	$F_{4,18} = 1.277$	$F_{4,36} = 0.724$	$F_{4,36} = 4.605^*$	$F_{8,36} = 0.948$
Non-grass monocots ($n = 6$)	$F_{2,18} = 13.167^{**}$ U > L	$F_{2,18} = 0.205$	$F_{2,36} = 31.443^{**}$ L > E & M	$F_{4,18} = 0.518$	$F_{4,36} = 5.573^{**}$	$F_{4,36} = 0.617$	$F_{8,36} = 0.890$
<i>Commelina</i> spp. Mid & Late	$F = 4.657$ $P < 0.023$	$F = 3.909$ $P < 0.039$	$F_{2,36} = 6.293$	$F_{4,18} = 0.548$	$F_{2,18} = 0.832$	$F_{2,18} = 1.353$	$F_{4,18} = 0.353$

Log, $\log(x + 1)$ transformation was used to rectify heterogeneity of variances; $F_{2,12}$ indicates F -value, denominator d.f.; F -values without an asterisk are not significantly different at $P > 0.01$; * $P < 0.01$; ** $P < 0.001$; *Early & Late*, indicate seasons of collection used in analysis where data transformation did not resolve variance heterogeneity for other seasons. *non-parametric*, the non-parametric Kruskal-Wallis ANOVA by ranks used for fire history and soil treatment, and Friedman ANOVA by ranks for seasonal fluctuations, where variance heterogeneity could not be resolved by data. Results from a Scheffe's post-hoc test (Mann-Whitney U -test for Kruskal-Wallis ANOVA and Wilcoxon matched pair test for Friedman ANOVA) of significant differences between soil treatments and soil depths are provided. E, early dry season; H, soil heated in oven at 85°C for 45 min; L, late dry season; M, mid dry season; S, exposure to smoke at ambient temperature for 30 min; U, untreated soil; W, wet season.

grass *Digitaria breviglumis*, declined as a result of soil heat treatment (Table 3).

Exposure to smoke at ambient temperature significantly enhanced the germination of native species, upright perennial forbs, grasses as a group and the common grasses *D. breviglumis* and *H. triticeus* from the seed bank (Table 3).

In the germinable seed bank, the densities of natives, the exotic subshrubs *T. rhomboidea*, upright perennial forbs, ephemeral forbs and grasses were significantly greater in soil collected during the late rather than early dry season (Table 3). The seed bank of exotic species was significantly greater in the mid and late, than early dry season. The seed bank of *H. triticeus* was larger in the mid than late dry season and that of the non-grass monocots was greater during the late dry season than both early and mid dry seasons (Table 3).

Significant interactions were demonstrated between recent fire history and soil treatment for subshrubs and fire history and season of soil collection for exotics, subshrubs and non-grass monocots (Table 3). Total seed bank density, exotic species and *H. triticeus* displayed a significant interaction between soil treatment and season of collection. A significant interaction was also detected between the combination of all three factors in the subshrub seed bank.

DISCUSSION

The germinable soil seed bank of eucalypt savanna at Cape Cleveland was dominated by grasses and forbs, while seed banks of trees and shrubs were scarcely detected. The dominance of herbaceous species in the seed bank has previously been reported in other eucalypt woodlands and forests (Drake 1979; Hodgkinson *et al.* 1980; Vlahos & Bell 1986; McIvor 1987; Clifford *et al.* 1996; Melzer 1996; Odgers 1996; Enright *et al.* 1997; Lunt 1997; Wang 1997; Read *et al.* 2000; Grant & MacGregor 2001; Hill & French 2003). The paucity of tree and shrub seed bank is consistent with the generalization by Higgins *et al.* (2000) that savanna trees produce short-lived seed banks and seedling recruitment may only result when appropriate environmental conditions coincide with seed fall. Most trees at Cape Cleveland drop mature seed at the most appropriate time for germination, that is prior to and during the wet season (Williams 2003). This indicates a lower investment of stored reproductive potential, in the form of seed banks, for the longer-lived trees and shrubs than for shorter-lived herbs. However, the longevity of trees and many shrubs in tropical savanna provides an avenue of population persistence without regular seedling recruitment (Bond & Midgley 2001).

The seed density at Cape Cleveland, ranging from 58 to 792 seeds per square metre, was similar to seed

bank densities documented in southern Queensland eucalypt forests, such as 28–433 seeds per square metre (Drake 1979) and 231–7021 seeds per square metre (Melzer 1996). However the Cape Cleveland seed bank density was low in comparison to other studies in eucalypt communities which have recorded seed density as high as 1360–13 800 seeds per square metre (Hodgkinson *et al.* 1980) and of the annual grasses *Sorghum intrans* and *Schizachyrium fragile*, that dominate some savannas of Cape York and the Northern Territory and which produce over 2000 seeds per square metre (Andrew 1986; Crowley & Garnett 1999).

The seed bank density at Cape Cleveland is also lower than documented in grazed pastures in the Townsville region. Seed banks ranging from 3600 to 11 000 seeds per square metre were recorded in a tropical savanna that was cleared and over-sown with exotic grasses and legumes at Lansdown, approximately 50 km to the south-west of Cape Cleveland (McIvor 1987). Densities of 210–9770 seeds per square metre were documented in native pastures near Collinsville, approximately 150 km to the south of Cape Cleveland (McIvor & Gardener 1994). However, the bulk of seed at Lansdown was provided by a few, mainly exotic, species (McIvor 1987). Similarly, the seed bank at Collinsville was dominated by exotic species, such as *Bothriochloa pertusa*, although some natives, such as *Eragrostis sororia* and *Cyperus iria* which do not grow at Cape Cleveland, were also abundant in the Collinsville seed bank (McIvor & Gardener 1994).

The Cape Cleveland seed bank contained 19 species common to McIvor (1987) Lansdown seed bank and seven species common to McIvor and Gardener (1994) Collinsville seed bank. All of these species at Lansdown produced average seed banks of less than 60 seeds per square metre, with most less than 10 seeds per square metre. The maximum seed density in any sample for the shared species at Collinsville was *Vernonia cinerea*, with 400 seeds per square metre. Native perennial grasses produced low seed bank densities in all of the Lansdown, Collinsville and Cape Cleveland studies. This suggests that the low to moderate seed bank density documented at Cape Cleveland is typical for the species that are present and that native perennial grasses in particular do not generally produce dense seed banks in the tropical savannas in the Townsville region.

The exposure to heat shock or smoke significantly increased the germination of several common species and species groups, providing indirect evidence that fire releases seed from dormancy. Heat shock has proved effective in promoting the germinable soil seed bank of a range of fire-prone communities across Australia, demonstrating its value as a treatment for assessing soil seed bank composition and its

importance in understanding seed dormancy mechanisms (Warcup 1980; Hopkins & Graham 1984; Skull 1992; Enright *et al.* 1997; Williams 2000; Hill & French 2003). Smoke has been reported to increase germination from the soil seed bank in a range of eucalypt woodland flora, including grasses and forbs (Enright *et al.* 1997; Roche *et al.* 1998; Lloyd *et al.* 2000; Read *et al.* 2000). However this is the first report of the positive stimulus of smoke on the germination of the widespread tropical grass *H. triticeus*.

Seasonal fluctuations were detected in the germinable soil seed bank, increasing through the dry season to a maximum, for many species, in the late dry season. The seasonal dynamics of seed banks were consistent with the timing of annual seed production at Cape Cleveland (Williams 2003). Peak seed production occurred during the early to mid dry season, so that the accumulation of seeds reached a maximum by the end of the dry season. These seasonal patterns correspond with McIvor's (1987) Lansdown study.

Soil seed banks of eucalypt forests in south-eastern Queensland display less distinct seasonal patterns and show strong variation among species (Drake 1979; Clifford *et al.* 1996; Melzer 1996; Odgers 1999). This lack of seasonality in seed banks of south-east Queensland may be due to the less distinct wet and dry seasons compared to north-eastern Queensland.

Ephemeral forbs, including *I. hirsuta*, were present in the seed bank during the third year after fire, when there were very few standing plants (Williams *et al.* 2003a). This highlights the importance of soil seed banks for population persistence of these species.

Recent fire history had limited effects on seed bank density in general, with two species groups being more abundant in longer unburnt savanna, and the ephemeral forb, *I. hirsuta*, more abundant in savanna burnt during the early dry season of the year prior to collection. This suggests the seed banks of most species are capable of being replenished in the year following burning.

The abundance of several species in eucalypt savanna of north-eastern Australia is promoted by fire, especially fires in the late dry season (Williams *et al.* 2003a). The results from this paper and Williams *et al.* (2003b, 2004) indicate that fire plays a crucial role in breaking seed dormancy in a range of savanna species and that late dry season fires provide a greater stimulus than early dry season fires for releasing seed from dormancy. This paper also shows the seasonal fluctuations in the seed bank can result in the availability of more seeds during the late dry season. Therefore the reason that late dry season fires promote the greatest increase in the abundance of some grasses and forbs (Williams *et al.* 2003a) may be due to both the greater dormancy-breaking stimulus of the higher intensity late fires (Williams *et al.* 2003b, 2004) and because more

seeds are available at that time of year to be affected by fire.

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