

Effect of fire regime on plant abundance in a tropical eucalypt savanna of north-eastern Australia

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Abstract Changes in plant abundance within a eucalypt savanna of north-eastern Australia were studied using a manipulative fire experiment. Three fire regimes were compared between 1997 and 2001: (i) control, savanna burnt in the mid-dry season (July) 1997 only; (ii) early burnt, savanna burnt in the mid-dry season 1997 and early dry season (May) 1999; and (iii) late burnt, savanna burnt in the mid-dry season 1997 and late dry season (October) 1999. Five annual surveys of permanent plots detected stability in the abundance of most species, irrespective of fire regime. However, a significant increase in the abundance of several subshrubs, ephemeral and twining perennial forbs, and grasses occurred in the first year after fire, particularly after late dry season fires. The abundance of these species declined toward prefire levels in the second year after fire. The dominant grass *Heteropogon triticeus* significantly declined in abundance with fire intervals of 4 years. The density of trees (>2 m tall) significantly increased in the absence of fire for 4 years, because of the growth of saplings; and the basal area of the dominant tree *Corymbia clarksoniana* significantly increased over the 5-year study, irrespective of fire regime. Conservation management of these savannas will need to balance the role of regular fires in maintaining the diversity of herbaceous species with the requirement of fire intervals of at least 4-years for allowing the growth of saplings >2 m in height. Whereas late dry season fires may cause some tree mortality, the use of occasional late fires may help maintain sustainable populations of many grasses and forbs.

Key words: eucalypts, fire regime, northern Australia, plant abundance, savanna.

INTRODUCTION

Tropical savannas that are dominated by eucalypts (*Eucalyptus* and *Corymbia*, Myrtaceae) cover extensive areas of northern Australia and are prone to fires during the dry season, between May and November (Mott *et al.* 1985; Williams *et al.* 2002a). Fire regimes have been demonstrated to affect primarily plant species abundance rather than generating significant species replacement in these communities (Bowman *et al.* 1988; Fensham 1990; Lonsdale & Braithwaite 1991; Russell-Smith *et al.* in press; Williams *et al.* in press).

The abundance of savanna species is influenced by fire frequency. Some species, such as the annual grass *Sorghum stipoides* and the sprouting shrub *Grevillea goodii*, increase in abundance with annual burning, whereas others, such as the perennial grass *Alloteropsis semialata* and the obligate seeder shrub *Acacia holosericea*, are more abundant after longer fire intervals

(Russell-Smith *et al.* in press; Williams *et al.* in press). The density of some savanna trees (>2 m tall), especially non-eucalypts such as *Acacia* spp., *Melaleuca viridiflora* and other broad-leaved species, can increase with fire intervals of 3 or more years (Bowman *et al.* 1988; Fensham 1990; Bowman & Panton 1995; Crowley & Garnett 1998; Williams *et al.* 1999). Increasing tree density with fire-free intervals of several years has been documented in some eucalypts, including *Eucalyptus tetrodonta*, whereas the density of *E. miniata* remained stable after 21 years of fire exclusion (Fensham 1990; Bowman & Panton 1995; Russell-Smith *et al.* in press).

As progressive curing of grasses through the dry season results in higher intensity fires in the late than in the early dry season (Gill *et al.* 1996), the timing and intensity of fire are interrelated factors that can affect plant abundance. The mortality of many woody species is directly related to fire intensity (Williams *et al.* 1999). The season of fire can have important implications on plant responses depending on whether it occurs prior to seed set, or whether fire coincides with periods of plant growth, because wet season burning can reduce

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the abundance of some perennial and annual species (Stocker & Sturtz 1966; Williams & Lane 1999). Late dry season fires can promote the abundance of some grasses, such as *Heteropogon contortus*, whereas earlier dry season fires may promote others, including *Themeda triandra* (Shaw 1957; Walker *et al.* 1989; Orr *et al.* 1991). The abundance of many woody and herbaceous species has also been correlated with climatic, edaphic and topographic variables (Fensham 1990; Williams *et al.* 2002a).

The fire response at a community level can be assessed by examining different plant growth form groups. These groups often possess differing traits to survive in a regularly burnt community, such as bud protection from thick bark in trees or root suckering by some subshrubs and herbs (Whelan 1995). Data are most prevalent for dominant woody and grass species of tropical savannas than other growth forms, which may respond differently to fire regime. For example, some ephemeral forbs of sandstone shrubby communities are most abundant following fire (Russell-Smith *et al.* 2002; Williams *et al.* 2002b).

Much of the research into fire effects on the flora of Australian tropical savannas has centred on the monsoonal regions of the Northern Territory, particularly savannas dominated by annual grasses such as *Sorghum* spp. (Bowman *et al.* 1988; Fensham 1990; Williams & Lane 1999; Williams *et al.* 1999) and Cape York Peninsula (Crowley & Garnett 1998, 2001). In the present paper we examine the influence of fire regime on plant abundance in a tropical savanna of north-eastern Australia, with a ground layer dominated by perennial grasses and forbs. Questions that are addressed are:

1. Does fire regime influence plant abundance?
2. Does fire regime influence species richness at the 1-m² and 100-m² scales?
3. Are the results similar to those observed in other regions of northern Australia?

METHODS

Study site

The influence of fire regime on plant abundance in eucalypt savanna in north-eastern Australia was assessed within a 10-ha site at Cape Cleveland, Bowling Green Bay National Park, approximately 25 km east of Townsville (19°16'30''S, 147°02'30''E). Townsville experiences summer wet seasons, with 78% of the 1143 mm mean annual rain falling between December and March. Rainfall records for Cape Cleveland during the study period (1997–2001), recorded by the Australian Bureau of Meteorology at a location approximately 10 km south of the study site, are provided in Fig. 1. The annual rainfall in Townsville was above the average during 1997, 1998 and 2000, and below average in 1999 and 2001 (Fig. 1).

The study site is on level ground at approximately 5 m a.s.l. It was grazed by a low density of free-ranging cattle from the early 1900s to the 1970s (C. Adams. pers. comm., 1997). Unpublished Queensland Parks and Wildlife Service records indicate that the eucalypt savanna of Cape Cleveland has a history of regular fires, with intervals ranging from one to five years and typically occurring between May to December. The

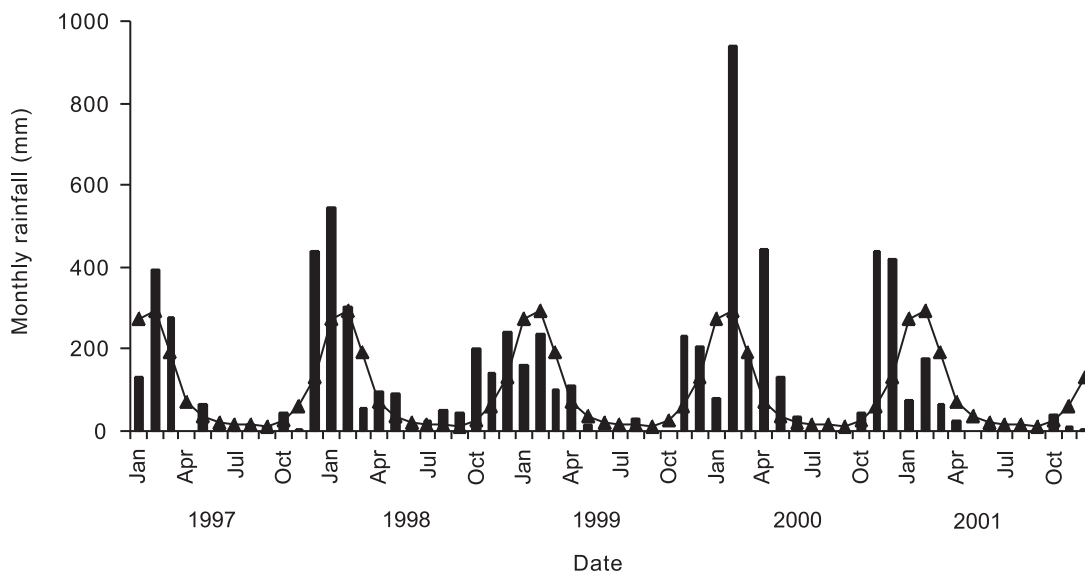


Fig. 1. Monthly rainfall at Cape Cleveland between 1997 and 2001, recorded by the Bureau of Meteorology 10 km south of the study site (columns), and mean monthly rainfall for Townsville, 25 km west of the study site (▲).

trial site was burnt prior to the present study by unplanned fires in December 1990 and December 1994.

Three experimental fire regimes were imposed across the Cape Cleveland site between 1997 and 2001:

1. Control: savanna burnt mid-dry season (July) 1997 only.
2. Early burnt: savanna burnt mid-dry season 1997 and early dry season (May) 1999.
3. Late burnt: savanna burnt mid-dry season 1997 and late dry season (October) 1999.

The entire 10-ha study site was intentionally burnt in the mid-dry season of 1997 (Table 1), after the establishment of permanent survey plots (see below). The fuel load was estimated from 15 0.5-m² samples prior to the fire and intensity was calculated from the average rate of fire spread measured at 10 points across the 10-ha site. This initial mid-dry season fire was undertaken across the entire site to provide prefire floristic data, which was particularly valuable for plots that remained unburnt for the remainder of the study.

Following the July 1997 fire, the 10-ha 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. A 20-m wide buffer zone was established along a roadside boundary, perpendicular to the main blocks, and was burnt annually during the dry season from 1997 to 2000, to create a fire break. Each fire treatment was imposed on three of the nine 1-ha blocks. The blocks were allocated to treatments using a randomized block design. One replicate of each treatment was randomly allocated a position in each of blocks 1–3, 4–6 and 7–9. Blocking was undertaken rather than a full randomization to account for a floristic gradient across the study site detected in initial field inspections, prior to establishing plots in 1997. That is, a few common species, most notably *Eucalyptus platyphylla* and *Heteropogon contortus* (taxonomy follows Henderson 2002), occurred in greatest abundance in blocks 7–9. Visual assessment of surface soil samples detected no corresponding textural gradient in the topsoil.

After the 1999 floristic abundance survey, the three 1-ha blocks assigned to the early burnt treatment were burnt simultaneously in May 1999, and those assigned to the late burnt treatment were burnt simultaneously in October 1999 (Table 1). Fuel loads were estimated prior to burning from three 0.5-m² samples, in each 1-ha block. Fire intensity was calculated from the average rate of fire spread measured at two or three points in each 1-ha block.

No cattle were present within the trial area during the study, although native herbivores, specifically agile wallabies (*Macropus agilis*), were present throughout the 5 years. The moderate time span of the present study (5 years) may limit the ability to detect some fire effects. However, the fire responses of herbaceous

Table 1. Characteristics of fires implemented in eucalypt savanna of Cape Cleveland

Fires	Time of ignition and date of fire	Temperature at ignition (°C)	Relative humidity at ignition (%)	Wind speed at ignition (km h ⁻¹)	Fuel load (t ha ⁻¹)	Intensity (kW m ⁻¹)
Mid dry season 1997	13.00 hours, 15 July	25	54	8	10.5	1176
Early dry season 1999	10.30 hours, 24 May	27.5	70	<5	8.9	1534
Late dry season 1999	08.10 hours, 13 October	28	53	10	11.7	5511

species, detected over 21 years in eucalypt savanna at Munmarlary, Northern Territory, were generally evident within the initial 5 years (Russell-Smith *et al.* in press).

Plot layout

Changes in species abundance were assessed using five annual surveys (1997–2001) of permanently marked plots, as repeat measure surveys have been successful in detecting significant floristic dynamics in response to fire regimes in savannas of the Northern Territory (Hoare *et al.* 1980; Russell-Smith *et al.* in press; Williams *et al.* in press). Four randomly located 100-m² plots were used to sample each of the nine 1-ha blocks, providing a total of 36 plots. This sampling effort was designed to assess the herbaceous layer effectively and hence most species within the community, although it is acknowledged that larger plots may be more useful for documenting changes in tree densities.

Plant measures

The abundance of all species in each plot was recorded using a stratified random sampling technique involving 20 throws of a 1-m² quadrat from 20 points of equal spacing around the plot perimeter. The presence of all species within (or growing across in the case of twining forbs) each quadrat was recorded. Thus plant abundance for all species was based on a frequency score out of 20 per plot in each annual survey.

Additional species in each plot that were not present within the 20 quadrats were recorded to document species richness at the 100-m² scale. The number of trees >2 m in height was also counted, and their circumference at breast height measured, in each of the 36 100-m² plots during the annual surveys. All of the 36 plots were surveyed annually for 5 years (1997–2001), in the late wet to early dry seasons (March to May) to ensure detection of annual species. Thus the five annual surveys provided a total of 180 survey records.

Statistical analyses

Species richness and abundance

The unit of comparison for this experiment is the fire regime encompassing the 5 years of study, with some assessment also made of immediately before and after the 1999 fire season treatments. No analyses were undertaken on plant responses to the 1997 fire in isolation, which was not replicated. This experimental

design replicates fire regimes of mixed intervals, intensity and season, typical of the Townsville region, in contrast to several previous savanna fire trials that assessed repeated fixed fire treatments (e.g. successive annual early dry season fires), and did not reflect contemporary fire regimes (Russell-Smith *et al.* in press).

Analyses were undertaken to examine the effect of fire regime on species richness (at 1-m² and 100-m² scales), individual species and species groups. Species were grouped according to growth form to aid the interpretation of community fire response, and their abundance scores were summed to provide the abundance of each growth form. Eight growth form groups were derived by separating woody species into three groups: (i) subshrubs (<2 m in height at maturity), (ii) woodland trees and shrubs, and (iii) rainforest trees and shrubs; and herbaceous species into five groups: (i) grasses, (ii) all non-grass monocotyledons, (iii) twining perennial forbs, (iv) upright perennial forbs, and (v) ephemeral forbs. The latter typically complete their life cycle within a year, although a few individuals of these species may survive into a second year.

In addition to the eight growth form groups, species were also classified as 'natives' or 'exotics' as identified by Henderson (2002) to assess whether exotic species were advantaged over natives by particular fire regimes. Twenty-four species, out of the total 118, were present in at least 1% of quadrats and were individually examined for evidence of a fire response.

The short-term effect of the 1999 fire season treatments on species richness, and the abundance of species groups and common species, were analysed using an analysis of covariance (ANCOVA) performed on the 2000 survey data using the 1999 prefire data as a covariate (Zar 1999) to assess the change before and immediately after the fire treatments (unburnt control, early and late dry season burnt).

To provide an assessment of the overall effect of fire regime from 1997 to 2001, an ANCOVA was performed on the 2001 survey data using the 1997 prefire data as a covariate. This allowed the assessment of changes over the course of the 5-year study, by analysing the differences at the end of the trial (2001) once adjusted for differences present at the start of the trial (1997).

In each of these analyses, the four 100-m² plots in each of the three replicate 1-ha blocks were considered nested within the fire treatments. The nested plots were treated as random factors, with fire treatments as fixed factors. Where the variation among treatment replicates of separate blocks was low ($P > 0.25$), the block replicates were pooled to increase the power of the tests (Underwood 1997).

The ANOVA assumptions of homogeneity of variances among treatments were checked using Cochran's test (Underwood 1997) and, where significant differ-

ences were detected, analyses were performed on log ($x + 1$) transformed data. Where data transformation did not resolve significant heterogeneity of variances, non-parametric tests were used. Separate Kruskal–Wallis ANOVA by ranks tests were performed to check for significant fire treatment differences in each of the 1999, 2000 and 2001 surveys. This enabled an assessment of pre-existing differences as well as differences in the first and second years postfire. No nesting option is available in this analysis, and therefore all 100-m² plots were treated as independent replicates. Where a significant difference was found, a Mann–Whitney *U*-test was used as a post hoc test, with a Bonferroni adjustment of the significance level for multiple comparisons (Sokal & Rohlf 1995).

The change in overall abundance of exotic and native species over the study period was calculated and a Mann–Whitney *U*-test was used to examine the statistical significance of differences between these two species groups. The large number of separate analyses from the same species abundance data sets increased the probability (alpha) of incorrectly rejecting the null hypothesis (Type I error; Ter Braak & Wiertz 1994). To account for this, a conservative probability level ($P < 0.01$) was set for the species abundance analyses. Although this increases the probability of incorrectly rejecting a significant result, it is less likely to result in an inappropriate claim of significant fire effects, enabling greater confidence when ascribing a fire response (Zar 1999).

Tree density and basal area

The influence of fire regime on the density and basal area of trees (>2 m in height) was analysed for all trees combined, and the four most abundant species. A repeated measures ANOVA was performed for fire treatment, with three levels (control, early burnt and late burnt) and year of survey as the repeated measure. The repeated measure factor 'year' contained five levels (1997–2001) for the tree density analyses and four levels (1998–2001) for basal area analyses, as circumference measurements were only available from 1998 to 2001. Due to the small number of trees within each of the 100-m² plots, data from the four 100-m² plots were pooled for each replicate 1-ha block to reduce variance. A significance level of $P < 0.05$ was used for assessing fire regime effects on tree density and basal areas.

RESULTS

Species richness and abundance

Fire regime did not significantly affect species richness at the 100-m² scale (Table 2). However, in the first year

following the 1999 fires, species richness at the 1-m² scale progressively increased from the unburnt control plots, to the early dry season burnt plots, to the highest in the late dry season burnt plots. There were no differences in species richness at the 1-m² scale by 2001.

The abundance of several common species and growth form groups, especially grasses, twining perennial forbs and ephemeral forbs, increased immediately after fire but declined by 2001 (Table 2). The abundance of both native and exotic species fluctuated over the 5 years, and was higher in 2001 than 1997. The mean percentage increase of combined exotic species (668%, SE 98) was significantly greater than that of natives (130%, SE 4; $U_{70} = 142.000$; $P < 0.001$). There was no significant fire effect on the abundance of the native species as a whole. Late dry season fires were associated with an increased abundance of combined exotic species in 2000. This difference disappeared by 2001.

Woodland trees and shrubs as a group showed no significant differences in abundance among fire treatments using the 1-m² quadrat-based abundance measure. Neither were any significant differences detected in the common trees *Corymbia clarksoniana* and *Planchonia careya*. Likewise, no significant effect could be detected for rainforest trees and shrubs, as a group, or the common rainforest tree *Canarium australianum*.

Subshrubs, as a group, did not differ in abundance among fire treatments. However, the late dry season fires of 1999 significantly enhanced the abundance of the common subshrub *Breynia oblongifolia* over unburnt controls. This difference was not apparent by 2001. There was a greater abundance of the exotic subshrub *Triumfetta rhomboidea* in both unburnt control and late dry season burnt plots, than in early dry season burnt plots in 2000; however, this difference was no longer apparent by 2001.

Upright perennial forbs as a group showed no significant fire effects. A short-term increase in the abundance of twining perennial forbs was evident following the late dry season fires relative to unburnt control plots in 2000. The abundance of the dominant twiner *Galactia tenuiflora* was significantly enhanced by burning and was the only species to show a significantly greater enhancement after early rather than late dry season burning. The exotic twining perennial forb *Passiflora foetida* was significantly more abundant after late dry season fires than early dry season fires or unburnt controls, in both 2000 and 2001.

Ephemeral forbs, as a group, showed a pulse of abundance following fire with greater abundance in the first year after both early and late dry season fires compared with unburnt control plots. Few ephemeral forbs were present in the 2001 survey and consequently there were no treatment differences in that year. There

Table 2. Mean (SE) species richness and abundance of species groups, and common species showing a significant fire response, and statistical results, for fire regime treatments in eucalypt savanna at Cape Cleveland

Dependent factors	Regime	Species richness and annual abundance means for each treatment (n = 12)					Statistical results	
		1997	1998	1999	2000	2001	2000 ANCOVA of fire regime (1997 data as covariate)	2001 ANCOVA of fire regime (1999 data as covariate)
Species richness per 100 m ²	C	29.25 (1.05)	36.92 (1.10)	36.08 (1.07)	35.92 (0.93) ^a	37.17 (0.98) ^z	$F_{2,6} = 1.104$	$F_{2,6} = 0.545$
	E	31.00 (1.72)	34.75 (1.41)	35.33 (1.50)	37.25 (1.90) ^a	35.83 (1.85) ^z		
Species richness per 1 m ²	L	30.08 (1.27)	35.17 (1.27)	34.75 (1.27)	39.75 (1.49) ^a	35.50 (4.95) ^z	Kruskal–Wallis 2000 $H_2 = 160.97^{**}$ $F_{2,6} = 5.820$ Log, pooled $F_{2,6} = 25.341^{**}$ Pooled $F_{2,6} = 4.776$ Log, pooled $F_{2,6} = 2.976$ Pooled $F_{2,6} = 1.177$ Log, pooled $F_{2,6} = 5.660^*$ Log, pooled $F_{2,6} = 9.243^*$ Pooled $F_{2,6} = 0.083$ Pooled $F_{2,6} = 0.83$ Pooled $F_{2,6} = 0.785$	
	C	4.68 (0.09)	7.75 (0.16)	6.92 (0.12)	6.27 (0.11) ^a	6.54 (0.12) ^z		
	E	4.44 (0.10)	7.33 (0.14)	7.20 (0.13)	7.94 (0.15) ^b	6.59 (0.12) ^z		
	L	4.60 (0.09)	7.76 (0.14)	6.78 (0.13)	9.22 (0.18) ^c	7.25 (0.13) ^y		
Native species	C	84.08 (2.74)	141.42 (8.35)	112.08 (6.45)	99.42 (6.62) ^a	103.67 (6.23) ^z	Kruskal–Wallis 2001 $H_2 = 24.33^{**}$ $F_{2,6} = 0.143$	
	E	80.75 (4.46)	135.33 (5.87)	117.58 (6.22)	133.83 (8.73) ^a	107.42 (5.25) ^z		
	L	85.33 (4.17)	138.83 (7.02)	109.92 (9.42)	147.83 (12.44) ^a	111.25 (7.52) ^z		
	C	9.50 (2.17)	11.83 (1.56)	26.25 (2.61)	25.83 (2.23) ^a	27.25 (2.68) ^z		
Exotic species	E	6.92 (1.96)	10.42 (2.25)	26.08 (3.15)	22.83 (2.60) ^a	24.08 (2.39) ^z	Log, pooled $F_{2,6} = 25.341^{**}$ Pooled $F_{2,6} = 4.776$ Log, pooled $F_{2,6} = 2.976$ Pooled $F_{2,6} = 1.177$ Log, pooled $F_{2,6} = 5.660^*$ Log, pooled $F_{2,6} = 9.243^*$ Pooled $F_{2,6} = 0.083$ Pooled $F_{2,6} = 0.785$	
	L	6.75 (2.34)	15.58 (4.53)	26.17 (3.88)	37.08 (4.52) ^b	33.58 (3.01) ^z		
	C	12.08 (1.37)	9.08 (1.32)	11.58 (1.52)	10.33 (1.27) ^a	8.50 (2.06) ^z		
	E	10.08 (1.77)	9.42 (1.81)	9.083 (1.71)	7.42 (1.38) ^a	5.667 (1.60) ^z		
Woodland trees and shrubs	L	10.33 (1.86)	9.92 (1.56)	8.33 (1.38)	10.25 (1.83) ^a	7.67 (1.01) ^z	Kruskal–Wallis 2000 $H_2 = 12.922^*$ Kruskal–Wallis 2001 $H_{2,6} = 7.651$	
	C	3.50 (1.10)	3.42 (0.81)	4.20 (0.73)	4.08 (0.91) ^a	3.00 (0.75) ^z		
	E	2.00 (0.94)	1.83 (0.73)	1.83 (0.80)	2.25 (0.91) ^a	1.75 (5.24) ^z		
	L	4.08 (1.42)	4.67 (1.25)	4.08 (1.31)	5.50 (1.26) ^a	4.67 (1.38) ^z		
Rainforest trees and shrubs	C	6.75 (1.01)	9.33 (1.96)	8.17 (1.64)	7.92 (1.64) ^a	7.92 (1.45) ^z	Log, pooled $F_{2,6} = 2.976$ Pooled $F_{2,6} = 1.177$ Log, pooled $F_{2,6} = 5.660^*$ Log, pooled $F_{2,6} = 9.243^*$ Pooled $F_{2,6} = 0.083$ Pooled $F_{2,6} = 0.785$	
	E	5.17 (1.15)	6.67 (1.41)	7.33 (1.79)	7.92 (1.60) ^a	7.92 (1.67) ^z		
	L	6.50 (1.71)	10.0 (1.11)	10.33 (0.95)	13.17 (1.59) ^a	13.0 (1.40) ^z		
	C	3.58 (0.97)	4.50 (1.18)	1.67 (0.43)	1.00 (0.33) ^a	1.17 (0.35) ^z		
<i>Breyenia oblongifolia</i>	E	2.42 (0.84)	2.50 (0.87)	1.25 (0.49)	3.42 (1.05) ^{ab}	3.08 (1.14) ^z	Kruskal–Wallis 2000 $H_2 = 12.922^*$ Kruskal–Wallis 2001 $H_{2,6} = 7.651$	
	L	4.58 (1.16)	5.25 (1.11)	2.58 (0.89)	4.25 (0.97) ^b	3.00 (0.67) ^z		
	C	0.92 (0.34)	2.08 (0.53)	3.58 (0.92)	4.33 (1.15) ^a	4.58 (0.89) ^z		
	E	0.58 (0.29)	1.58 (0.96)	3.42 (1.23)	1.42 (0.80) ^b	1.67 (0.75) ^z		
<i>Triumfetta rhomboidea</i>	L	0.67 (0.19)	2.08 (0.73)	5.08 (1.32)	4.58 (0.74) ^a	5.50 (0.97) ^z	Log $F_{2,6} = 1.153$	
	C	2.92 (0.92)	9.42 (1.75)	6.17 (1.39)	6.25 (6.25) ^a	5.08 (0.93) ^z		
	E	3.25 (0.62)	8.17 (1.87)	8.19 (1.52)	10.08 (1.71) ^a	4.75 (1.01) ^z		
	L	3.67 (1.26)	8.17 (2.32)	6.67 (2.52)	9.42 (2.51) ^a	5.42 (1.66) ^z		
Upright perennial forbs	C	24.17 (2.63)	36.67 (3.32)	46.25 (3.82)	36.50 (3.00) ^a	43.08 (2.90) ^z	Log $F_{2,6} = 1.153$	
	E	26.17 (2.66)	37.42 (3.07)	52.42 (3.17)	48.83 (3.53) ^b	47.92 (3.22) ^z		
	L	21.25 (2.06)	34.67 (3.18)	41.92 (2.37)	49.08 (3.40) ^b	49.17 (2.94) ^z		
	C	6.58 (1.69)	9.25 (1.86)	7.83 (1.70)	4.58 (1.23) ^a	5.50 (1.20) ^z		
Twining perennial forbs	E	11.25 (1.75)	14.17 (1.69)	12.83 (1.63)	14.50 (1.85) ^b	11.17 (1.42) ^z	Kruskal–Wallis 2000 $H_2 = 12.922^*$ Kruskal–Wallis 2001 $H_{2,6} = 7.651$	
	L	7.58 (1.72)	10.83 (1.70)	8.58 (1.50)	9.00 (1.58) ^c	9.58 (1.55) ^z		
	C	5.33 (1.57)	6.08 (1.19)	10.58 (1.29)	8.58 (0.75) ^a	10.25 (0.83) ^z		
	E	3.92 (1.55)	4.67 (0.86)	8.83 (1.22)	9.75 (0.87) ^a	12.75 (1.01) ^z		
<i>Galactia tenuiflora</i>	L	3.08 (1.77)	4.92 (0.96)	8.33 (1.06)	16.42 (0.87) ^b	16.50 (0.84) ^y	Log, pooled $F_{2,6} = 8.428^*$	
	C							
<i>Passiflora foetida</i>	L						Log, pooled $F_{2,6} = 8.428^*$	
	C							

Table 2. (continued)

Dependent factors	Regime	Species richness and annual abundance means for each treatment (n = 12)				Statistical results	
		1997	1998	1999	2000	2001	2000 ANCOVA of fire regime (1997 data as covariate) 2001 ANCOVA of fire regime (1999 data as covariate)
Ephemeral forbs	C	1.42 (0.51)	19.75 (3.83)	2.75 (0.98)	1.33 (0.98) ^a	1.33 (0.50) ^z	Log $F_{2,6} = 41.117^{**}$ $F_{2,6} = 1.715$
	E	1.50 (0.36)	25.25 (2.84)	5.75 (1.52)	17.25 (3.74) ^b	3.17 (0.78) ^z	
	L	1.59 (0.79)	23.58 (2.99)	4.25 (1.12)	27.17 (4.67) ^b	1.25 (0.52) ^z	
<i>Indigofera hirsuta</i>	C	0.33 (0.22)	9.67 (1.83)	0.00 (0.00)	0.17 (0.11) ^a	0.08 (0.08) ^z	Kruskal-Wallis 2000 $H_{2,6} = 25.308^{**}$ $H_{2,6} = 6.049$
	E	0.83 (0.27)	13.92 (1.08)	0.83 (0.32)	7.25 (1.39) ^b	0.50 (0.15) ^z	
	L	0.17 (0.11)	11.33 (1.48)	0.08 (0.08)	12.50 (2.17) ^b	0.17 (0.11) ^z	
Grasses	C	35.33 (1.61)	38.67 (2.23)	44.17 (2.18)	37.5 (1.86) ^a	38.17 (2.13) ^z	Pooled $F_{2,6} = 8.55^{*}$ $F_{2,6} = 2.790$
	E	30.75 (1.99)	34.75 (2.37)	40.0 (2.5)	40.08 (2.42) ^{ab}	40.17 (2.02) ^z	
	L	33.33 (1.59)	33.83 (1.66)	38.92 (2.56)	43.92 (2.7) ^b	43.08 (2.04) ^z	
<i>Heteropogon triticeus</i>	C	16.58 (1.25)	18.16 (0.90)	18.50 (0.79)	13.83 (1.30) ^a	9.75 (0.90) ^z	Kruskal-Wallis 2000 $H_{2,6} = 7.988$ $H_{2,6} = 13.884^{**}$
	E	17.42 (1.48)	19.00 (1.00)	19.25 (0.66)	18.83 (0.99) ^b	17.92 (1.04) ^y	
	L	14.58 (2.50)	15.25 (2.30)	15.33 (2.28)	15.00 (2.36) ^{ab}	12.50 (2.11) ^{yz}	
Non-grass monocots	C	7.42 (1.5)	26.92 (2.17)	14.83 (1.81)	21.33 (2.59) ^a	23.83 (1.53) ^z	Log, pooled $F_{2,6} = 0.110$ $F_{2,6} = 0.848$
	E	8.75 (1.81)	22.25 (2.75)	18.92 (1.25)	22.83 (1.97) ^a	20.17 (1.9) ^z	
	L	11.5 (1.47)	29.58 (2.28)	21.58 (2.3)	26.42 (3.69) ^a	20.67 (2.37) ^z	

Common species are listed under relevant growth form groups.

Regime: C, control, burnt July 1997 only; E, burnt July 1997 and early dry season 1999; L, burnt July 1997 and late dry season 1999.

Significantly different treatments for the separate 2000 and 2001 ANCOVA at $P < 0.01$ are indicated by different superscript lower-case letters.

Statistical results: $F_{2,6}$ indicates F value, denominator d.f., numerator d.f.; F and H values: $^{*}P < 0.01$; $^{**}P < 0.001$; 'log': log ($x + 1$) transformation used to rectify heterogeneity of variances; 'pooled': block P value > 0.25 and replicates pooled; 'block': significant block effect at $P < 0.01$; 'Kruskal-Wallis': non-parametric Kruskal-Wallis ANOVA by ranks test used instead of parametric ANOVA, where variance heterogeneity was unresolved.

was significantly greater abundance of the ephemeral forb *Indigofera hirsuta* in early and late burnt plots than unburnt controls in 2000.

The grasses, as a group, were significantly more abundant in late dry season burnt plots than unburnt controls in 2000. In 2001, the dominant grass *Heteropogon triticeus* was significantly more abundant in early dry season burnt plots than control plots, which had remained unburnt for 4 years by that time. No significant fire effects were detected for the non-grass monocots.

Tree density and basal area

Total density of trees (>2 m in height) increased between 1997 and 2001 ($F_{4,24} = 4.93$; $P < 0.01$) with a significant interaction between fire and year (Fig. 2; $F_{8,24} = 2.507$; $P < 0.05$). Tree density increased in plots that remained unburnt after 1997, but was stable or declined slightly in early and late burnt sites after the 1999 fires. No statistically significant differences among fire treatments, or year of survey, were found for any of the four most abundant trees over the 5 years of investigation.

There were no significant fire effects on tree basal area (Fig. 3; $P > 0.05$). This was because the increase in tree density resulted from the growth of saplings above 2 m in height, which added little to the overall basal area compared with the larger trees. The basal area of the dominant tree *Corymbia clarksoniana* significantly increased over the course of the study in all treatments (Fig. 3; $F_{3,18} = 5.15$; $P < 0.01$). No other statistically significant differences in basal area were detected for the four most abundant trees ($P > 0.05$).

DISCUSSION

Species richness and abundance

Late dry season fires increased above-ground species richness at the 1-m² scale in the year following fire, but there was no corresponding effect at the 100-m² scale (Table 2). This probably reflects an increase in the density, rather than number of species in the savanna (Whelan 1995). The documented species richness of 30–40 species per 100-m² is similar to that of eucalypt savanna in the Northern Territory (Fensham 1990).

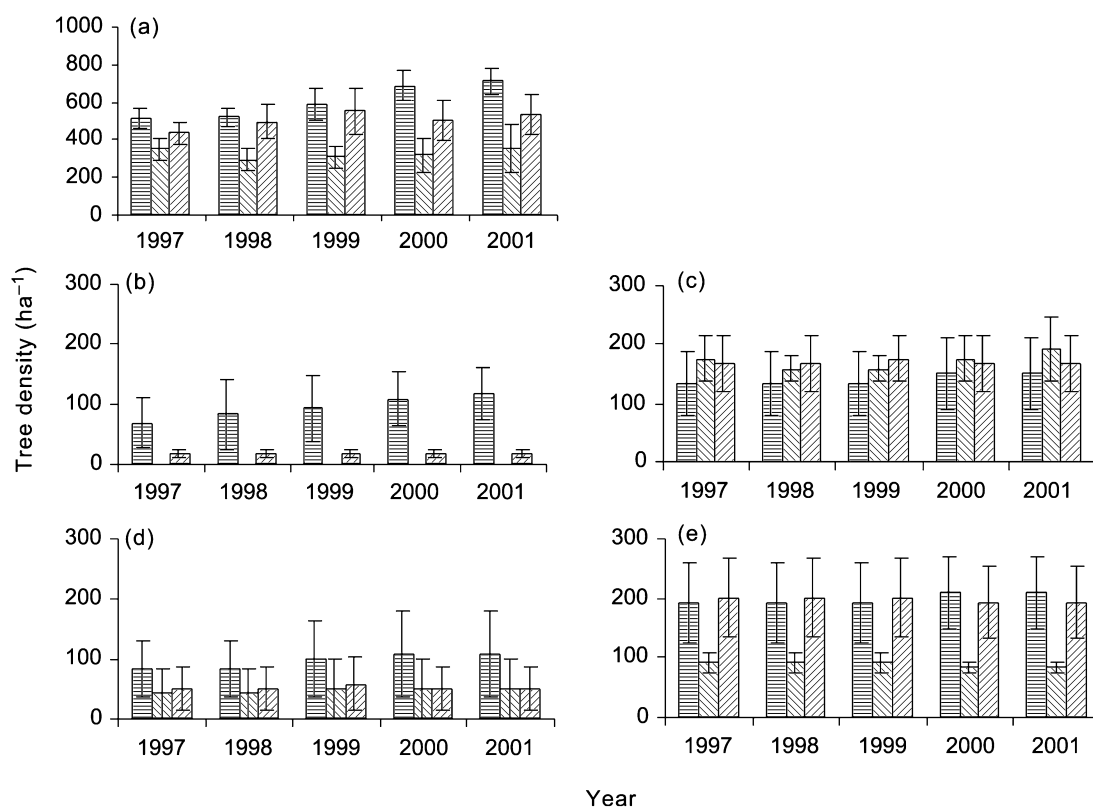


Fig. 2. Mean (\pm SE) tree density in (□) control, (▨) early and (▩) late dry season burnt eucalypt savanna at Cape Cleveland, between 1997 and 2001 for (a) combined trees ($n = 10$ species; 199 plants); (b) *Canarium australianum* ($n = 16$ plants); (c) *Corymbia clarksoniana* ($n = 61$ plants); (d) *Corymbia tessellaris* ($n = 25$ plants); and (e) *Planchonia careya* ($n = 60$ plants).

However, Fensham (1990) detected significantly lower species richness at the 100-m² scale in plots unburnt for 10 years, compared with regularly and irregularly burnt savanna. It is not known whether a similar decline in species richness occurs in savannas of north-eastern Australia after longer fire-free intervals than those examined in the present study.

Fire regime was found to affect the abundance of several species groups and common species in eucalypt savanna at Cape Cleveland (Table 2). A postfire flush of abundance was detected for the subshrub *Breynia oblongifolia*, combined twining perennial forbs, the common twiners *Galactia tenuiflora* and *Passiflora foetida*, combined ephemeral forbs, *Indigofera hirsuta*, and grasses as a group. Late dry season fire typically produced the greatest change in abundance, although for *Galactia tenuiflora*, the greatest abundance was produced under early dry season burning. The increase in species abundance in the first year after fire corresponded with the period of lowest fuel load, suggesting a competitive inhibition by dense ground cover. Whereas most fire effects were undetectable by the second year after fire, *Passiflora foetida* maintained a higher abundance in recently burnt plots and the dominant grass *Heteropogon triticeus* significantly declined with the absence of fire for 4 years in comparison with early burnt plots.

Fire regime has been demonstrated to affect the abundance of herbaceous species in some Australian tropical savannas (Bowman *et al.* 1988; Fensham 1990; Williams & Lane 1999; Russell-Smith *et al.* in press). However, the significant effect of dry season fire regime on both species richness and the abundance of herbaceous species in the current study contrasts with the findings of Williams *et al.* (in press), who did not detect clear fire effects on grasses and forbs during a 5-year experiment in eucalypt savanna at the Kapalga research station in the Northern Territory. Neither the abundance of herbs nor species richness responded directly to fire regime at Kapalga, but were correlated with fluctuations in wet season rainfall and the cover of annual *Sorghum* species. Part of the reason for these differences between Kapalga and Cape Cleveland may be the contrast in seedling recruitment ecology. Many forbs and grasses at Kapalga germinate at the start of each wet season irrespective of fire (Andrew & Mott 1983; Brennan 1996; Williams & Lane 1999; Williams *et al.* in press). In contrast, Cape Cleveland is dominated by perennial grasses and forbs that display fire-trigger seedling recruitment rather than mass germination at the start of each wet season (Williams 2002).

Frequent fires over two decades have been shown to promote the dominance of a few annual grasses in

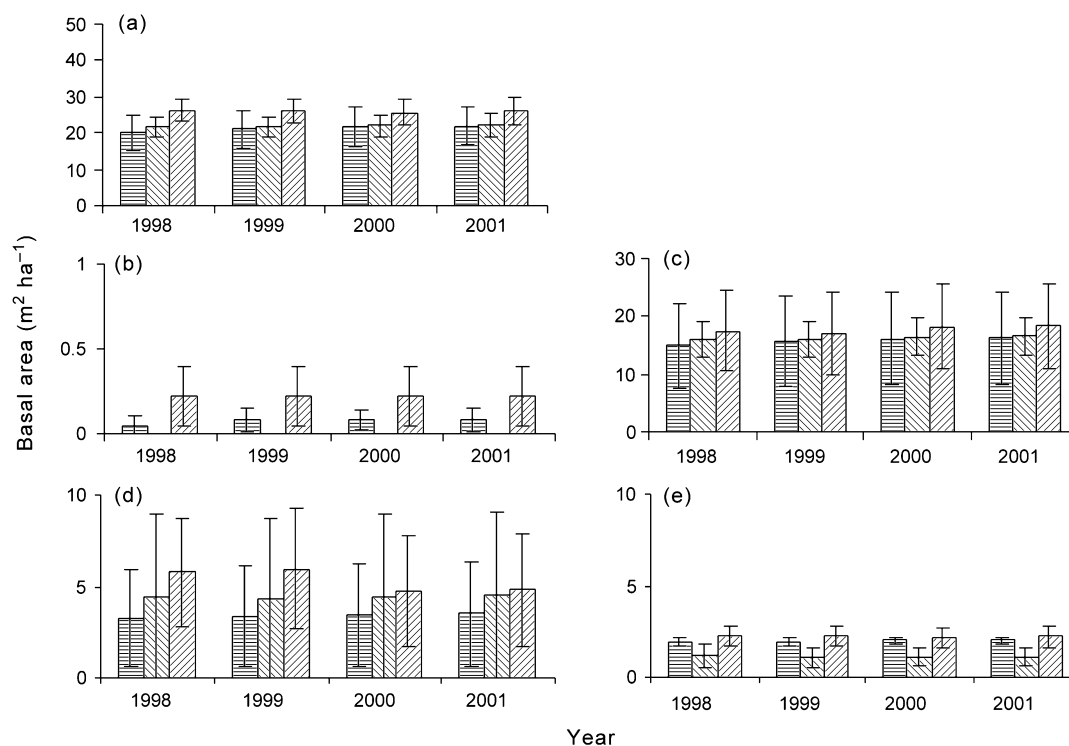


Fig. 3. Mean (\pm SE) tree basal area in (■) control, (▨) early burnt and (▩) late dry season burnt eucalypt savanna at Cape Cleveland between 1997 and 2001 for (a) combined trees ($n = 10$ species; 199 plants); (b) *Canarium australicum* ($n = 16$ plants); (c) *Corymbia clarksoniana* ($n = 61$ plants); (d) *Corymbia tessellaris* ($n = 25$ plants); and (e) *Planchonia careya* ($n = 60$ plants).

eucalypt savanna of the Northern Territory (Russell-Smith *et al.* in press). An increased abundance of perennial grasses has also been documented in recently or frequently burnt tropical savanna (Shaw 1957; Norman 1963; Sandercoe 1989; Walker *et al.* 1989; Orr *et al.* 1991). Whereas some attention has been given to *Heteropogon contortus*, less research has examined the larger *H. triticeus*. It often occurs at greatest abundance in frequently or most recently burnt plots (Sandercoe 1989; Fensham 1990). However, *H. triticeus* has also increased simultaneously in annually burnt and unburnt savanna of the Northern Territory (Russell-Smith *et al.* in press), and has been documented at reduced abundance in recently burnt plots on Cape York Peninsula, in the presence of free-ranging stock (Crowley & Garnett 1998). Differences in response may result from edaphic, climatic and biotic factors, including competitive interactions and variation in grazing pressure following fire, and the examination of population processes is crucial to resolving the reasons for these differences.

Tropical forbs respond variously to fire regime (Bowman *et al.* 1988; Fensham 1990). Some forbs, such as the leguminous *Crotalaria* spp. are more abundant in frequently burnt savanna, whereas the ephemeral *Polygala orbicularis* has shown contrasting responses to fire frequency (Bowman *et al.* 1988; Fensham 1990). Fire-enhanced short-term pulses of forb abundance have also been documented in sandstone heathy woodlands of the Northern Territory (Russell-Smith *et al.* 2002) and north-western Queensland (Williams *et al.* 2002b).

Tree density and basal area

The total density of trees taller than 2 m significantly increased with a 4-year absence of fire at Cape Cleveland, although this was not significant for any individual species and may have been influenced by competition from mature trees (Fensham & Bowman 1992). The increase in tree density resulted from the growth of saplings to greater than 2 m in height. Burning during the early and late dry seasons inhibited an increase in tree density over the course of the study, although the basal area of the dominant tree *Corymbia clarksoniana* significantly increased over the 5-year study, irrespective of fire regime. The low levels of tree mortality and insignificance of fire regime is in contrast to research in the Northern Territory (Williams *et al.* 1999), and may have resulted from the lower fire intensities experienced at Cape Cleveland.

The apparent dissimilarity of the results of the frequency-based abundance measure, which found no significant tree response to fire regime, and density, which found trees increased with fire protection, is because tree density was driven by the growth of existing saplings into the >2 m height category,

whereas the frequency-based abundance measure documented both large and small woody plants. These combined results suggest that the number of woody plants remained unchanged and that some saplings grew above 2 m in height in the absence of fire for 4 years.

The lack of short-term fire effects detected for rain-forest trees and shrubs is consistent with the results of other studies in Australian tropical savannas (Bowman *et al.* 1988; Fensham 1990; Bowman 1993; Bowman & Panton 1995; Russell-Smith *et al.* in press; Williams *et al.* in press). However, assessment of fire effects on different life events, such as seedling emergence and survival, and growth rates of saplings, is needed to shed further light on the long-term influence of fire regime on this group.

Higgins *et al.* (2000) suggested variation in fire intensity is a key factor governing tree density in savannas, with the escape of stunted saplings from the 'flame zone' depending on fire frequency and intensity. Data from Cape Cleveland provide evidence that fire frequency influences the release of stunted saplings. However no evidence was found that fire intensity affected sapling release, as saplings (i.e. <2 m tall) of all tree species sprouted from the base after both higher intensity late dry season fires and lower intensity early and mid-dry season fires. As a result, tree density did not increase in early burnt sites that experienced only low intensity fires during the study.

In conclusion, this study has demonstrated that the abundance of several savanna species was influenced by fire regime. The effects of fire regime were most evident in the herbaceous layer in promoting ephemeral and twining perennial forbs and grasses in the first year following burning, especially late dry season fires. Fire intervals of 4 years led to a significant decline in abundance of the dominant grass *Heteropogon triticeus*, and an increase in the density of trees (>2 m tall), due to the growth of saplings into the >2 m height category.

Clearly, variation in fire regime will be required to maintain species diversity and structure in this savanna, and no single fire regime will suit all species (Williams *et al.* 2002a). Details of the fire-related mechanisms that determine floristic abundance are required to understand better the effects of fire regimes. Future papers will systematically examine the effect of fire on critical life events on a range of coexisting savanna species of the Townsville region, to provide an insight into the processes whereby fire influences species abundance.

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