

Does long-term fire exclusion in an Australian tropical savanna result in a biome shift? A test using the reintroduction of fire

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Abstract The structure of tropical savanna ecosystems is influenced by fire frequency and intensity. There is particular interest in the extent to which long-term fire exclusion can result in a shift from savanna to forest vegetation that is not easily reversed by the reintroduction of fire. This study examined changes in the structure and composition of a long-unburnt site within the northern Australian savannas following an extended period of active fire exclusion (>20 years), and the effect of the reintroducing fire through experimental fire regimes, including fires in the early and late dry season at a range of frequencies. After the long period of fire exclusion, the vegetation community was characterized by a well-developed midstorey and canopy layer, low grass cover, substantially higher densities of woody sprouts and saplings than frequently burnt savanna. The community composition included a high proportion of rainforest-affiliated species. Three years of experimental fires had no detectable effect on the overall composition of grass layer and woody plants but had an effect on woody vegetation structure. Continued fire exclusion further increased the density of woody stems, particularly in the midstorey (2.0–4.99 m), whereas moderate-intensity fires (>800 kW m⁻¹) significantly reduced the density of midstorey stems. The reintroduction of higher moderate intensity fire events resulted in the vegetation in some compartments reverting to the open savanna structure typical of frequently burnt sites. Such rapid reversibility suggests that in general, the woody thickening resulting from long-term fire exclusion did not represent a biome shift to a non-savanna state. However, there was a small proportion of the site that could not sustain the fires applied to them because grass cover was very low and patchy and therefore appeared to have crossed an ecological threshold towards closed forest.

Key words: biome shift, fire, fire behaviour, resprout, savanna, tropical woodland, woody thickening.

INTRODUCTION

State-and-transition models are useful for describing the range of complex ecosystem processes and multiple vegetation states observed in tree-grass ecosystems (Westoby *et al.* 1989; Angassa & Oba 2008). According to state-and-transition theory, vegetation can shift from one stable state to another, and this shift can be irreversible without dramatic intervention. Substantial changes in composition and structure may occur within a vegetation state, but negative feedbacks reinforce ecosystem stability, and changes are easily reversed by removing the stressor/s that drove the initial change (Bestelmeyer *et al.* 2003; Briske *et al.* 2006).

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In extreme cases a transition from one state to another can involve such a transformation in ecosystem structure and function that it represents a shift from one biome to another. This is the case throughout the seasonal tropics, where savanna and forest represent contrasting biomes in regions of high rainfall (Bond & Parr 2010). Savanna vegetation is dominated by fire-resistant, shade-intolerant, sclerophyllous tree species that form an open canopy over a continuous grass layer, whereas forest is dominated by fire-sensitive, shade-tolerant mesophyll tree species that form a closed canopy with little or no grass cover (Ratnam *et al.* 2011). Long-term fire exclusion sees a transition from savanna to forest, as juvenile woody plants recruit into the midstorey layer, and the increased shade reduces grass biomass (Silva *et al.* 2001; Russell-Smith *et al.* 2003; Woinarski *et al.* 2004). The reduction in grass biomass results in

reduced fire frequency, which reinforces the transition from savanna to forest (Russell-Smith *et al.* 2003; Ratnam *et al.* 2011).

Alternatively, frequent burning has been shown to reverse woody thickening, particularly in combination with drought and browsing by large herbivores (Roques *et al.* 2001; Midgley *et al.* 2010). Most savanna woody species are capable of re-sprouting after fire, although high mortality occurs in response to higher-intensity fires, particularly of the smallest and largest individuals (R.J. Williams *et al.* 2003; Midgley *et al.* 2010). Conversely, dry season burning generally has little effect on grass-layer plants, with compositional change attributed to inter-annual rainfall variability (O'Connor & Everson 1998; Williams *et al.* 2003b). Site and stand characteristics, and the interaction between these, may alter these responses because they determine fire behaviour and the response of the vegetation community to fire behaviour (R.J. Williams *et al.* 2003).

Open savanna communities characterized by a continuous understorey of C₄ grasses and a scattered overstorey of *Eucalyptus* species dominate northern Australia (Hutley & Setterfield 2008). These communities are frequently burnt every 1–3 years (Andersen *et al.* 2005). Within the savanna matrix are small (typically <5 ha) pockets of closed monsoon rainforest (Russell-Smith 1993; Russell-Smith & Setterfield 2006). A range of studies in the north Australia savannas has documented transition towards closed forest in the long-term absence of fire, characterized by increases in stem density, development of the midstorey or subcanopy, decrease in grass cover and increase in rainforest-associated species (Russell-Smith *et al.* 2003; Williams *et al.* 2003a; Woinarski *et al.* 2004). However, it is unclear at what point along this transition the shift from savanna to forest can be considered to have occurred. One approach to addressing this is to focus on the ease with which vegetation change is reversible. If the reintroduction of fire results in a rapid reversion to open savanna then it can be argued that a biome shift has not yet occurred.

Here we use this approach to assess if more than 20 years of active fire exclusion at a savanna site in northern Australia has resulted in a biome shift. First, we describe the state of the vegetation in the long-term absence of fire, with the expectation that it will have characteristics of forest structure, composition and function, such as a substantial proportion of forest species, a relatively closed canopy, and patchy grass cover (and therefore a low capacity to carry fire). We then assess the vegetation response to the reintroduction of fire focussing on the extent to which these forest characteristics are reversed.

METHODS

Study area

The study was undertaken within the Territory Wildlife Park at Berry Springs, 30 km southeast of Darwin, Northern Territory, Australia (12°41'42.25"S, 130°58'50.36"E). The region has a monsoonal tropical climate, with a hot summer wet season (October–March), and a mild winter dry season (April–September). Mean annual rainfall at the Middle Point Automatic Weather Station (36 km to the north-east) is 1399 mm, of which 90% falls in the wet season. Rainfall recorded at the Park during the study (2004–2007) was 17% higher than the long-term average, principally as a result of a cyclone-related rainfall event in April 2006 (Bureau of Meteorology, unpubl. data 2007).

Fire had been actively excluded from the Park since at least 1981 with only two patchy fires in the study site between 1981 and 2004. In 1980, vegetation structure at the site was typical of the broader region; *Eucalyptus tetrodonta* F.Muell. and *Eucalyptus miniata* A.Cunn. ex Shauer were dominant overstorey trees over a sparse midstorey (approx. 2–5 m high) and a grass layer of tall perennial (*Heteropogon triticeus*) and annual (*Sorghum intrans*) grasses (Sivertsen *et al.* 1980). In 2004, a moderately to well-developed midstorey was present throughout the site (Fig. 1), particularly in association with the Quaternary colluvial sediments of the permanent lagoon in the south (Scott *et al.* 2009).

Experimental design

The fire experiment consisted of a line of 18 1-ha compartments located in the north-western corner of Territory Wildlife Park, arranged in three contiguous blocks (North, Centre and South) to accommodate the environmental variability at the site (see Scott *et al.* 2009 for a detailed description). In summary, soil moisture content of the surface soil was significantly higher in the North and Central blocks where the soils were gravelly clay loams on a small ridge, and exhibited an horizon of massive laterite of Tertiary origin, 10–50 cm below the surface (Scott 2008). In the South block, soils were sandy loams associated with Quaternary colluvial sediments of a permanent lagoon, significantly less gravelly (25% gravel >2 mm in the upper 5 cm soil surface), positioned at the foot of the ridge, and did not contain massive laterite in the upper 1 m of the soil profile (Scott 2008). Vegetation structure varied along the edaphic gradient, with significantly higher density of woody stems in the midstorey in the South block (approx. 2000 stems ha⁻¹) compared with the North and Central blocks (approx. 1050 stems ha⁻¹).

Fire regimes were allocated as treatments to three compartments each, one per block, according to a randomized complete block design. This allowed variation in edaphic characteristics to be assessed in the experiment. Fire regimes were: unburnt (UN), annual early fires (Annual Early), a single early season fire in 2004 (Early 04), a single early season fire in 2005 (Early 05) and biennial late (Biennial Late). All fire regimes were first applied in 2004, with the exception of the Early 05 regime, which was first burnt in 2005 (Table 1). Experimental fires were lit with drip torches

a)



b)



Fig. 1. The Territory Wildlife Park study site with savanna with a *Eucalyptus* dominated overstorey and a (a) moderate to (b) well-developed midstorey.

along the leeward sides of each compartment to be burnt (back fire). After the fire had established within the compartment, fire lines were lit on the windward side unless the backfire was intense and moving rapidly to the windward side. This paper reports on changes in vegetation in the first three years following the reintroduction of fire. The early season fires were typically lower intensity, and therefore lower flame height, than late season fires which reflects the fire

behaviour in this region (Table 1; Setterfield *et al.* 2010). The exception was the Early 05 treatment which had a moderate intensity fire, and contrasted with the early fires in other treatments. There was variability within fire regimes due to the edaphic and vegetation differences between compartments and blocks. For example, very low fire intensities occurred in some compartments, particularly in the South block, where there was sparse grass cover (Fig 1b).

Table 1. Burning schedule for experimental fire regimes at the Territory Wildlife Park

Fire regime	Year		
	2004	2005	2006
Annual Early	144.0 (18.1)	77.7 (36.7)	125.3 (54.1)
Early 04	n/a	–	–
Early 05	–	1110.3 (569.0)	–
Biennial Late	808.4 (625.0)	–	2121.3 (975.3)

Values are mean intensity (Kw m⁻¹) with 1 SE in parenthesis (data unavailable for Early 04). – indicates no fire event.

Plant composition and abundance

To determine if the reintroduction of fire caused a substantial change in structure and composition of woody plants, surveys were completed in May 2004, before fire regimes were first implemented, and again in March 2007. Sampling was undertaken within two parallel belt transects (80 × 6 m, approx. 30 m apart) within each compartment, where the abundance of woody plant species (including standing dead stems) was recorded. For stems <2 m, abundance was categorized according to two height strata: sprouts (0–0.49 m) and small saplings (0.5–1.99 m) (collectively known as the grass-layer stratum). For stems >2 m tall (and >3 cm d.b.h.), the height and d.b.h. of each individual were recorded, and categorized into the following height strata: lower midstorey (2.0–4.99 m), upper midstorey (5.0–9.99 m) and overstorey (10.0 m+). Stems >2 m and <3 cm d.b.h. were classified as large saplings. The precise height of large saplings was not measured, although they were typically <5 m (i.e. in the lower midstorey), and contributed only a very small proportion (2.4%) of the total woody stem density (and therefore basal area). Basal area (m² ha⁻¹) was calculated by multiplying stem area (obtained from d.b.h. measurements) by stem density, considering each woody stem >2 m height and >3 cm d.b.h.. Eight uncommon vine species were present but were not included in the site assessment. In the 2007 survey, each stem was noted for the presence of basal sprouting and survival of the main stem.

To assess the effect of fire regimes on the grass-layer species, the abundances of grass, sedge and forb species were sampled annually in the late wet season from 2004 to 2007. The density of each species was counted within 18 2-m² permanent quadrats per compartment; nine quadrats were spaced, every 10 m, along the centre line of each belt transect. Tree litter and canopy cover were also assessed annually at these quadrats. Cover of grass and leaf litter was estimated visually (to the nearest 5%), and canopy cover recorded using the mean of four cardinal points on a forestry densitometer immediately outside each quadrat (Lemmon 1956).

Sampling occurred in the late wet season (March–May) when the ability to detect and identify grass-layer plants was highest given the presence of mature, flowering individuals. A slightly later sampling period in 2004 made for unreliable identification of annual species (grasses, forbs and sedges), because they had already set seed and begun to cure. With the exception of perennial grasses and selected annual grass species, most analyses therefore consider the surveys of 2005 to 2007 inclusive.

For some other plants, identification to species level was not possible given the absence of flowering material during the sampling period. Such species were included as aggregates of two or more species with a similar vegetative appearance: *Eriachne agrostidea* F.Muell included *Eriachne ciliata* R.Br.; *Panicum mindanaense* Merr. included *Yakirra nulla* Lazarides & R.D. Webster and *Urochloa polyphylla* (R.Br.) R.D. Webster; *Eriachne trisetata* Nees ex Steud. included *Aristida holathera* Domain and *Eriachne burkittii* Jansen; and *Eriachne avenacea* R.Br. included *Eriachne major* (Ewart & O.B. Davies Lazarides).

Statistical analysis

Analysis of variance was used to assess changes in the abundance of woody vegetation within each height stratum, species richness, and basal area. Data from transects were averaged and the variables were analysed with multivariate ANOVA with the following factors: Year (fixed), Regime (fixed), Block (random), with Block nested in Regime. Variables were square-root or log-transformed if necessary, in this and all other analyses, to satisfy the normality and variance homogeneity assumptions of ANOVA. Analyses of woody stem abundance were also conducted separately (in each stratum) for the rainforest-affiliated species (defined by Liddle *et al.* 1994 as species that are 'either exclusive to, or typically components of, perennially or seasonally closed canopy vine-forest or vine-thicket vegetation'), given expected differences in their responses to fire compared with savanna species. Analyses of woody stem abundance were also conducted for species based on the height of those species when they are mature individuals (grass-layer species (<2 m), six spp.; shrub species (2–10 m), 58 spp.; tree species (>10 m), 12 spp.).

Two-way ANOVA was used to determine whether fire regime influenced the incidence of basal sprouting. The number of woody stems exhibiting the basal sprouting response (as a proportion of the total live stem density) was compared between fire regime treatments in a design consisting of Regime (fixed), and Block (random), with Block nested in Regime.

To make generalizations on grass-layer plant responses, species were categorized according to life form: annual or perennial grasses (Poaceae), non-leguminous forbs, sedges (Cyperaceae) and legumes (Fabaceae). Grass cover, species richness (2 m² scale), total density, and the density of each life form group, were analysed with a repeated measures

ANOVA to assess change over time within fire regime treatments. Factors comprised Regime (fixed factor), Block (random factor), Transect (random factor) and Year (repeated measure, fixed factor), with Transect nested in Regime and Block.

Patterns of woody and grass-layer species composition at the site were analysed separately with ordination and ANOSIM (analysis of similarity) using *Primer 6* (Clarke & Gorley 2001). The number of individuals within each sampling unit was converted to a density value, and then averaged to the compartment level. Data were log ($x + 1$) or square root transformed, and resemblance matrices constructed using the Bray–Curtis measure of similarity. One-way ANOSIM was used to determine whether species composition differed between fire regime treatments and blocks at the end (2007) of the sampling period.

Canopy, grass and litter cover prior to fire were compared between blocks using one-way ANOVA. Tukey's honestly significant difference *post hoc* tests were used to identify which blocks were significantly different from each other. Litter and Canopy cover were compared between fire regime treatments in each survey year (2004–2007 inclusive) using a non-parametric Kruskal–Wallis Ranks test (as a result of positively skewed distributions with zero counts).

RESULTS

The two woody vegetation surveys recorded 84 plant species at a mean density of 9945 stems ha^{-1} . Approximately half of the species (34 spp.), and a third of the stems overall (36.1%), were rainforest-associated species. Rainforest species had a greater prominence in the grass-layer strata, where they comprised 38.5% of the stems, compared to 19.1% in the midstorey and 15.9% in the overstorey. The overwhelming majority of woody stems were sprouts (73.6%), followed by small saplings (12.6%), stems in the lower (7.1%) and upper (3.5%) midstorey, large saplings (2.4%) and overstorey trees (0.7%).

Site characteristics varied along the edaphic gradient prior to the reintroduction of fire. Canopy cover in 2004 was significantly lower in the North ($58.6 \pm 3.8\%$) and Central ($57 \pm 2.1\%$) blocks compared to the South block ($80.6 \pm 5.3\%$; $F_{2,15} = 9.5$, $P < 0.01$). Similarly litter cover in 2004 was significantly lower in the North ($22.8 \pm 2.5\%$) and Central ($23.6 \pm 4.5\%$) blocks compared to the South block ($43.4 \pm 3.9\%$; $F_{2,15} = 9.62$, $P < 0.01$).

Edaphic conditions were clearly an important influence on vegetation with a significant effect of block evident for abundance of sprouts, small saplings and stems in the upper midstorey and overstorey (Table 2). Abundance of these groups was higher in the South block (sandy loams soils) than the North or Central block (lateritic soils; Fig. 2). This trend was particularly evident for rainforest species in these strata (Fig. 3; Table 2).

Leaf litter cover increased at a similar rate between 2003 and 2007 in the Annual Early, Early 04 and UN regimes, demonstrating that lower fire intensities had little effect on litter accumulation (Fig. 4). By contrast, the higher-intensity fire in the Early 05 regime in 2006, and late dry season fires in the Biennial Late regime, markedly reduced litter cover (Fig. 4). As a consequence, there was a significant difference in litter cover between regimes in 2005 ($H_{(4, n=30)} = 15.25$, $P < 0.01$) and 2007 ($H_{(4, n=30)} = 17.34$, $P < 0.01$), after some of the higher-intensity fires.

Canopy cover remained relatively constant during the study period in the UN regime and in regimes with low-intensity or infrequent fires (i.e. Annual Early and Early 04 regimes, Fig. 4). In contrast, canopy cover decreased (by approx. 15%) in the first year after the moderate-intensity Early 05 fire, and decreased (by approx. 10%) in response to the second fire of the Biennial Late regime, the most intense fire of the experiment, resulting in a significant difference in canopy cover between regimes in 2007 ($H_{(4, n=30)} = 10.92$, $P < 0.05$).

Effect of fire on woody plant species

The reintroduction of fire altered stand structure through reduced abundance of the large saplings and the lower midstorey stems, although the magnitude of this change was determined by fire intensity resulting in Year \times Regime interactions (Table 2). The abundance of large sapling stems increased or remained relatively stable within most plots, but decreased with the repeated moderate-intensity fires of the Biennial Late regime (Fig. 5). The abundance of lower midstorey stems decreased within the fires of the Early 05 and Biennial Late regimes but was maintained or increased within the UN, and lower intensity Annual Early and Early 04 regimes (Fig. 5). A similar pattern occurred for the abundance of the tree species, with the latter also demonstrating a significant year by regime interactions (Table 2). The mean abundance of lower midstorey stems overall (and tree species in that group) showed a significant effect of year overall (Table 2). Stems in the upper midstorey strata and overstorey strata were more resilient to burning than those in the lower midstorey, showing no effect of Year, nor a Year \times Regime interaction (Table 2; Fig. 5).

The fire regimes in this experiment had little effect on the sprout layer with increases in mean sprout abundance evident in all fire regime treatments over time (Fig. 6); resulting in a significant Year effect. The significant increase was evident for the rainforest, midstorey and overstorey groups in the sprout layer (Table 2). The abundance of overstorey species in the sprout layer decreased in the higher-intensity Early 05 regime in contrast to the increases observed within all

Table 2. Summary ANOVA results for variation in species richness, and the abundance of woody plants in each stratum between 2004 and 2007

Response variable	<i>F</i> -ratios				
	Year (Y)	Fire regime (R)	Block (B)	Y × R	Y × B
	<i>F</i> _{1,10}	<i>F</i> _{4,10}	<i>F</i> _{10,15}	<i>F</i> _{4,10}	<i>F</i> _{10,15}
Species richness	12.98**	1.49	2.24	2.37	1.46
Standing dead stems	23.91***	0.66	4.53**	1.27	2.41
Live stem abundance					
Grass-layer					
Sprouts (0.0–0.49 m)	11.28**	0.76	5.19**	1.58	1.56
Rainforest	10.52**	0.73	8.13***	1.81	1.14
Ground-layer	1.10	0.31	1.67	2.14	0.44
Shrub	10.62**	0.73	3.41*	1.34	2.40
Tree	9.31*	0.74	4.24**	4.98*	0.07
Small saplings (0.5–1.99 m)	5.39*	1.04	12.35***	1.24	3.76*
Rainforest	1.25	0.04	11.84***	1.58	0.55
Shrub	3.68	0.76	11.16***	1.22	2.76*
Tree	19.27**	1.82	2.62*	2.41	0.50
Midstorey					
Large saplings (>2.0 m & <3 cm d.b.h.)	0.32	0.54	1.96	3.89*	1.70
Rainforest	0.49	0.45	4.57**	2.31	1.08
Shrub	<0.01	0.42	2.01	3.42	1.46
Lower midstorey (2.0–4.99 m)	7.07*	3.44	2.13	5.19*	5.42**
Rainforest	5.27*	0.44	6.32***	1.30	7.96***
Shrub	4.78	3.56*	1.80	4.45*	3.47*
Tree	17.09**	1.45	2.68*	12.64***	0.37
Upper midstorey (5.0–9.99 m)	2.46	0.37	3.38*	2.18	3.44*
Rainforest	0.75	0.19	7.03***	1.77	3.37*
Shrub	1.03	0.42	2.01	1.86	5.62**
Tree	4.39	1.29	1.13	1.37	0.54
Overstorey (10.0 m+)	2.50	0.79	3.58*	2.91	1.42

Basal area, species richness and standing dead stems consider all strata together, whereas abundance variables are categorized by stratum for all species combined (e.g. sprouts, 0–0.49 m), and then by species groups based on the maximum height that they grow too (i.e. ground-layer, shrub, tree species) within each stratum. Abundance was also analysed for rainforest species). Significant *F*-ratios are indicated by asterisks (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Grass-layer species in the small sapling stratum, overstorey species in the large sapling stratum, and monsoon forest species in the overstorey stratum, were too uncommon for separate analysis.

other fire regimes, resulting in a significant year by regime interaction (Table 2). The abundance of small saplings also showed a significant increase over time, primarily due to the increase in overstorey species (Table 2).

Despite the reduction in large saplings and midstorey stems, basal area was not significantly affected by Year, Regime or Block. However, there were significant inter-annual changes in species richness and stem abundance. Species richness increased significantly over time within all but the Biennial Late regime (Fig. 7), from a mean of 24.7 species per transect in 2004, to 27.1 species per transect in 2007. There was no significant effect of Regime or Block, or interaction between factors (Table 2).

Rainforest species showed a significant effect of Block in all strata (Table 2), reflecting the general pattern observed for the community (Fig. 3). Rainforest species in the sprout and lower midstorey strata

showed a significant effect of Year, whereby sprouts increased considerably over time (particularly in the Annual Early and UN regimes) and lower midstorey stems decreased, particularly in the higher-intensity regimes (Early 05 and Biennial Late; Fig. 8).

The abundance of standing dead stems tripled during the experiment, resulting in a significant effect of Year and Block but no difference was detected between fire regimes (Table 2). The mean number of dead stems was 38.5 stems ha⁻¹ in 2004 (ranging from 82.3 stems ha⁻¹ in the South block to 10.4 stems ha⁻¹ in the North block), to a mean of 160.8 dead stems per hectare in 2007 (ranging from 259.4 stems ha⁻¹ in the South block to 59.4 stems ha⁻¹ in the North block). Despite this increase, standing dead stems (represented by 59 species) still only comprised a small proportion (1%) of the total number of stems in 2007. The species with the highest proportion of standing dead stems (with $n > 10$ individuals in total) were

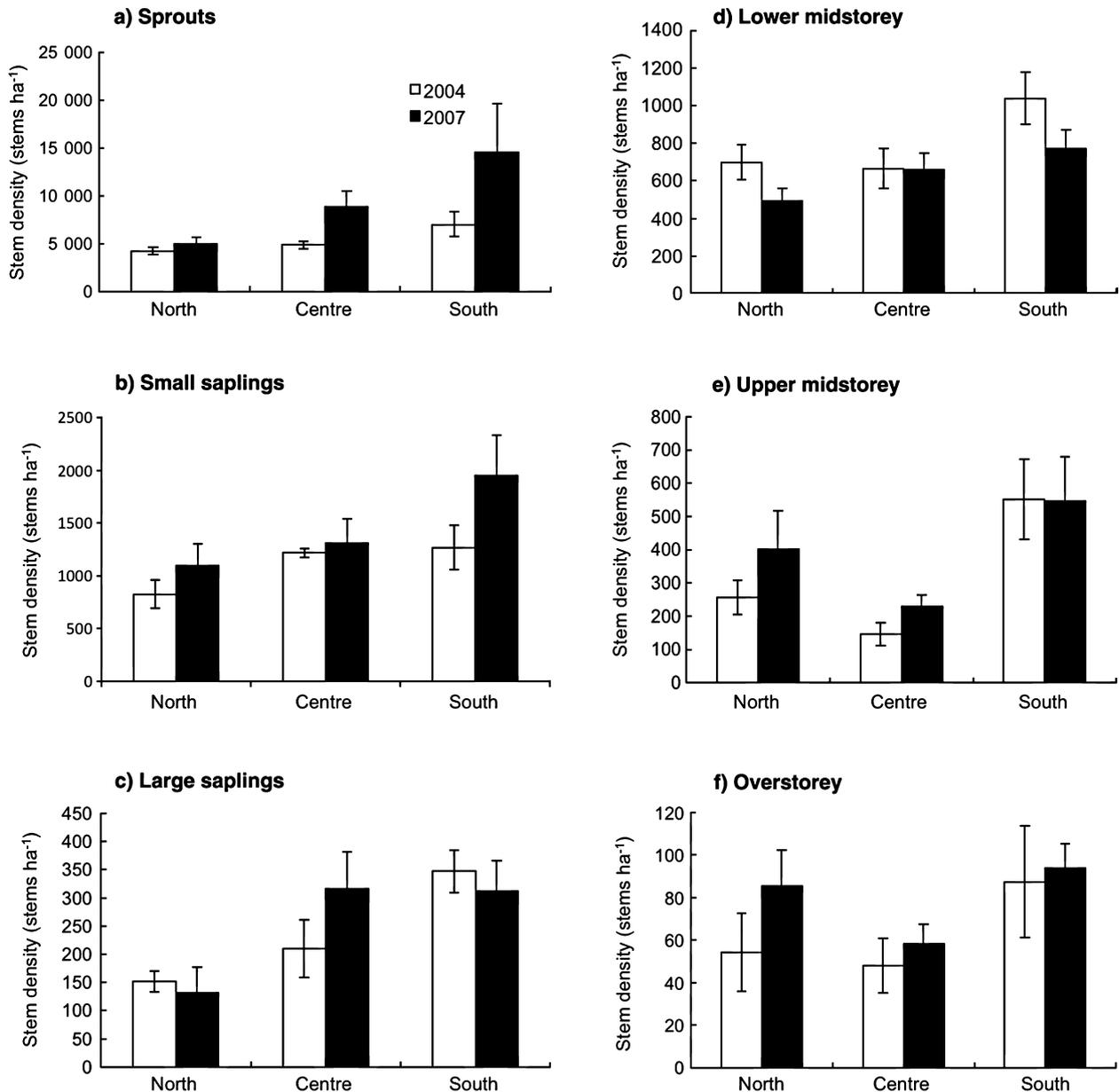


Fig. 2. Total abundance of woody stems within each height stratum (sprouts, <0.5 m; small saplings, 0.5–1.99 m; large saplings, >2 m but <3 cm d.b.h.; lower midstorey, 2.0–4.99 m; upper midstorey, 5.0–9.99 m; overstorey, 10.0+ m), in 2004 before regime treatments were first implemented (white bars), and 3 years later in 2007 (black bars). Data are presented by block: (a) North (woodland), (b) Centre (woodland) and (c) South (ecotone). Data are mean stem density \pm SE, where transect ($n = 10$) is the unit of replication. Note differences in scale.

Calytrix exstipulata (Myrtaceae; 8.0%), *Acacia holosericea* (Mimosaceae; 7.6%) and *Acacia oenocarpa* (Mimosaceae; 7.3%) in the grass layer, and *Grevillea peridifolia* (Proteaceae; 44.4%), *Alphitonia excelsa* (Rhamnaceae; 42.2%) and *Acacia latescens* (Mimosaceae; 23.1%) in the midstorey/overstorey.

In 2007, basal sprouting was evident on 59 species. Basal sprouting occurred on 7.4% of the woody stems. There was a significant difference between fire regime treatments in the proportion of individuals that exhib-

ited basal sprouting ($F_{4,10} = 6.98$; $P < 0.01$; Fig. 9). The lowest proportion of basal sprouting was observed in the UN and the Early 04 regime (4% of total stems in the regimes), whereas basal sprouters comprised about 10% of stems in the Annual Early and Early 05 regimes, and 20% in the higher-intensity Biennial Late regime. The species for which basal sprouters were most common (with $n > 10$ individuals in total) included *Lophostemon lactifluus* (Myrtaceae; 43.8%), *Syzygium eucalyptoides* subsp. *bleeseri* (Myrtaceae;

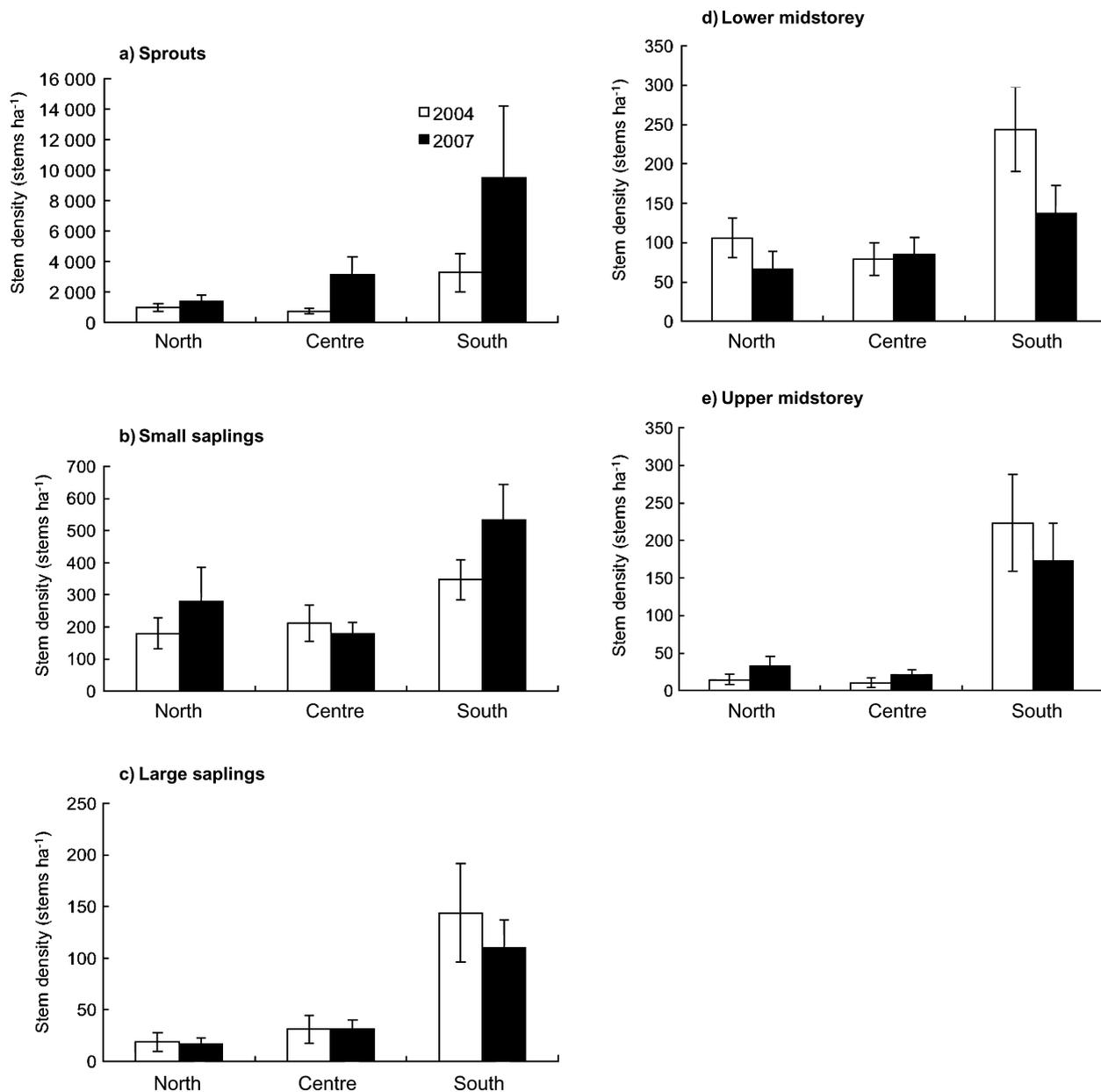


Fig. 3. Total abundance of woody stems of monsoon forest species (*sensu* Liddle *et al.* 1994) within each height stratum (sprouts, <0.5 m; small saplings, 0.5–1.99 m; large saplings, >2 m but <3 cm d.b.h.; lower midstorey, 2.0–4.99 m; upper midstorey, 5.0–9.99 m), in 2004 before regime treatments were first implemented (white bars), and 3 years later in 2007 (black bars). Data are presented by block: (a) North (woodland), (b) Centre (woodland) and (c) South (ecotone). Data are mean stem density \pm SE, where transect ($n = 10$) is the unit of replication. Rainforest species were very uncommon in the overstorey stratum and data are not presented. Note differences in scale.

32.6%) and *Corymbia bleeseri* (Myrtaceae; 31.4%) for stems in the grass layer, and *S. eucalyptoides* subsp. *bleeseri* (Myrtaceae; 40.0%), *Acacia lamprocarpa* (Mimosaceae; 28.1%) and *Acacia mimula* (Mimosaceae; 19.6%) in the midstorey/overstorey.

Effects on grass and legumes species

In total, 116 herbaceous grass-layer plant species were identified during the annual surveys, at a mean density

of 70 individuals m⁻² (range: 0–1802 per square metre). The grass layer was dominated by annual grasses (36.9% of total density, 17 spp.) and annual forbs (28.9%, 56 spp.). Sedges (14.9%, 11 spp.), perennial grasses (13.4%, 18 spp.) and legumes (5.9%, 14 spp.) together comprised the remaining one-third of the grass-layer plants. The most common species (according to density) were the annual grass *Pseudopogonatherum contortum* (Poaceae; 11.7 ± 1.1 SE individuals per square metre), sedge *Fimbristylis* sp.

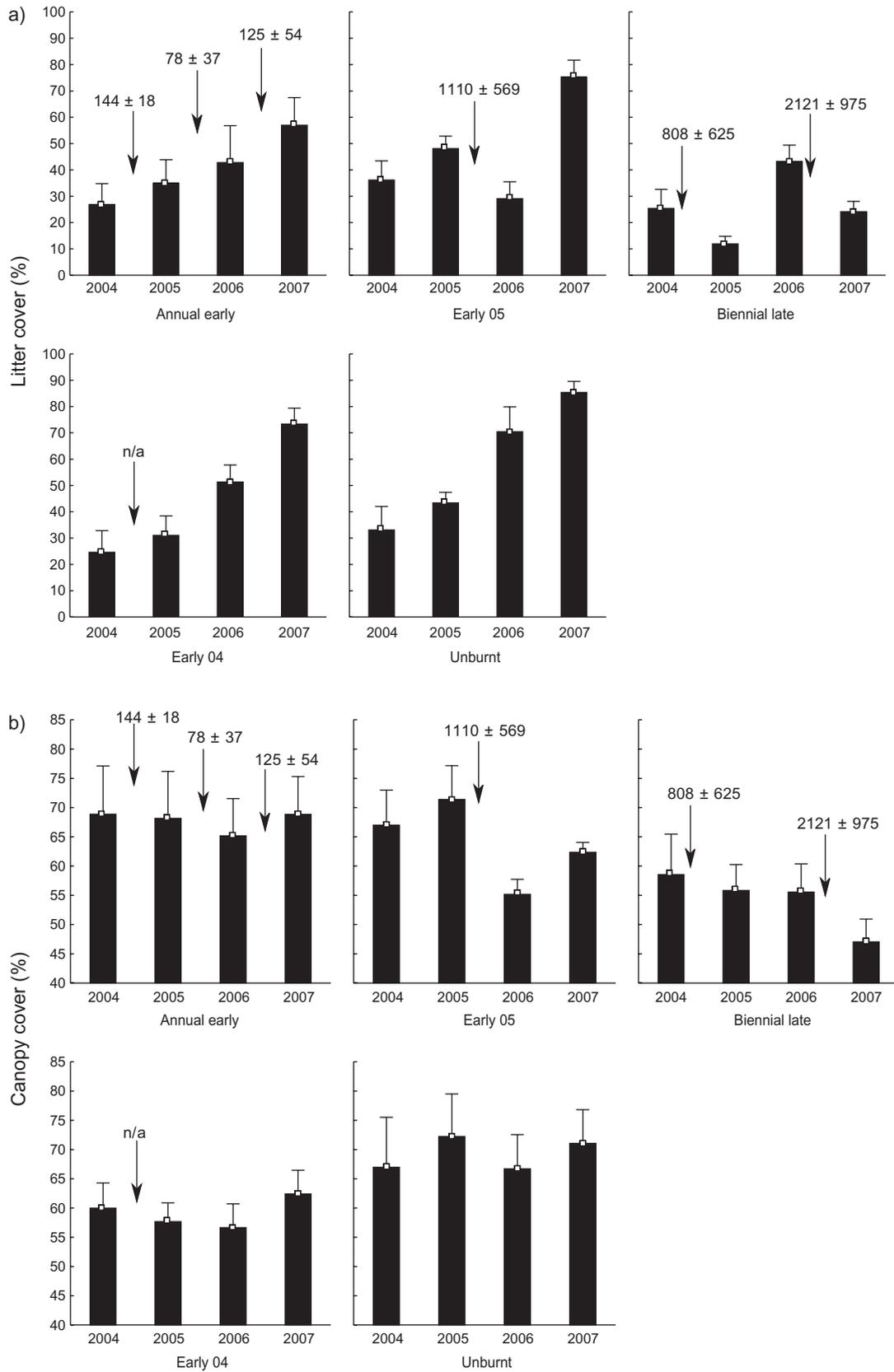


Fig. 4. Mean (+1 SE) values of (a) litter cover and (b) canopy cover, during the 4 years (2004–2007) of the manipulative fire experiment. Arrows and associated numbers indicate the timing of fires for each treatment and their intensity, and ‘n/a’ indicates that fire intensity was not assessed ($\text{kW m}^{-1} \pm 1 \text{ SE}$; see Table 1).

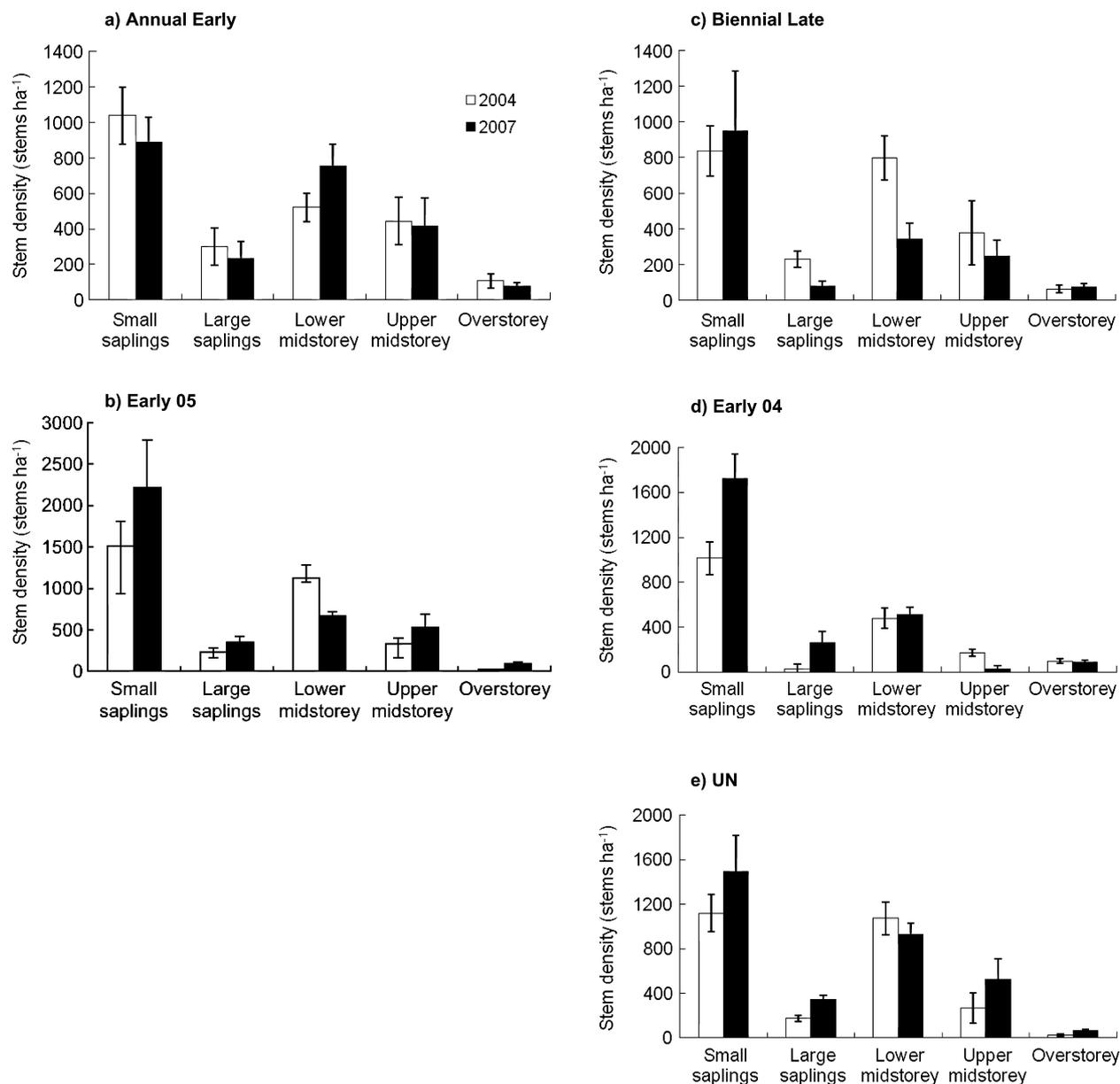


Fig. 5. Total abundance of stems within each height stratum above the sprout layer (small saplings, 0.5–1.99 m; large saplings, >2 m but <3 cm d.b.h.; lower midstorey, 2.0–4.99 m; upper midstorey, 5.0–9.99 m; overstorey, 10.0+ m), in 2004 before regime treatments were first implemented (black bars), and 3 years later in 2007 (white bars). Data are presented by fire regime treatment: (a) Annual Early, (b) Early 05, (c) Biennial Late, (d) Early 04 and (e) Unburnt (UN) (see Table 1 for details of intensity and frequency). Data are mean stem density \pm SE, where transect ($n = 6$) is the unit of replication. Note differences in scale.

Charles Darwin (Cyperaceae; 7.0 ± 0.7 per square metre) and perennial grass *E. trisetia* (Poaceae; 6.1 ± 0.3 per square metre).

Grass cover was low in 2004 ($12.9 \pm 2.2\%$) with a small overall increase to $18.0 \pm 2.3\%$ after the 3 years for experimental fires. There was no significant increase in grass cover in the higher-intensity Biennial Late regime, where cover increased from $11.7 \pm 7.1\%$ in 2004 to $27.9 \pm 3.1\%$. However, the total density of individuals in the grass layer, and the density of annual

grasses and legumes specifically, showed a significant effect of year overall, with density increasing over time (Table 3). The mean density of all life forms, except sedges, progressively increased in each year of the experiment (Table 4). For both annual grasses and total density, a significant Year by Regime interaction was not evident (Table 3), indicating that these increases occurred in spite of the different fire regime treatments applied. Total grass-layer density and annual grass density increased by approx. 45% and

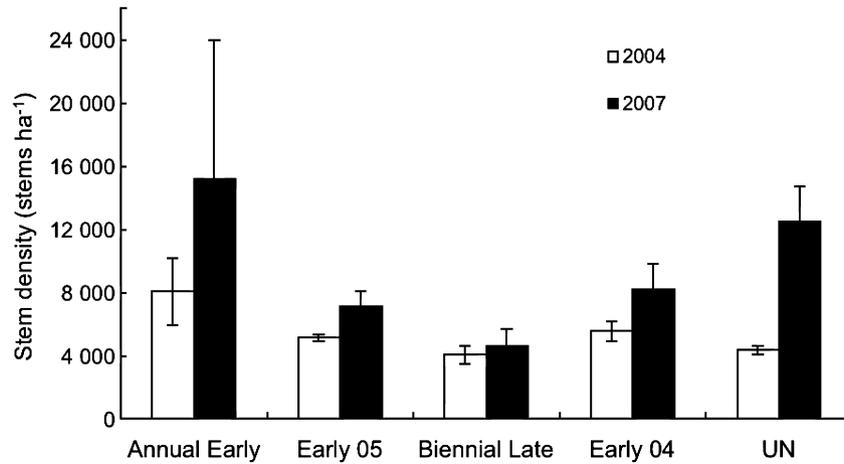


Fig. 6. Total abundance of sprouts (0–0.49 m) within each of the fire regime treatments (see Table 1 for details of intensity and frequency) of the experiment, in 2004 before regimes were first implemented (white bars), and 3 years later in 2007 (black bars). UN, unburnt.

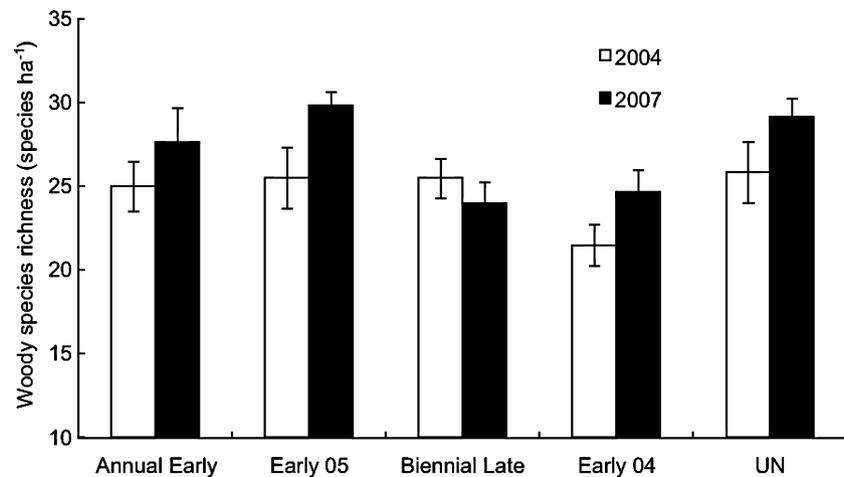


Fig. 7. Species richness of all woody species within each of the fire regime treatments (see Table 1 for details of intensity and frequency) of the experiment, in 2004 before regimes were first implemented (white bars), and 3 years later in 2007 (black bars). UN, unburnt.

100% respectively over the sampling period. The increase in density during the experiment coincided with an increase in the total rainfall and number of rain days during the wet season (November to February inclusive) prior to sampling (from 2005 onwards; Table 4). The increase in grass-layer plant density also coincided with a decrease in the total rainfall and number of rain days in the late dry season (August to October inclusive) prior to sampling. Species richness and the density of all life form groups showed a significant effect of block overall (Table 3).

Perennial grasses and legumes showed a significant Year \times Regime interaction, with changes in density over time determined by the fire regime treatment imposed (Table 3). Perennial grass density increased gradually in the UN regime, to double within 3 years. A similar

pattern occurred within the Early 04 regime which was burnt early in the experiment but protected from fire thereafter (Fig. 10a). Regular burning and regimes with higher-intensity fires tended to limit population increases; perennial grass density in such regimes (e.g. Biennial Late) remained relatively stable during the experiment.

The significant Regime \times Year interaction of legume density was the result of a substantial increase in density in the first year after fire, particularly after the higher-intensity fires of the Early 05 and Biennial Late regimes (Fig. 10). The post-fire response was smaller after lower-intensity fires of the Annual Early regime, and no increases were evident in the UN regime. Indeed, density tended to decrease after the initial post-fire increases (e.g. Fig. 10, Early 05, 2006–2007).

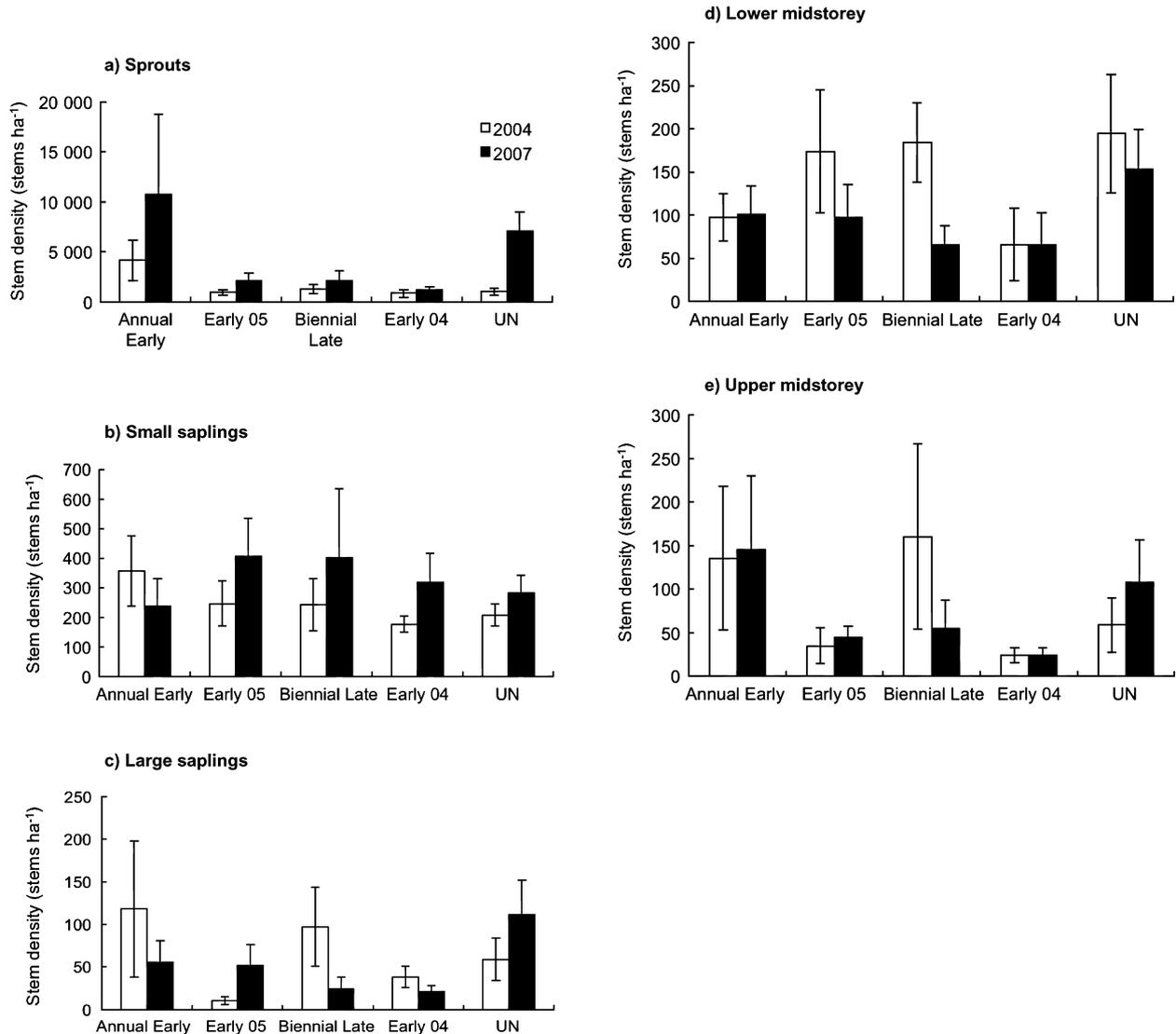


Fig. 8. Total abundance of woody stems of monsoon forest species (*sensu* Liddle *et al.* 1994) within each height stratum (sprouts, <0.5 m; small saplings, 0.5–1.99 m; large saplings, >2 m but <3 cm d.b.h.; lower midstorey, 2.0–4.99 m; upper midstorey, 5.0–9.99 m; overstorey, 10.0+ m), in 2004 before regime treatments were first implemented (white bars), and 3 years later in 2007 (black bars). Data are presented by fire regime treatment: (a) Annual Early, (b) Early 05, (c) Biennial Late, (d) Early 04 and (e) Unburnt (UN) (see Table 1 for details of intensity and frequency). Data are mean stem density \pm SE, where transect ($n = 6$) is the unit of replication. Note differences in scale.

Density of the annual grass *S. intrans* was low (≤ 0.06 individuals m^{-2}) before burning commenced and remained so 3 years after the application of fire treatments. There was, however, a notable increase in abundance towards the end of the experiment, apparently unrelated to fire regime (Fig. 10).

Floristic composition

After 2 years, there was no significant difference in woody ($R = -0.079$; $P = 0.721$) or grass-layer ($R = -0.119$, $P = 0.756$) species composition between fire regime treatments. At this time, however, there was a

strong, significant effect of Block evident for both components, with the open forest community in the North and Central block separating from the South block (woody plants, $R = 0.369$, $P = 0.002$; grass-layer plants, $R = 0.606$, $P = 0.002$). This dissimilarity of the woody component was primarily due to the differences in midstorey taxa (Table 5), with five of the six species that contributed more than 3% towards the dissimilarity being midstorey species, and the other being a canopy tree. Four of these species (including three rainforest species) were most common in the ecotone community of the South block. Most grass-layer plant species that contributed to the dissimilarity in composition between the wood-

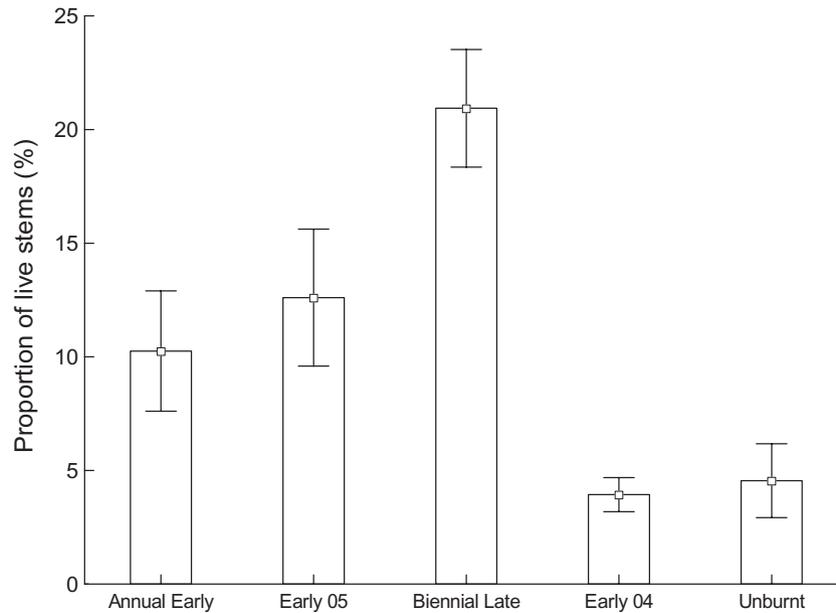


Fig. 9. The abundance of basal resprouts in 2007 as a proportion of live stems within each of the fire regime treatments (Annual Early, Early 05, Biennial Late, Early 04 and Unburnt).

Table 3. Summary for the repeated measures ANOVA analysis of grass-layer species richness, total density and the density of individual life form groups

Response variable	Source of variation and <i>F</i> -value						
	Fire (R)	Block (B)	Year (Y)	R × B	R × Y	B × Y	R × B × Y
	$F_{4,8}$	$F_{2,15}$	$F_{2,4}$	$F_{8,15}$	$F_{8,16}$	$F_{4,30}$	$F_{16,30}$
Species richness	2.4	74.0***	4.0	5.9**	2.1	7.9***	3.0**
Abundance							
Total	2.0	18.1***	16.1*	1.9	1.2	4.0*	2.2*
Annual grasses	0.9	28.3***	27.9**	4.1**	1.8	6.4***	3.6**
Perennial grasses [†]	2.2	77.9***	$F_{3,6} = 4.1$	4.4**	$F_{12,24} = 2.2^*$	$F_{6,45} = 3.2^*$	$F_{24,45} = 1.5$
Forbs	2.3	27.8***	1.1	2.5	2.2	2.6	0.7
Sedges	1.7	18.3***	5.7	1.9	0.9	2.6	2.4*
Legumes	3.7	34.9***	8.0*	4.1**	3.9**	4.8**	3.7**

Statistically significant test statistics are indicated by asterisks (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). [†]Data examined annual surveys between 2004 and 2007 inclusive; all other variables examined data between 2005 and 2007 inclusive; late sampling in 2004 precluded the sampling of some life form group.

land (North and Central blocks) and ecotone (South block) were more abundant in the woodland, with the notable exception of *E. trisetata*, which was much more abundant in the ecotone (Table 5).

DISCUSSION

Vegetation structure after long-term fire exclusion

The high density of woody plants at the site at the commencement of the study, particularly in the lower

midstorey, suggests that a significant change in vegetation structure occurred during the period of fire exclusion. The density of woody sprouts and small saplings at the site (500–1000 stems ha⁻¹) was considerably higher than typically occurs in Australian savannas (Bowman & Panton 1995; Vigilante & Bowman 2004). In contrast, woody stem density was similar to that at another Australian savanna site (Munmarlary; 1400 midstorey stems per hectare) where fire had been excluded for >20 years, and where midstorey stems were previously absent (Russell-Smith *et al.* 2003). At our site, edaphic characteristics strongly affected the development of the midstorey, with significantly higher

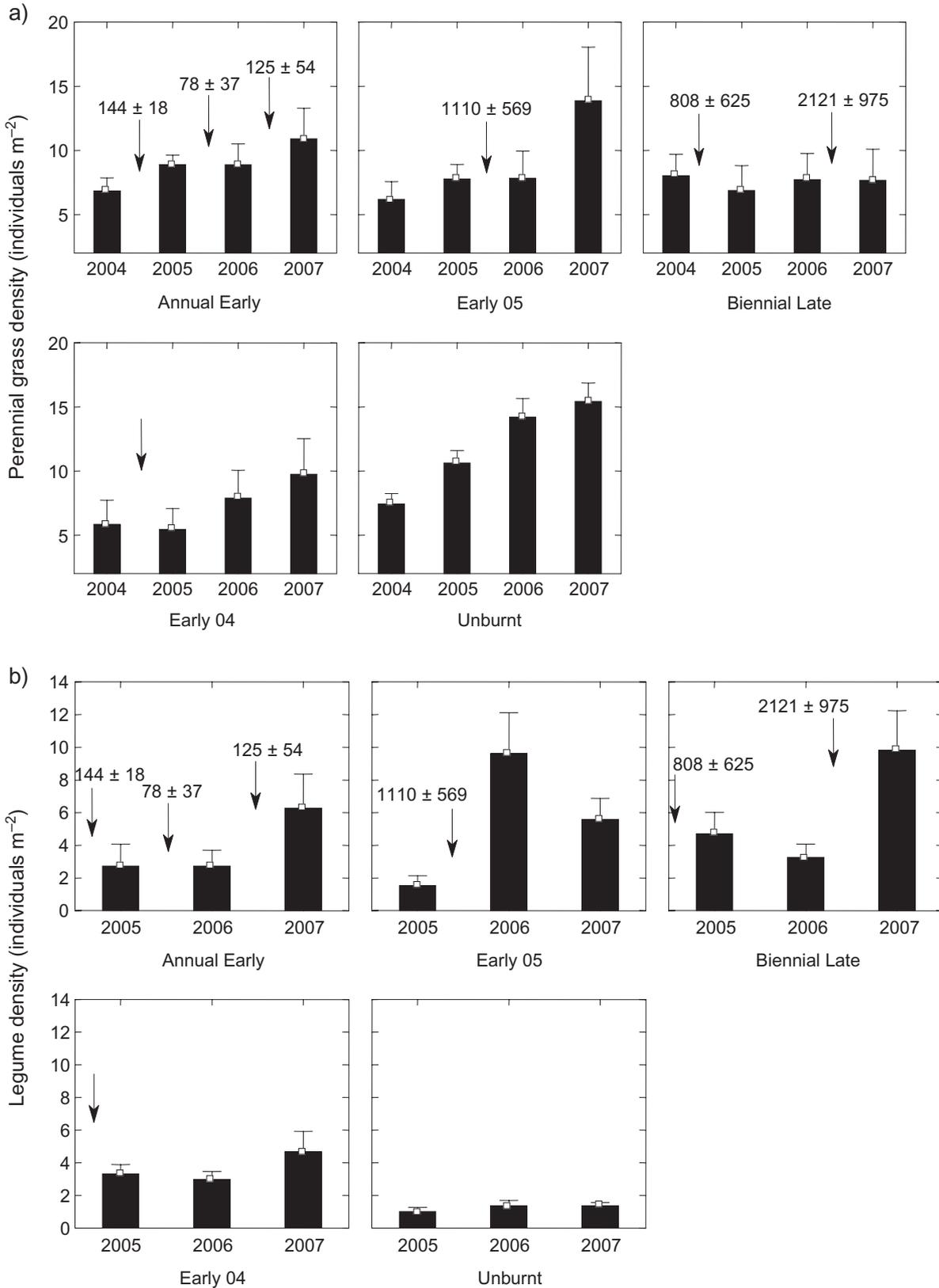


Fig. 10. Mean (+1 SE) density of (a) perennial grasses (b) legumes, and (c) *Sorghum intrans*, categorized by fire treatment and year. Perennial grasses and legumes showed a significant regime × year interaction in the experiment (see Table 1), whereas *S. intrans* did not. Arrows and associated numbers indicate the timing of fires for each treatment and their intensity (kW m⁻¹ ± 1 SE; R. Williams, unpubl. data 2004–2006; see Table 1).

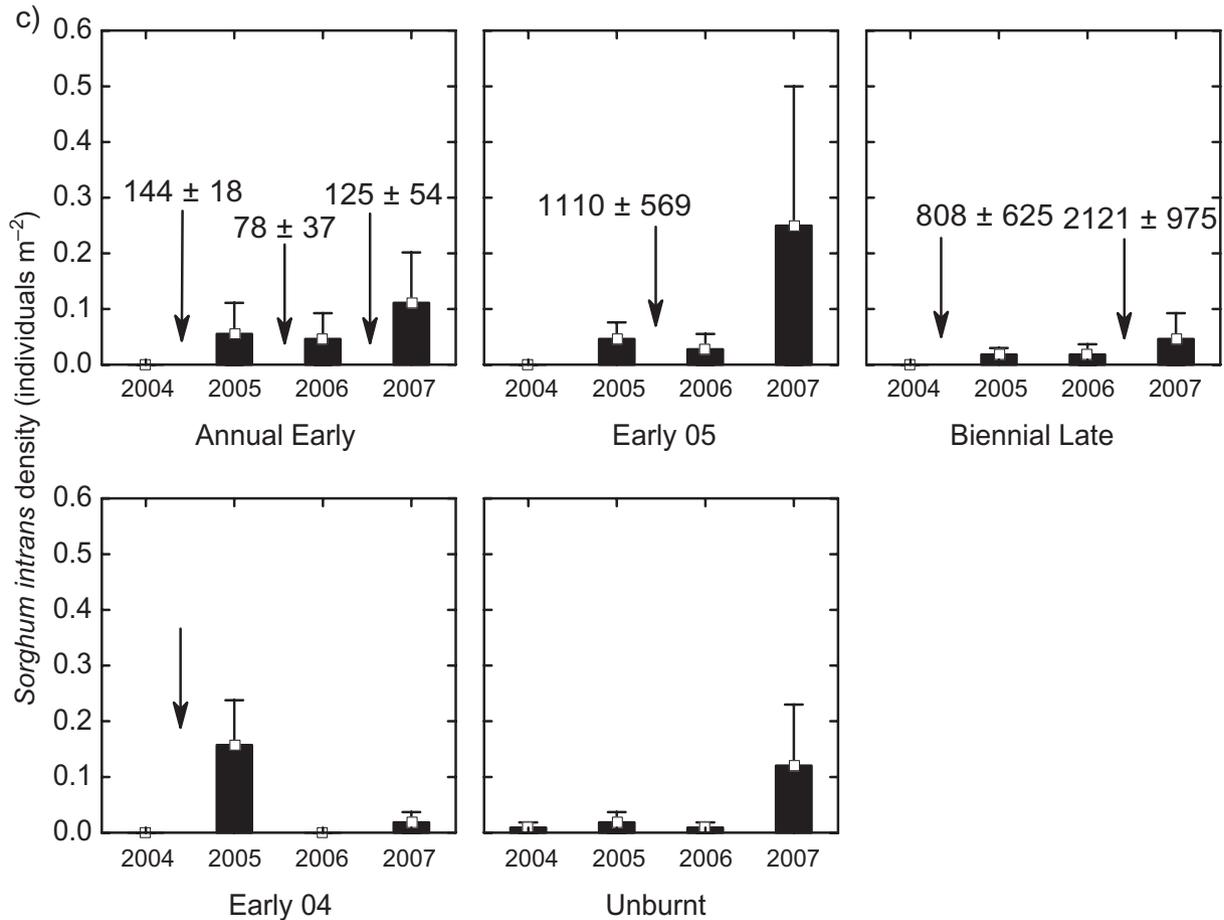


Fig. 10. Continued

Table 4. Inter-annual variation in the abundance of grass-layer plants (categorized by life form; fire regimes pooled) and rainfall in the late dry season (August to October inclusive) and wet season (November to February inclusive)

	Year			
	2004	2005	2006	2007
Abundance (individuals m ⁻² ± 1 SE)				
Total	–	60.1 (7.0)	62.2 (7.0)	86.7 (11.7)
Annual grasses	–	16.0 (3.0)	23.8 (4.7)	38.3 (6.0)
Perennial grasses	7.0 (0.6)	7.7 (0.6)	9.1 (0.8)	11.3 (1.1)
Forbs	–	17.6 (2.9)	18.5 (3.0)	24.1 (7.0)
Sedges	–	15.8 (2.8)	6.8 (1.4)	8.5 (1.9)
Legumes	–	3.0 (0.5)	3.9 (0.7)	5.4 (0.7)
Rainfall (mm)				
Late dry season prior [†]	64	101	33	2
Wet season prior [‡]	1050	581	789	1115
Rainfall (no. rain days)				
Late dry season prior	7	6	5	1
Wet season prior	80	62	67	78

Abundance data for most life-form groups are unavailable for 2004, as many annual species had already cured by the time of sampling. [†]Rainfall collected within 2 km of the study site. [‡]Rainfall at the site was not consistently recorded in one wet season (2007) and so data presented are from Middle Point Automatic Weather Station 36 km to the north-east (Bureau of Meteorology, unpubl. data 2004–2007). Mean rainfall at Middle Point Automatic Weather Station (for the period 1957–2004) is 71 mm on 9 rain days in the late dry season period, and 965 mm on 72 rain days for the wet season period (Bureau of Meteorology, unpubl. data 2004–2007)

Table 5. Mean density (untransformed) of woody and grass-layer plant species in 2007, in each block at the Territory Wildlife Park study site, which contributed at least 3% of the dissimilarity in species composition between blocks

Species	Structural / lifeform group	Mean density by block (stems ha ⁻¹ , woody plants; individuals ha ⁻¹ , grass-layer plants)			Dissimilarity (%)	Cumulative dissimilarity (%)
		North (woodland)	Centre (woodland)	South (ecotone)		
Woody plants						
<i>Exocarpus latifolius</i> [†]	Shrub	319	4 587	13 507	10.05	10.05
<i>Petalostigma pubescens</i>	Shrub	125	17	3 208	5.82	15.87
<i>Calytrix exstipulata</i>	Shrub	1 975	2 885	2 007	4.93	20.8
<i>Alphitonia excelsa</i> [†]	Shrub	152	160	2 535	4.77	25.57
<i>Petalostigma quadriloculare</i>	Shrub	1 034	1 590	1 424	3.76	29.33
<i>Syzygium eucalyptoides</i> [†]	Tree	194	28	1 198	3.09	32.43
Grass-layer plants						
<i>Pseudopogonatherum contortum</i>	Annual	282 824	159 861	0.0	10.5	10.5
<i>Thaumastochloa major</i>	Annual	98 611	64 907	3 380	5.64	16.15
<i>Eriachne trisetata</i>	Perennial	20 278	57 732	139 676	5.45	21.6
<i>Schizachyrium fragile</i>	Annual	98 519	6 296	3 796	5.18	26.77
<i>Fimbristylis</i> sp. <i>Charles Darwin</i> (JL Egan 5300)	Sedge	65 972	60 000	1 574	3.72	30.49
<i>Spermacoce exsertata</i>	Herb	9 352	106 065	79 398	3.65	34.14

Species in bold font were most abundant in the ecotone community (Southern block). Note separate SIMPER analyses were conducted for woody plants and grass-layer plants. [†]Monsoon forest species (Liddle *et al.* 1994).

midstorey stem density in the South block, where the sandy loam soils with low gravel content are likely to result in higher plant available moisture compared with the North and Central blocks where the soils are clay loams with high gravel content and a shallow lateritic layer (Scott *et al.* 2009). The South block is located close to a permanent freshwater lagoon, and therefore the watertable is likely to be higher throughout the dry season than on the ridge in the north (Scott *et al.* 2009). This process of woody thickening is also supported by the trends documented in the UN regime during the 3 years of this study, when stem density increased throughout most strata. An increase in the midstorey during this period is consistent with previous fire experiments in the savannas of northern Australia, Africa and South America, where fire exclusion has enabled the recruitment of woody sprouts into the midstorey above the flame zone and away from the competition of grass-layer plants (Brookman-Amissah *et al.* 1980; San José & Farinas 1991; Silva *et al.* 2001; Russell-Smith *et al.* 2003; Woinarski *et al.* 2004).

A large proportion of individuals at the site, particularly in the grass layer, were rainforest species; however, it is unclear the extent to which this reflects species composition prior to fire exclusion, or recruitment after. Many of the most common rainforest-associated species (e.g. *A. excelsa* and *Ac. lamprocarpa*) also occur in frequently burnt savannas, but show a strong association with fire protection over time (Bowman & Panton 1995; Woinarski *et al.* 2004). Edaphic characteristics were critically important in the

composition of the midstorey, with substantially higher representation of rainforest species in the South block. These edaphic characteristics clearly influenced the structure and composition of the midstorey within this study site irrespective of fire regime.

Grass-layer plant composition has changed during the period of long-term fire exclusion since 1981. Vegetation surveys at the time showed that the grass layer was dominated by the tall annual *Sarga intrans* (Andersen & Hoffmann 2011), and this species remains dominant immediately outside the Park (Scott 2008). Therefore, in the long-term absence of fire, the composition of the grass understorey changed to dominance by the smaller perennial *E. trisetata* and low-growing annuals (e.g. *P. contortum* and *E. agrostidea*). This change has been documented elsewhere in northern Australia (Russell-Smith *et al.* 2003; Williams *et al.* 2003a; Woinarski *et al.* 2004). Mechanistic experiments have independently shown the negative influence of canopy shading and litter cover on the establishment and seed production of grasses, including annual *Sorghum* (Scott *et al.* 2010a).

Effects of reintroducing fire

Reintroducing moderate intensity fire to the long-unburnt savanna caused the vegetation to transition back towards open savanna structure, principally through a reduction in lower midstorey stem density. However, fire intensity was the important factor deter-

mining this change. The abundance of midstorey stems increased or remained similar in the UN regime and with repeated, low-intensity fire (Annual Early, mean fire intensity = 116 kW m^{-1}), demonstrating woody plant density had not peaked during the 20 years of fire exclusion. By contrast, the abundance of large saplings decreased in the Late regime (808 and 2121 kW m^{-1}), and the number of lower midstorey stems decreased considerably in both the Biennial Late and Early 05 regime (1110 kW m^{-1}). At least part of this reduction in midstorey stem density could be attributed to top-kill, where individuals remained alive, but were redistributed into smaller size classes (e.g. sprouts). Minimal changes to basal area were recorded (Table 2), indicating that most structural change involved individuals with thin stems (i.e. in the midstorey).

In general, the resilience of sprouts and small saplings, response of midstorey stems and resistance of overstorey trees to fire in this study is well known in northern Australia. The susceptibility of midstorey stems to burning is consistent with the notion that smaller (lower d.b.h.) plants experience greater rates of stem mortality (top-kill) and have a lower probability of surviving fire (Williams *et al.* 1999; Werner *et al.* 2006; Liedloff & Cook 2007). The fire intensities in this study were low. Had fire intensities been higher (e.g. $>5000 \text{ kW m}^{-1}$), mortality and top-kill may have been much higher and basal area significantly reduced, as a consequence of mortality in large overstorey trees, as evidenced by the landscape-scale Kapalga fire experiment (Williams *et al.* 1999).

The reintroduction of fire had a limited effect on grass-layer species composition. Populations of grass-layer plants are highly resilient to fire as a consequence of vegetative regeneration and the annual input of seeds into fire-protected, dry season seed banks (Belsky 1992; O'Connor & Pickett 1992; Williams *et al.* 2003a; Scott *et al.* 2010b). The increase in perennial grass density in compartments remaining unburnt for several years appears to reflect increased seedling recruitment in the absence of fire because there was a uniformly low mortality rate of common, adult perennial grasses recorded at the site in the UN regime and the burnt regimes (Scott *et al.* 2010c). Enhanced seedling recruitment in the unburnt areas could have resulted from an increase in seed production or seed viability, or lower rates of seed or seedling mortality, in those compartments. The marked increase in legume density after fire (Fig. 10b) was a direct result of elevated temperatures in the soil overcoming physical dormancy (Auld & O'Connell 1991; Bell & Williams 1998). The response of seeds to heating has been documented for several legume species in north-eastern Australia, including those at the study site (Williams *et al.* 2003b; Scott *et al.* 2010b). However, even though perennial grasses and

legumes showed significant changes in abundance over time according to fire regime, these life forms were only minor components of the vegetation and so did not significantly influence composition overall.

Inter-annual rainfall variability was strongly related to the density of grass-layer plants (Table 4). Rainfall variability has been demonstrated to affect grass-layer savanna species composition, particularly in response to long periods of drought (O'Connor 1994; O'Connor & Everson 1998; Bisigato & Bertiller 2004). Seedlings of grass-layer plants are vulnerable to desiccation, so mortality would be exacerbated in drier wet seasons with prolonged periods of low rainfall intensity or frequency (Andrew & Mott 1983; O'Connor 1994). A later start to the wet season, as occurred in 2006–2007, could conversely enhance seedling survival by allowing most seed germination to occur closer to the mid-wet season period of reliable rainfall, thereby minimizing post-germination mortality (Crowley & Garnett 1999).

Reversibility of change following long-term fire exclusion

State-and-transition conceptual models accommodate the possibility that different stable vegetation states are possible within a location, and vegetation state persists unless there is a significant change in an ecosystem driver (Bestelmeyer *et al.* 2003). An open savanna state is maintained by burning. Fire results in some mortality of midstorey and overstorey stems, and the suppression of woody sprouts in the grass layer. The open canopy supports a continuous grass layer, which, due to an annual cycle of fuel accumulation and curing, reinforces the regime of frequent burning (R.J. Williams *et al.* 2003). At the beginning of this study, the savanna structure reflected the effects of a long period of fire exclusion with a well-developed midstorey (2–10 m) represented by approx. $500\text{--}1000 \text{ stems ha}^{-1}$. In our study, fires of moderate intensity ($1000\text{--}2000 \text{ kW m}^{-1}$) reduced the density of the midstorey, with a decrease from 800 to $350 \text{ stems ha}^{-1}$ in the Biennial Late regime, and from approx. 1100 to $650 \text{ stems ha}^{-1}$ in the Early 05 regime. This study showed, however, that fire intensity and frequency are critical to these processes, with a maintenance (at approx. $1000 \text{ stems ha}^{-1}$) of the midstorey in the UN regime and increased development of the midstorey (from approx. 500 to $750 \text{ stems ha}^{-1}$) in the low intensity Annual Early regime. Moderate or high intensity fires over several years may be required to achieve the sparse midstorey characteristic of frequently burnt savanna in this region, and fully restore the

structure and/or function of frequently burnt communities typical of the region's *Eucalyptus* dominated savanna.

The reduction in lower midstorey stems in higher-intensity regimes was driven by the responses of canopy and rainforest species in particular (Table 2). It would seem, therefore, that both canopy and rainforest species experience a recruitment bottleneck in the lower midstorey in these regimes. For the short term at least, this has little consequence for canopy species because of the resilience and longevity of trees already in the overstorey. Over the longer-term, however, fire-free periods will be required for recruitment into the overstorey (Setterfield 2002). Similarly, fire-free periods would be required for rainforest species to dominate the midstorey and overstorey vegetation layers.

Even if the flammable annual grass *S. intrans* was replaced by less flammable grasses such as the perennial *E. trisetata*, the changes still indicate the presence of a pre-threshold state across most of the experimental catchments because the resulting composition carried fires that modified vegetation structure (positive feedbacks). This change in composition and others, such as the increase in perennial grass density with fire exclusion (Fig. 10a) and increase in legume density after fire (Fig. 10b), did not cause any structural or functional degradation of the ecosystem. In the time-frame examined, the loss of *S. intrans* was unidirectional; the reintroduction of fire was unable to reinstate its former dominance. This suggests some longer-term implications, given poor seed dispersal and a lack of long-term seed dormancy within the seed bank (Andrew & Mott 1983). The immediate (1 year) post-fire increase in the abundance of *Sorghum ecarinatum* Lazarides reported on the Arnhem Plateau was probably a result of its occurrence in over half of the quadrats prior to the fire (Russell-Smith *et al.* 2002).

A small proportion of the site appears to have already crossed an ecological threshold, characterized by the predominance of positive feedbacks which reinforce a change between open woodland and closed forest states. There were patches in the South block (approx. 1000 m²) where woody plant density was very high (approx. 10 500 woody stems per metre), presumably a result of more favourable edaphic conditions supporting this midstorey development in the absence of fire (Bowman & Minchin 1987; Medina & Silva 1990; Scott *et al.* 2009). As a consequence, the higher canopy shading and higher amounts of litter (see Fig. 8) resulted in a fuel layer dominated by litter with significantly fewer herbaceous grass-layer plant species (Scott *et al.* 2009). These litter patches acted as a network of firebreaks, and despite efforts to re-ignite them, were unable to sustain fire. A dominance of litter in the fuel layer therefore reinforced woody thickening on a transition towards closed forest.

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