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RESPONSE OF *EUCALYPTUS*-DOMINATED SAVANNA TO FREQUENT FIRES: LESSONS FROM MUNMARLARY, 1973–1996

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Abstract. We assess a replicated fire plot experiment undertaken between 1973 and 1996 in two *Eucalyptus*-dominated savanna vegetation formations (open forest, woodland), at Munmarlary, in monsoonal northern Australia. Four treatments, each with three replicates, were imposed on each vegetation type: annual early dry-season burning; annual late dry-season burning; biennial early dry-season burning; and unburned controls. Treatments were imposed faithfully, with noted exceptions, on 1-ha plots. Fire intensities were typically low (<1000 kW/m) to moderate (1000–2500 kW/m), varied significantly between treatments, and generally were greater in woodland. In both woodland and open forest, pH was significantly lower and NO_3-N was significantly higher in unburned plots. Organic C was not significantly greater in unburned treatments. Effects of fire regime on other soil chemical properties differed between open forest and woodland sites. Among the grasses, invariant frequent burning led to the dominance of a small number of annual species, notably regionally dominant *Sorghum*. In the absence of burning, annuals declined generally, whereas some perennials increased while most decreased. These responses usually were apparent within the first five years of the experiment. At the relatively small spatial scale of the grass sampling regime, there was high turnover of both annual and perennial grasses. Under low- to moderate-intensity, frequent burning regimes, woody vegetation dominated by mature eucalypts is structurally stable. In the absence of burning for at least five years, there was release of the non-eucalypt, woody component into the midstory; this occurred more rapidly in open forest. Accession of rain forest species occurred on some woodland plots, especially the unburned treatment. In contrast, eucalypts were not released significantly from the understory. Rather, as suggested by other studies, recruitment of eucalypts into the canopy appears to involve significantly reduced root competition through death of dominant eucalypts. Although the Munmarlary experiment provides invaluable quantitative data for exploring relationships between fire regimes and the responses of north Australian savanna systems, it has been less successful in meeting the complex information requirements of regional fire managers. Replicated experimental fire plot designs, no matter how elegant and rigorously implemented, may substantially fail the test of management relevance, given the fundamental requirement for savanna biodiversity managers to experience the integrated effects of fire regimes that vary idiosyncratically over multiple time and spatial scales. We suggest that such information requirements are better met through modest, targeted ''adaptive management'' studies, involving collaborative partnerships between managers and researchers.

Key words: adaptive management; Australia; eucalypts; Eucalyptus *spp.; fire experiment; fire intensity; fire plot; fire regime; northern Australia; savanna; tropical savanna.*

INTRODUCTION

It is widely recognized that along with seasonal water availability, nutrients, and herbivory, fire regimes play a critical role in regulating the floristic composition, vegetation structure, function, and dynamics of savanna systems (Walker 1985, Skarpe 1992, Scholes and Walker 1993). For example, it is commonly observed that prolonged absence of fire in savanna results in invasion by species sensitive to fire and increases in woody plant density (Rose Innes 1972, Archer et al. 1988, San Jose and Farinas 1991, Swaine et al. 1992, Moreira 2000), particularly when associated with heavy grazing (Trollope 1982, Hopkins 1983, Harrington and Hodgkinson 1986, Archer 1995, Roques et al. 2001, Silva et al. 2001). Conversely, under fire regimes dominated by frequent, especially intense fires, her-

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baceous species (especially grasses) are promoted, populations of woody species sensitive to fire are greatly reduced or eliminated, woody vegetative resprouts may proliferate in lower strata, and juveniles and upper strata are depleted (Rose Innes 1972, Hopkins 1983, Ratter 1992, Hoffmann 1999, Williams et al. 1999, 2002, Roques et al. 2001). Frequent, relatively intense fires result in the archetypal woody ''bottleneck'' savanna physiognomy (Walter 1971, Braithwaite and Estbergs 1985, Bond and van Wilgen 1996). The recent prominence of non-equilibrium models of tree–grass balance in savanna systems (Scholes and Archer 1997, Higgins et al. 2000) recognizes, in part, the significance of interactions between rainfall variability and fire regimes (and other disturbance) to long-term woody species recruitment.

The experimental study of the effects of fire regimes on savanna vegetation and soil properties typically has been undertaken with reference to plots from which fire has been excluded for extended periods, or to more elaborate designs involving one or more fire treatments as well as unburned controls. Much of this work has been undertaken in Africa. In summarizing over 40 years' experience from experimental fire plot studies in west Africa, Rose Innes (1972:159) concluded that: (1) fire retards woody development in savannas; (2) intense fires in the late dry season are particularly destructive of woody elements; (3) moderate-intensity fires in the early dry season are less destructive, but still allow for woody development; (4) fire also exerts a powerful selective influence on floristic composition, fire-tolerant species being encouraged and fire-sensitive ones eliminated; and (5) fire is a powerful tool for shaping vegetation toward chosen objectives. With regard to effects on grass layer composition and yield, O'Connor (1985) reviewed findings from over 70 fire experiments conducted in southern Africa. Although compositional changes were observed in most experiments, the effects of fire and rainfall were generally difficult to distinguish, given both high interannual rainfall variability and variation among replicate plots. Concerning effects on soil nutrients and organic matter, it is frequently (Moore 1960, Cass et al. 1984, Scholes and Walker 1993), but not universally (Fagenbro 1982, Coutinho 1990, Mistry 1998, Bird et al. 2000), observed that savanna fires have little measurable influence in the longer term.

In this paper, we present key results from a replicated fire experiment conducted over two decades in mesic savanna (>1000 mm/yr), at Munmarlary, in present-day Kakadu National Park, northern Australia. The experiment was established in 1972 with the objectives of providing regional land managers with permanent reference plots and a quantitative basis for studying the longer term responses of *Eucalyptus* open forest and woodland vegetation types to four imposed treatments (Hoare et al. 1980): annual early dry-season burning, annual late dry-season burning, biennial early dry-season burning, and fire protection. The experimental regime was maintained faithfully, with noted exceptions, from 1973 until the end of the field experiment in 1996. During that time, vegetation assessments were undertaken for the period 1973–1978 (Hoare et al. 1980) and in 1986 (Bowman et al. 1988). Other assessments have included ants on open forest plots in 1986 (Andersen 1991), birds on all plots in 1987 (Woinarski 1990), epiphytic orchids on woodland plots in 1989 (Cook 1991), and vegetation on unburned open forest plots vs. surrounding vegetation subject to the ambient fire regime in 1994 (Bowman and Panton 1995).

Hoare et al. (1980) and Bowman et al. (1988) found increases in woody stems, especially non-eucalypts, on unburned plots. In contrast to African studies, however, those authors found little evidence for structural and floristic differences between burned treatments in either open-forest or woodland vegetation, and no evidence for accession of more fire-sensitive, closed-forest species on unburned plots. The generality of these results was questioned by Lonsdale and Braithwaite (1991), who posited that the small sizes of treatment plots (100 × 100 m) would preclude the acceleration of fires in late dry-season treatments to maximum intensities possible under prevailing weather conditions. Nevertheless, more recent data obtained from an extensive northern Australian savanna grassland fire behavior experiment indicate that initial acceleration from a line of ignition is achieved rapidly, often within 15 seconds (Cheney et al. 1993).

The faunal studies of Woinarski (1990) and Andersen (1991) demonstrated that different functional groups of birds and ants, respectively, were generally advantaged by different fire regimes. For example, frugivorous birds or species that feed and/or nest in shrubby understories were more commonly observed in unburned vegetation, whereas regionally dominant, opportunist, and hot-climate specialist ant taxa were most abundant on annually burned plots, and cryptic taxa and generalized myrmecines dominated unburned plots. However, the small sizes of the experimental plots were found to be clearly inadequate for documenting landscape-scale processes such as faunal movements and grazing interactions (Andersen and Braithwaite 1992). Cook (1991) demonstrated that two species of epiphytic orchids occurring on the woodland site were particularly abundant on unburned plots. The vegetation study of Bowman and Panton (1995) found that, with reference to unburned plots on the open forest site, there were markedly fewer saplings, poles, and tree-sized individuals, but not sprouts, in surrounding vegetation subject to the ambient fire regime; after 22 years, there was still no evidence for rain forest succession on unburned plots.

The Munmarlary experiment is one of only two long-term replicated experiments examining the impacts of fire regimes on mesic *Eucalyptus*-dominated savanna in northern Australia. A separate landscape-scale ex-

periment, employing four treatments conducted over five years (1990–1994), was established at the former Kapalga Research Station, also in Kakadu National Park (Andersen et al. 1998). Data from Kapalga indicate that very intense savanna fires in *Eucalyptus*-dominated savanna vegetation result in differential effects on woody species and structural components (Lonsdale and Braithwaite 1991, Williams 1995, Williams et al. 1999, 2002). Despite the scientific merits of the Kapalga program, it has been recognized that, as with Munmarlary, the experiment failed to engage regional land managers because there was insufficient involvement of managers in the design, implementation, and ownership of the experiment (Andersen and McKaige 1997), and the set of applied treatments was relatively narrow.

A full assessment of the Munmarlary experiment using all available data for the period 1973–1996 is given in Russell-Smith et al. (2002*a*). Our purpose here is to report major findings from Munmarlary regarding the effects of alternative fire management regimes on (1) soil nutrients and organic matter; (2) grass species and life history (perennial, annual) compositional changes; and (3) effects on woody species floristics and structure. We conclude by examining management and methodological implications of these findings.

Methods

Study sites

Study sites were located in *Eucalyptus*-dominated open forest and woodland at Munmarlary in the north of present-day Kakadu National Park, northern Australia (12°28′ S, 132°30′ E). Such vegetation dominates savanna landscapes throughout northern Australia under a wide range of seasonal rainfall (<600 to >2000 mm/yr) and typically low-nutrient substrate conditions (Stocker and Mott 1981, Williams et al. 2002). By contrast with eucalypt woodland formations, open forest occurs in higher rainfall coastal and subcoastal areas, typically on deep, well-drained, and light-textured soils (Wilson et al. 1990). The selected sites were representative of Kay and Jay land systems (Story et al. 1969), by which names the open forest and woodland plots were respectively referred to throughout the life of the experiment. Detailed descriptions are given in Hoare et al. (1980) and Bowman et al. (1988). Plant species nomenclature follows Dunlop et al. (1995).

The open forest site is situated on slightly sloping terrain (<2°), with deep, well-drained, dark-reddish brown sandy loam soils. At the start of the experiment, the open forest site was dominated by *Eucalyptus tetrodonta*, with lesser *E. miniata* and *E. porrecta*, generally with a canopy height of 20–30 m. Canopy cover, estimated from low-level aerial photos, was 48%. The sparse midstory consisted of broad-leaved small trees (*Buchanania obovata*, *Gardenia megasperma*, *Planchonia careya*, *Xanthostemon paradoxus*) and legumes (*Erythrophleum chlorostachys*, *Acacia* shrubs). Understory components included relatively high densities of shrubs (predominantly <1 m) and a dense cover of perennial and annual grasses.

The woodland site is situated on a gently undulating, complex land surface with soils varying from poorly drained sandy clays to freely draining sands. Initially the site was dominated by *Eucalyptus confertiflora* with lesser *E. tectifica*, *E. tetrodonta*, and *E. polycarpa*. Canopy heights ranged generally between 10 and 20 m, providing 21% canopy cover. The midstory, comprising a variety of broadleaved small trees (e.g., *Brachychiton paradoxus*, *Gardenia megasperma*, *Planchonia careya*, *Terminalia ferdinandiana*, *Erythrophleum chlorostachys*) and the palm *Livistona humilis*, was better developed than on the open forest site. The understory consisted of relatively high densities of shrubs (predominantly <1 m) and a dense, floristically diverse cover of perennial and annual grasses

A Detrended Correspondence Analysis (DCA) of floristic presence/absence data collected from all plots in 1986 demonstrated that vegetation of the open forest and woodland sites is floristically distinct (Bowman et al. 1988). As noted both by Hoare et al. (1980) and Bowman et al. (1988), up until the mid-1980s the unfenced Munmarlary sites, particularly the woodland, supported high densities of feral Asian water buffalo (*Bubalus bubalis* Lydekker). These authors reported the occurrence of patches of trampled bare ground and dense stands of the exotic weed *Hyptis suaveolens* in the woodland experimental site. Since the late 1980s, nearly all feral buffalo have been removed from Kakadu National Park as part of a national bovine disease eradication program (Skeat et al. 1996).

As for northern Australia generally, the climate is characterized by marked rainfall seasonality, with >90% occurring in the wet-season months, November–March. No detailed climate data are available for the site. Mean annual rainfall, recorded from Gunbalanya, the nearest long-term weather-recording station some 45 km to the southeast, is ~1500 mm (Fig. 1a). Although annual rainfall is highly variable locally, the wet season is a highly reliable event (Taylor and Tulloch 1985). Thus, over the period of study, ≥50 mm of rainfall was recorded annually at Gunbalanya in at least four consecutive wet months (Fig. 1b). Mean monthly relative humidity at 1500 hours ranges from >70% during the wet season to <30% during September. Daily maximum temperatures average >30°C over the year; frosts have not been reported. Winds over the dry-season burning period are dominated generally by strong easterlies and southeasterlies; from about October, winds become more northerly and northwesterly, increasingly under the influence of the northwest monsoon (McAlpine 1976, Gill et al. 1996).

Experimental design and treatments

The fire regime treatments and abbreviations, as referred to in the following text, tables, and figures, were

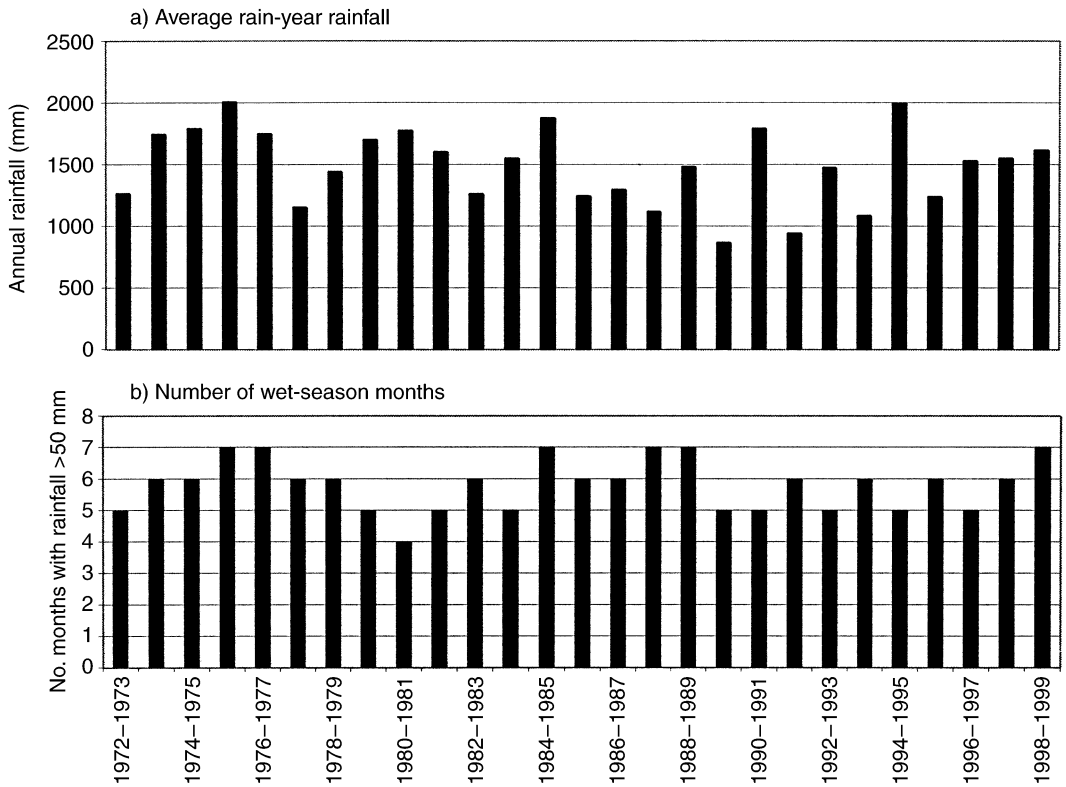

FIG. 1. Rainfall data, 1973–1999, Gunbalanya, Northern Territory, Australia: (a) mean rain-year (July–June) rainfall; (b) number of consecutive wet-season months with rainfall >50 mm. Source: Australian Bureau of Meteorology.

as follows: (1) EANN, annual early dry-season burning (May–June mostly), lit once the experimental sites became accessible by road after the wet season; (2) LANN, annual late dry-season burning (August–October mostly); (3) BIEN, biennial early dry-season burning, lit at the same time as annual early dry-season fires; and (4) UNBN, complete protection from fire.

In each of the open forest and woodland experimental sites, the four treatments were applied to ~100 × 100 m plots laid out systematically in three contiguous replicate square blocks (Fig. 2). The configuration of treatment plots per block was allocated randomly at each site separately, and then consistently across all three blocks at respective sites. Replicate plots (i.e., the same fire treatment on the same land system) were 0.3–0.6 km apart. Individual plots were separated by a double grid of graded firebreaks and intervening vegetation buffers; the latter were burned prior to early dry-season treatments. The open forest and woodland sites were all burned in September 1972, prior to the laying out of the experimental sampling subplots in October of that year. Vegetation sampling subplots, each 50 × 50 m, were established more or less in the center of each experimental plot. Treatments began in 1973. All woodland plots were burned in a wildfire in 1974, prior to scheduled early burn treatments. Treatments were otherwise maintained as scheduled until the final assessment in 1996, with the following exceptions: for woodland, one BIEN plot was burned out of sequence in 1986, and one UNBN burned inadvertently in 1986 and 1988; for open forest, one LANN plot was inadvertently burned early both in 1976 and 1987. In our estimation, these exceptions do not significantly detract from the validity of the long-term observations described here; thus, analyses of assembled data are presented as though the experiment was fully realized.

For the first few years, fires were lit from one ignition source upwind of the internal 50 × 50 m assessment plot. Subsequently, fires were ignited along the outer 100-m upwind margin to maximize rates of spread. Up until the mid-1980s, all litter fuels were consumed in fire treatments by burning any patches that escaped combustion. Subsequent practice involved leaving such patches, given the increasing difficulties with ensuring complete burns under light and patchy fuel conditions. The presence of small, remnant patches of unburned light fuels tended to apply, however, only to annual treatments (EANN, LANN) of open forest plots; this is considered unlikely to have significantly influenced vegetation dynamics.

Sampling and data availability

Initial inventory of the plots was undertaken prior to the commencement of the early-burning treatments

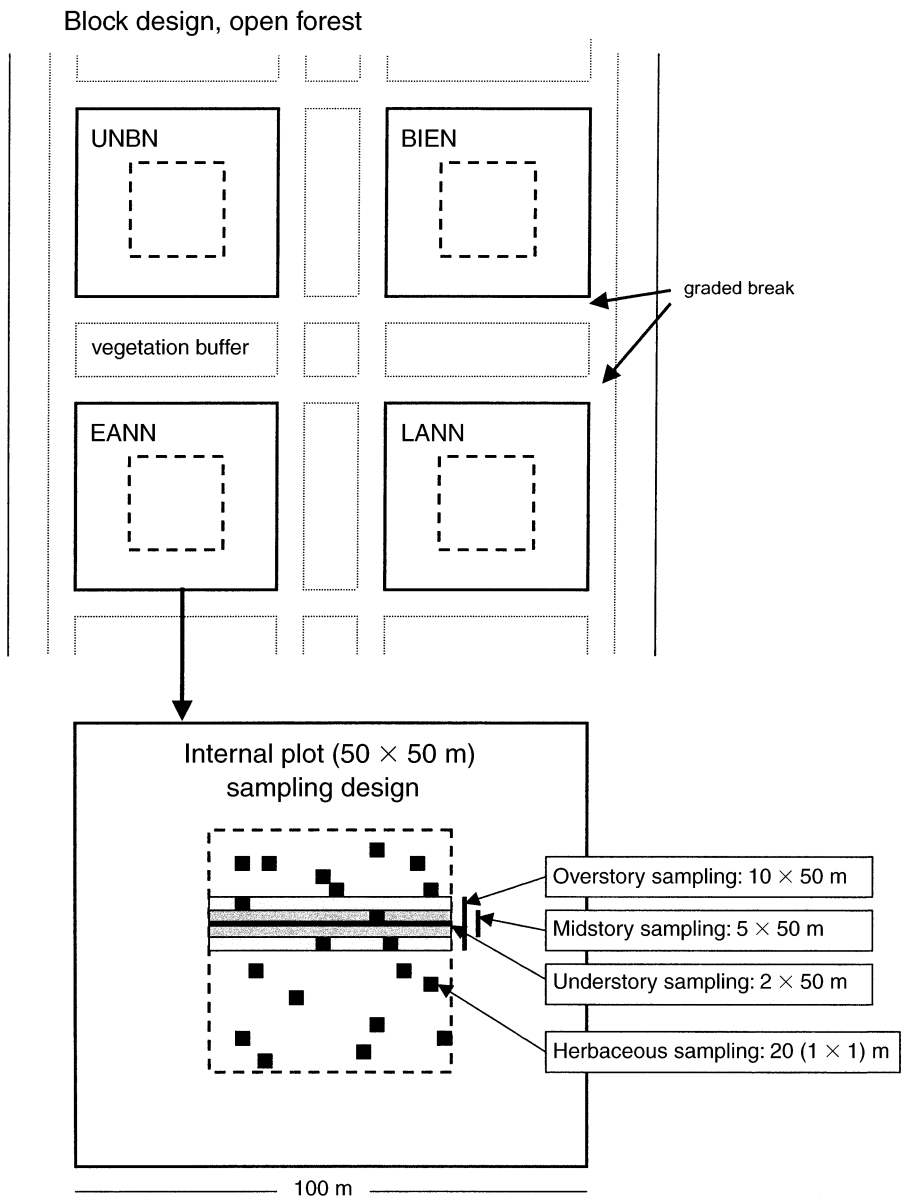

FIG. 2. Block and internal treatment plot designs for the open forest site; a slightly different, randomly selected configuration of treatment plots per block was applied at the woodland site. Note that locations of the internal 50 × 50 m sampling plot, sampling transects, and herbaceous sampling quadrats were all randomly assigned. Treatment abbreviations: EANN, annual early dry-season burning (mostly May–June); LANN, annual late dry-season burning (mostly August–October); BIEN, biennial early dry-season burning (mostly May–June); and UNBN, unburned (completely protected from fire).

in May 1973. Sampling was undertaken in the internal 50 × 50 m subplot of each 1-ha experimental plot. Sampling of the tree overstory (stems > 8 m) was undertaken along randomly located permanent transects of 50 × 10 m. Sampling of the midstory (2–8 m) and woody understory species (<2 m) was undertaken along transects of 50 × 5 m and 50 × 2 m, respectively, nested randomly within the tree sample transect. Sampling of the herbaceous ground layer was undertaken at 20 randomly located, permanent 1-m^2 quadrats. Sampling details of relevance for analyses presented here and data sets available for analysis, are outlined below for each stratum.

1) Trees were identified to species and the diameter at breast height (dbh) was measured. Tree stems were not permanently tagged. Tree (i.e., overstory) inventory data are available for 1973, 1978, and 1994 for open forest plots, and, for 1973 and 1996 for woodland plots.

2) Midstory stems were identified to species and counted. Stems were not tagged. Midstory inventory data are available for 1973, 1976, 1978, and 1994 for open forest plots, and for 1973, 1976, and 1996 for

woodland plots. Mean counts of stems per treatment (lacking species identification and measures of dispersion) are also available for woodland plots from 1978.

3) Woody understory stems in three height classes were identified to species and counted. Multistemmed individuals including clumps (clones) were counted as one individual. Full 50 × 2 m transect inventories are available for all open forest plots in 1973, 1976, and 1994, and for all woodland plots in 1973 and 1996. Mean counts of understory plants per transect (also lacking species identification and measures of dispersion) are also available for 1976 and 1978 for both open forest and woodland.

4) Ground-layer sampling of the occurrence (presence/absence) of herbaceous and woody species in each of 20 1-m^2 quadrats per plot was undertaken in 1973, 1976, 1978, and 1996, both for open forest and woodland. Ground-layer sampling in 1996 involved detailed floristic assessment of grasses only, given that sampling was undertaken in the mid-dry season following desiccation of aerial parts of herbaceous species. As a result, only analyses of grass data are presented here.

Data on fuel load and associated fire behavior were collected irregularly over the life of the experiment from both open forest and woodland plots. Fuel loads (oven-dry matter of grass and litter per square meter) were estimated from one sample per plot until the early 1980s; thereafter, at least three samples were taken per plot. Fuels were sampled immediately prior to burning treatments. However, in 1994 and 1996 at least, LANN samples were collected prior to early-annual treatments. Rates of fire spread were calculated throughout as the mean rate of spread (in meters per second) of the central and two flanking fire fronts, through the interior 50 × 50 m assessment subplot. Minimum data required for the calculation of Byram's (1959) fire line intensity (i.e., at least one fuel load estimate and mean rate of spread estimate per plot) are available for open-forest plots (EANN and LANN, 12 years; BIEN 7 years) and woodland plots (EANN, 9 years; LANN, 12 years; BIEN, 5 years).

Although soil chemical data (total N, total P, organic C) are available for some plots sampled in 1973, comparable data are not available from the end of the experiment. Instead, we present data (pH, exchangeable cations, available P, nitrate-N, organic C) derived from sampling undertaken by one of us (G. D. Cook) in August 1989. Soil samples (0–5 cm) were collected from within the internal 50 × 50 m subplot of each 1-ha experimental plot. Four random samples were taken, each consisting of bulked soil from three cores within 1 m^2. Soil pH was measured in a 1:5 soil water extract (McLean 1982). Organic carbon contents were determined by dichromate reduction. Exchangeable cations were measured by extraction with 1 mol/L ammonium acetate. Available P was measured following extraction with 0.005 mol/L H_2SO_4, and Nitrate-N following extraction with water.

Analysis

Fire intensity.—Intensity is given as Byram's fire line intensity (I), defined as the product of the rate of forward spread of the fire front, fuel load, and heat content of the fuel (Byram 1959). Following conventional usage in Australian studies (Gill and Knight 1991), the mineral-free heat of fuel combustion is taken to be 20 000 kJ/kg. Fire intensities (mean ± 1 SE) per treatment were plotted for available years of data. Given the noted data constraints, one-way ANOVA was performed on fire intensity data to test for differences between fire treatments and between blocks. Tukey's non-equal n hsd (Spjotvoll and Stoline 1973) was used to test for differences between respective pairs of treatments and pairs of blocks. Due to missing data for certain treatments in some years and the absence of obvious trends over the experimental period, treatment was tested by ANOVA with year as a covariate, thus increasing the sensitivity of the test to treatment differences. Preliminary tests of homogeneity of variance (Option HOVTEST in SAS Procedure GLM; SAS Institute 1989) and distributions of transformed and untransformed data indicated that assumptions of ANOVA were adequately met. An alpha level of 0.05 was applied here and in all other statistical tests.

Soils.—Untransformed data for respective treatments were pooled across blocks ($n = 36$) and analyzed by one-way ANOVA.

Grass species composition.—We analyzed variation in the frequency with which grass species were recorded in permanent plots by repeated-measures ANOVA (SAS Procedure GLM). Species frequency was calculated as the proportion of quadrats occupied (counts/20) and that proportion was arcsine-transformed. Initially, observations for all species were considered collectively to examine broad trends in the responses of annuals and perennials to the fire treatments, with life history strategy (LHS) being entered as a factor in models. Subsequently, all species that appeared in at least five of the 48 samples taken from the 20 by 1-m^2 arrays were assessed individually. Frequencies of annual and perennial species turnover were calculated separately for open forest and woodland sites and were compared among treatments. Variation in species turnover among treatments and with life-form (perennial or annual) was examined by chi-square analysis (SAS Procedure FREQ).

Woody species.—We used procedure GLM in the SAS system (SAS Institute 1989) for analyses of variation in stem density and basal area. The principal response of interest within both the woodland and open forest plots is a change in the number of woody stems with treatment, and the direction of that change through time. The rate of direct response of woody stems to the different fire treatments is likely to vary with the size and height of stems. For example, for the large mature stems of the overstory, responses may be rel-

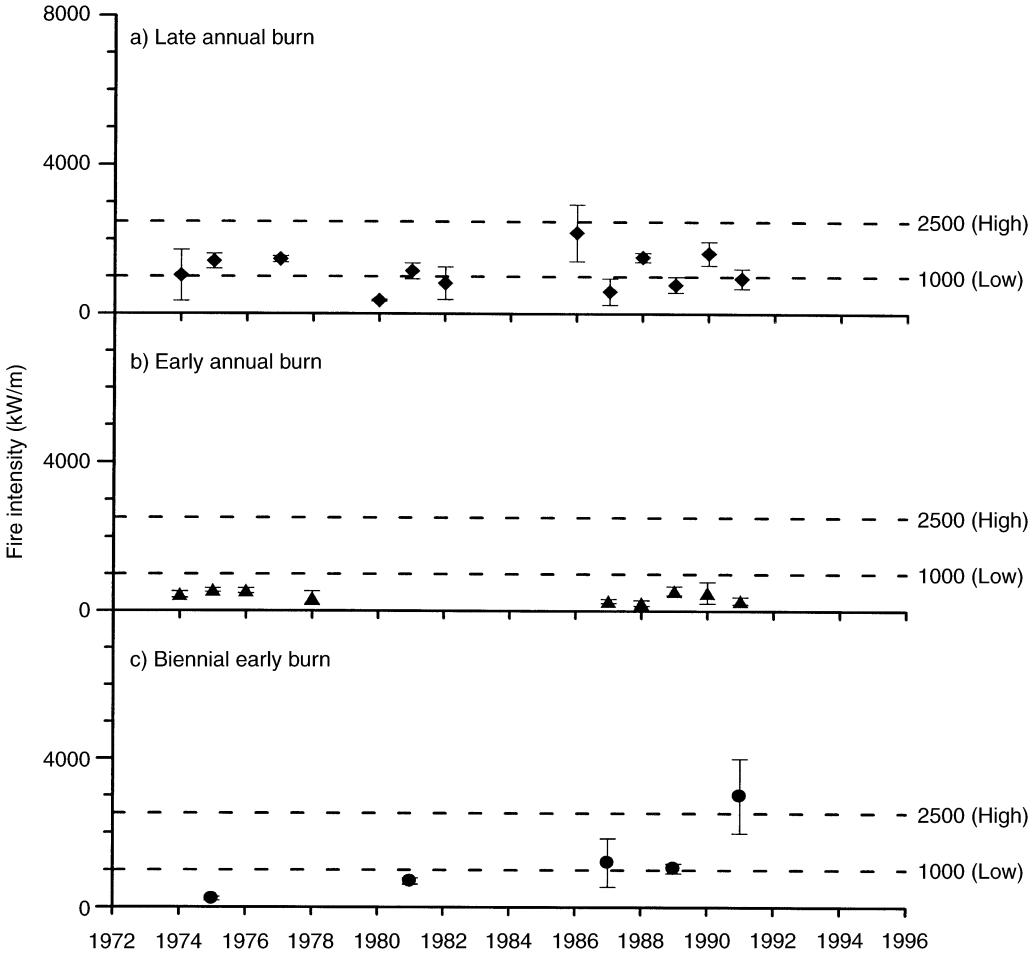

FIG. 3. Mean (± 1 SE) fire intensities under different fire treatments for open forest using all available quantitative data between 1973 and 1996.

atively slow, being measured in years or decades, whereas entry of new woody stems to the understory from suckers or seedlings may be an annual event. We therefore consider understory (<2 m height), midstory (2–8 m), and overstory (>8 m) separately. We also examine changes in overstory basal area with fire treatment through time. Because we do not have data for individual marked stems, we are unable to undertake direct quantitative analysis of the movement of stems between height classes, but these analyses of the temporal dynamics of stems do permit some weak inferences. For all analyses, we pooled data from different sampling plots to give a total stem count or basal area for each block. Prior to analysis, counts were $\log_e$-transformed after adding 1.0. Sources of variance in the responses of interest within each of the land systems are (1) treatment effects and (2) change over time, whether related or unrelated to treatment. Because data came from measures from the same sampling strata revisited from year to year, we used repeated-measures analysis to explore variation with time and interactions between time and treatment. Change in woody species composition (species turnover) on all treatments between the start and end of the experiment were calculated and compared similarly to grass species turnover.

RESULTS

Fire intensity

For open forest, mean fire intensities were consistently low (421 kW/m) for EANN treatments, mostly moderate (1177 kW/m) for LANN, and tending to increase through time for BIEN (1410 kW/m; Fig. 3). Mean fire intensities on woodland plots were greater than for open forest in EANN (804 kW/m) and LANN (2739 kW/m) treatments, and less for BIEN (997 kW/m; Fig. 4).

Mean fire intensities varied significantly between treatments, both for open forest and woodland; there were no significant block effects (Table 1 a, b). For open forest, mean fire intensities differed significantly between EANN and LANN, and between EANN and BIEN treatments, but not between LANN and BIEN

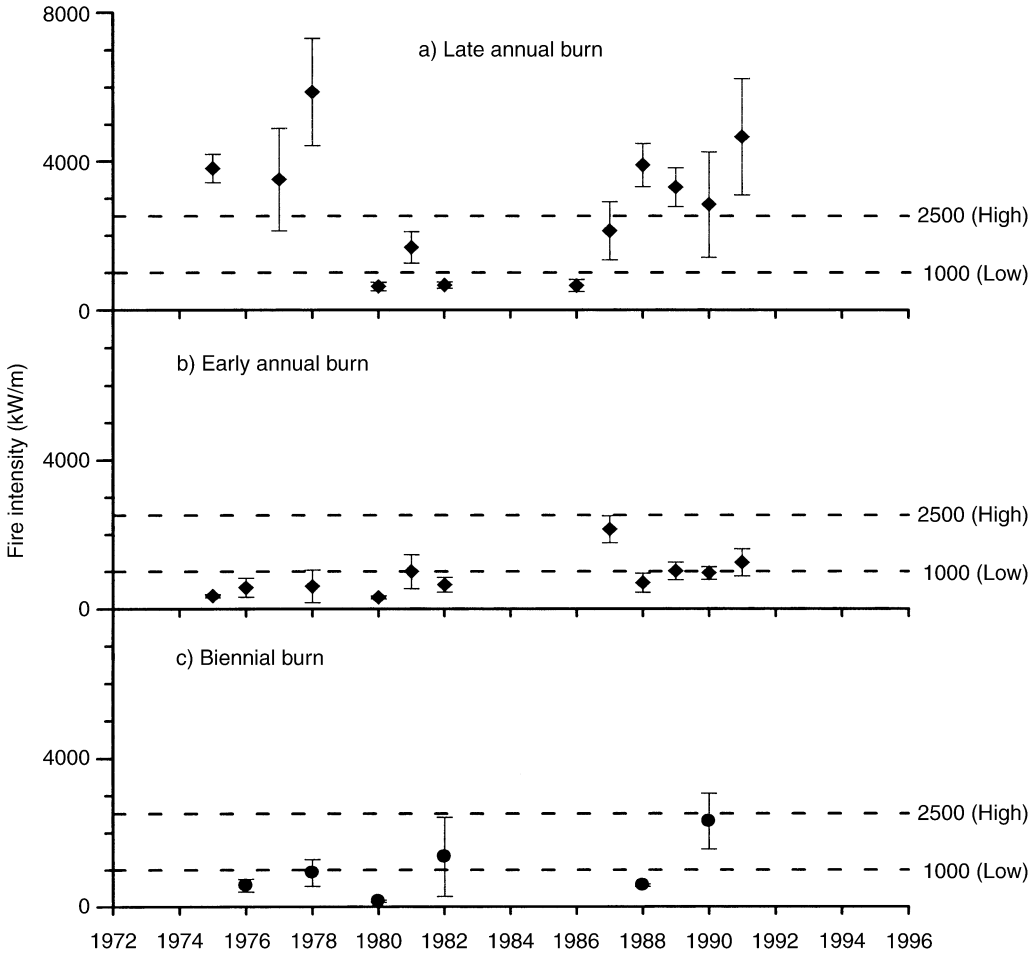

FIG. 4. Mean (± 1 SE) fire intensities under different fire treatments for woodland using all available quantitative data between 1973 and 1996.

TABLE 1. Assessment of differences in fire intensity (given as Byram's [1959] fire-line intensity, *I*) between fire treatments and blocks (one-way ANOVA, with Year as a covariate to Fire treatment), and comparisons between respective pairs of treatments for (a) open forest and (b) woodland, using all available data, 1973–1996.

Independent variable	Test	Treatment comparisons†	df	*F*	*P*
a) Open forest					
Fire treatment (covariate = year)	one-way ANOVA with covariate		2, 72	8.75	0.0004
	post hoc Tukey's unequal *n* HSD	EANN and LANN			0.0014
		LANN and BIEN			0.9795
		EANN and BIEN			0.0108
Block	one-way ANOVA		2, 73	0.71	0.4962
b) Woodland					
Fire treatment (covariate = year)	one-way ANOVA with covariate		2, 79	14.08	<0.0001
	post hoc Tukey's unequal *n* HSD	EANN and LANN			0.0001
		LANN and BIEN			0.0036
		EANN and BIEN			0.9711
Block	one-way ANOVA		2, 80	1.20	0.3060

† Treatment abbreviations are: EANN, annual early dry-season burning (mostly May–June); LANN, annual late dry-season burning (mostly August–October); and BIEN, biennial early dry-season burning (mostly May–June).

TABLE 2. Mean (n = 36) chemical properties of soil samples (0–5 cm) collected in 1989 from each of four treatments for (a) open forest and (b) woodland.

Treatment†	pH	NO_3-N (mg/kg)	H_2SO_4-P (mg/kg)	Exch. Ca‡ (cmol/kg)	Exch. Mg‡ (cmol/kg)	Organic C (%)
a) Open forest						
EANN	5.5^{b}	0.79^{b}	9.0^{a}	0.30	0.61^{b}	2.42^{b}
LANN	5.7^{c}	1.06^{b}	4.2^{c}	0.28	0.32^{d}	1.03^{c}
BIEN	5.5^{bc}	1.04^{b}	7.2^{ab}	0.44	0.76^{c}	1.46^{a}
UNBN	5.2^{a}	2.5^{a}	6.4^{cb}	0.27	0.45^{a}	1.73^{a}
P	<0.01	<0.01	<0.01	NS	<0.01	<0.01
b) Woodland						
EANN	5.6^{b}	1.2^{b}	10.4	1.57^{b}	0.53^{b}	1.41
LANN	6.4^{c}	1.0^{b}	9.8	2.63^{c}	0.72^{c}	1.09
BIEN	5.7^{b}	1.4^{b}	12.0	1.24^{b}	0.57^{b}	1.35
UNBN	5.1^{a}	2.6^{a}	9.0	0.48^{a}	0.17^{a}	0.85
P	<0.01	<0.05	NS	<0.01	<0.01	NS

Note: Within a column, different superscript letters depict significantly different means.

† Treatment abbreviations are: EANN, annual early dry-season burning (mostly May–June); LANN, annual late dry-season burning (mostly August–October); BIEN, biennial early dry-season burning (mostly May–June); and UNBN, unburned (completely protected from fire).

‡ Esch. = Exchangeable.

(Table 1a). For woodland, mean LANN fire intensities were significantly greater than for EANN or BIEN, with the latter two treatments showing no significant difference (Table 1b).

Soils

On the open forest site, the soil of the LANN plots had the highest pH values and the lowest organic C, total P, exchangeable Mg, and total exchangeable cations (Table 2a). For most soil properties, there were no significant differences between the EANN and BIEN plots, but the BIEN plots had lower organic C contents and higher exchangeable Mg levels than the annually burned plots.

On the woodland site, late annual fires resulted in the highest levels of soil pH, exchangeable Ca and Mg, and total exchangeable cations (Table 2b). UNBN plots had the lowest values of these properties, and there were no significant differences in these properties between the EANN and BIEN plots. The concentrations of soil nitrate were significantly higher in the UNBN plots than in the burned plots, but there were no other significant differences in measured soil properties.

Grasses

In total, 15 grass species comprising nine annuals and six perennials were recorded in open forest quadrats, and at least 40 species comprising 21 annuals and 19 perennials were recorded in woodland quadrats, over the life of the experiment. By treatment, woodland plots typically contained twice the number of annual grass species and 4–7 times the number of perennials (Fig. 5).

In the open forest sites, the frequency of grasses aggregated across species and life history strategy fell substantially during the experiment ($F_{3,45}$ = 33.54, P < 0.0001). Decline in annuals was much greater than in perennials (year by life-form interaction, $F_{3,45}$ = 34.78, P < 0.0001). There were significant treatment effects on these trends (year by treatment interaction, $F_{9,45}$ = 2.34, P = 0.043), with declines being least pronounced in EANN. In open forest, there was a significant decline (P < 0.05) in the frequency of occurrence of most annual species across all treatments over the study period (Fig. 5), the notable exception being *Sorghum stipoideum*. Effects on perennials tended to be less clear-cut (Fig. 5). When examined individually (through terms for the interaction between time and treatment), the responses of only four species showed significant variation in the extent and direction of change with fire treatment, namely: relatively lesser decreases in EANN treatments by *Brachiaria holosericea* (P = 0.023) and *Setaria apiculata* (P = 0.057); marked increase in UNBN by *Eriachne triseta* (P = 0.035); and a marked decrease in UNBN by *Sorghum stipoideum*, contrasting with an equally marked increase on all burned treatments (Fig. 6; time by treatment interaction, P = 0.023).

In woodland, overall frequency fell somewhat during the experiment ($F_{3,48}$ = 3.69, P = 0.028). As in open forest, the decline in annuals was much greater than in perennials (year by life-form interaction, $F_{3,48}$ = 9.72, P = 0.0002). There was no significant treatment effect on these trends (year by treatment interaction, $F_{9,39}$ = 1.62, P = 0.17). Consistent with this result, individual species of both annual and perennial grasses more often showed decreases over the study period than increases, and more annual species showed significant declines (Fig. 5). Significant declines in occurrence were recorded for annual species, particularly, on EANN, BIEN, and UNBN treatments, with relatively fewer declines recorded for perennial species across all treatments except LANN (Fig. 5). Responses of only three species showed strong and statistically significant (P

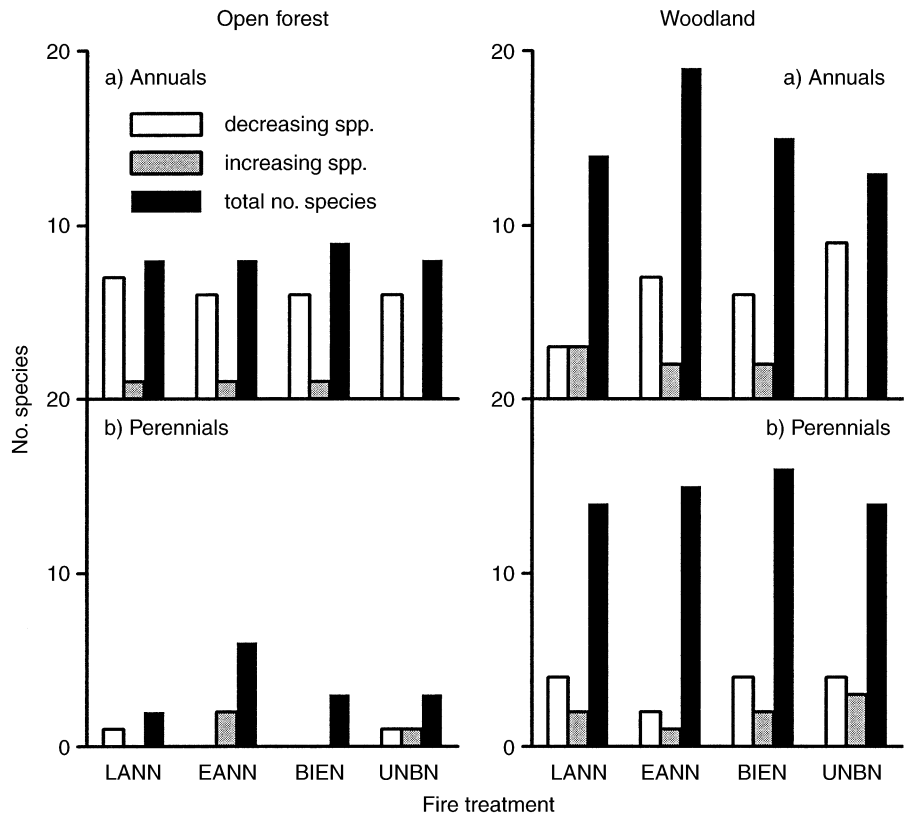

FIG. 5. Total number of (a) annual and (b) perennial grass species recorded from 1973 to 1996 in respective treatments (see Fig. 2), and the number of species that showed significant increases or decreases in frequency for open forest and woodland plots, respectively.

< 0.05) treatment effects, namely a marked increase by *Digitaria gibbosa* in LANN, a decrease in UNBN ($P = 0.012$) treatments; an increase by *Eriachne triseta* in UNBN ($P = 0.0019$), and a marked decrease by *Whitechloa capillipes* in UNBN ($P = 0.117$) (Fig. 6).

In open forest, grass species turnover over the life of the experiment (1973–1994) ranged among treatments from 14% to 88% for annuals and from 33% to 50% for perennials. Total species turnover summed over consecutive observations did not vary with treatment ($\chi^2 = 3.97$, $P = 0.265$), but did vary with life-form ($\chi^2 = 5.83$, $P = 0.016$), principally reflecting higher rates of turnover (and especially very much higher loss) of annual species ($\chi^2 = 8.88$, $P = 0.008$). Although the major loss of annual grass species occurred between 1978 and 1994, no similar trend is obvious for perennial species (Fig. 7). In woodland, grass species turnover ranged from 50% to 67% for annuals, and from 62% to 73% for perennials, in the various treatments over the life of the experiment. There was no significant difference in turnover rate among treatments ($\chi^2 = 1.09$, $P = 0.781$) for either annuals or perennials ($P > 0.05$). Loss of species accounted for most of the turnover ($\chi^2 = 12.60$, $P = 0.0004$), especially between 1973 and 1976 and 1978 and 1996 for annuals, and 1978 and 1996 for perennials (Fig. 8). There was no significant variation with life-form in the proportion of species lost or gained ($\chi^2 = 0.955$, $P = 0.329$).

Woody plants

We sampled 35 woody plant species from open forest plots: five tree species (>8 m tall) including three *Eucalyptus* (Myrtaceae), *Persoonia falcata* (Proteaceae), and *Terminalia ferdinandiana* (Combretaceae); 16 species that reached the midstory (2–8 m); and 14 understory species (<2 m). On woodland plots, 56 woody species were sampled as follows: 10 tree species including *Erythrophleum chlorostachys* (Caesalpinaceae), 5–6 *Eucalyptus* species, *Petalostigma pubescens* (Euphorbiaceae), *Terminalia ferdinandiana* and *Xanthostemon paradoxus* (Myrtaceae); 23 midstory species; and 23 understory species.

Structural change in woody plants: all species pooled

Open forest.—

1. *Understory*.—Repeated-measures analysis showed no consistent change in the density of stems within treatments ($F_{2,7} = 1.14$, $P = 0.374$) through time. There was

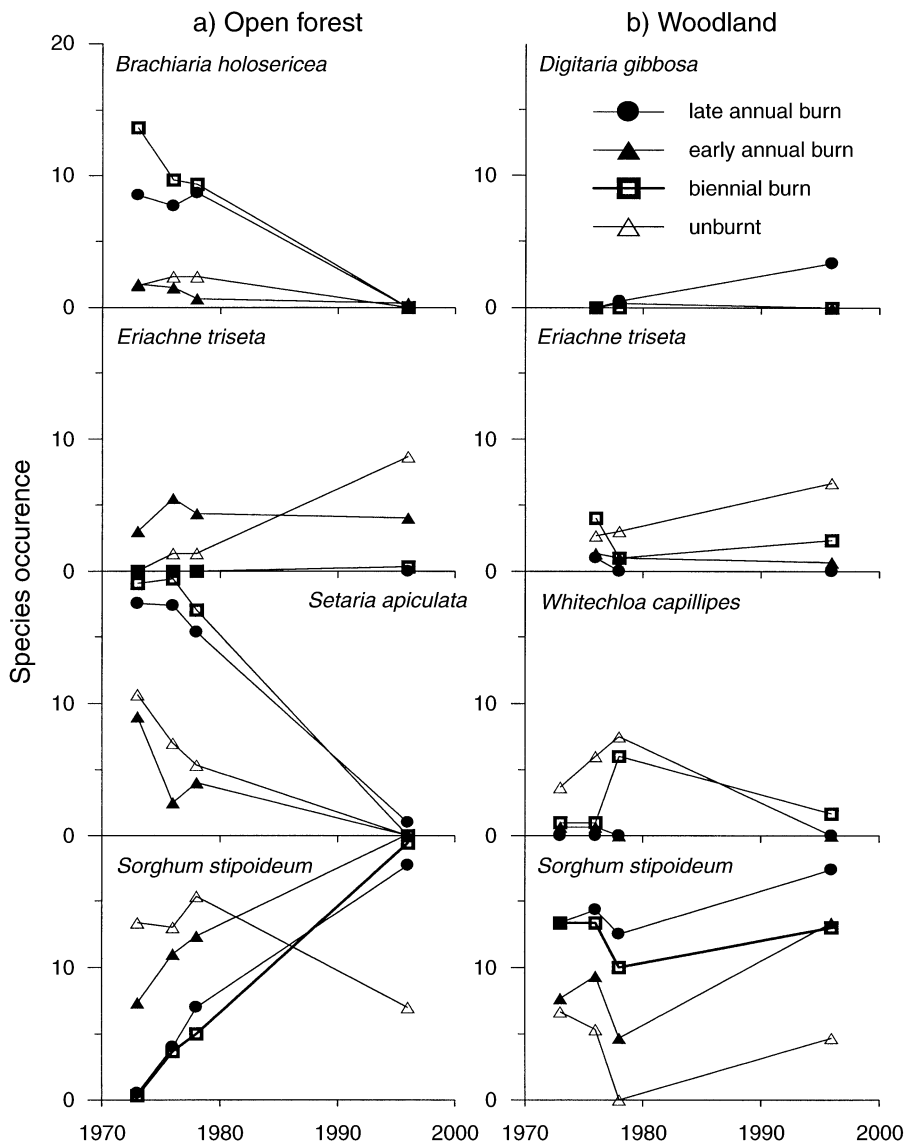

FIG. 6. Mean frequency of occurrence (n = 3 replicates per treatment) of grass species showing significant departures from the general trend in relative frequency over the sampling period for (a) open forest and (b) woodland plots, respectively. Note that *Sorghum stipoideum* is included in the woodland for reference only.

no variation in mean density of stems among treatments ($F_{3,8}$ = 1.85, P = 0.217), or in the time by treatment interaction ($F_{6,14}$ = 0.62, P = 0.710; Table 3). Total density of small stems of woody species appeared to be relatively constant and independent of fire treatment over a span of 21 years. Large numbers of potential recruits to larger (midstory and canopy) size classes remained present over more than two decades, irrespective of fire treatment (Fig. 9a).

2. *Midstory*.—There were striking changes in the density of midstory stems with time ($F_{2,6}$ = 554.1, P < 0.0001; Table 3). In 1973, no midstory stems (in the range 2–8 m tall) were present on any of the experimental plots, but 21 years later, many such stems were recorded (Fig. 9b). In addition, there were very significant treatment differences ($F_{3,7}$ = 108.4, P < 0.0001) and a significant treatment by time interaction ($F_{6,12}$ = 11.36, P < 0.0001). Increases were greatest, by a large margin, in the UNBN treatment. Increase was least in the LANN treatment. We interpret these results to indicate, in combination, substantial fire treatment effects on the entry of stems to the midstory by 1978, within five years of commencement of the treatments. The release of stems from the understory was much stronger in the UNBN treatments, but occurred to some extent in all fire treatments.

3. *Overstory*.—There was no change in the number of overstory stems through time ($F_{2,7}$ = 0.20, P =

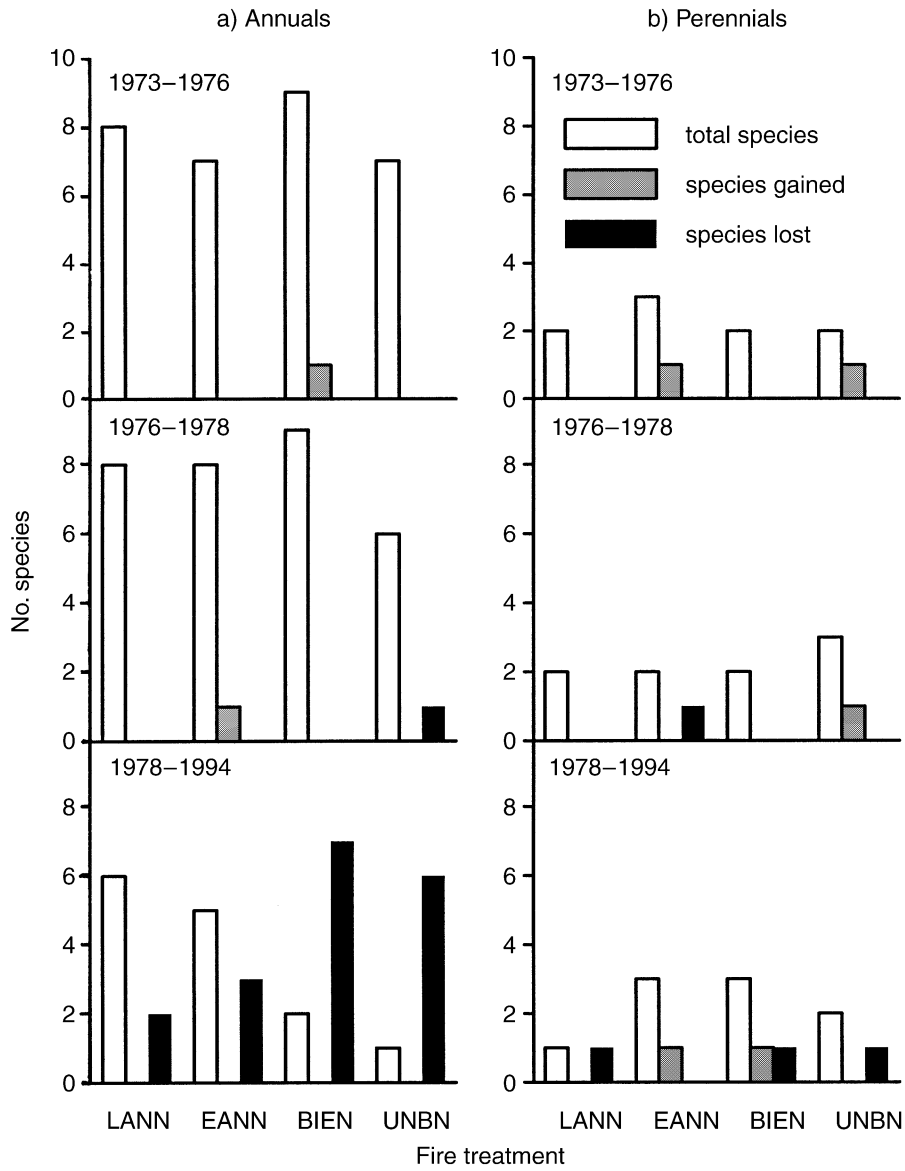

FIG. 7. Turnover of (a) annual and (b) perennial grass species on respective open forest treatment plots between 1973 and 1976, 1976 and 1978, and 1978 and 1994. Total species refers to the number of species remaining at the end of the assessment period. Abbreviations of treatments are as in Fig. 2.

0.820), nor were there significant differences among treatments ($F_{3,8}$ = 1.03, P = 0.429) (Fig. 9c; Table 3). Despite the lack of evidence of recruitment of additional stems to the overstory, there was a significant increase in basal area of stems over the 21 years of sampling ($F_{2,7}$ = 12.27, P = 0.005; Table 3). The rate and direction of basal area change varied with treatment ($F_{6,14}$ = 5.62, P = 0.004), with the increase being most evident in UNBN treatments (Fig. 9d).

Woodland.—

1. *Understory*.—There was a significant increase in pooled stem density with time ($F_{1,8}$ = 8.89, P = 0.018). This increase was most marked in EANN and BIEN treatments (Fig. 10a), but there were no significant treatment-related effects on change through time ($F_{3,8}$ = 1.88, P = 0.211; Table 4).

2. *Midstory*.—Total stem density was higher in later years, but the overall change was not significant ($F_{2,6}$ = 3.12, P = 0.118). However, stem density did vary among fire treatments ($F_{3,7}$ = 4.88, P = 0.039), which affected the direction of change (time by treatment interaction, $F_{6,12}$ = 5.33, P = 0.007; Table 4). Increase in stem density was particularly evident in UNBN treatments, contrasting with a slight decline in the LANN treatment (Fig. 10b). This result varies somewhat from responses seen in the open forest, where there was entry

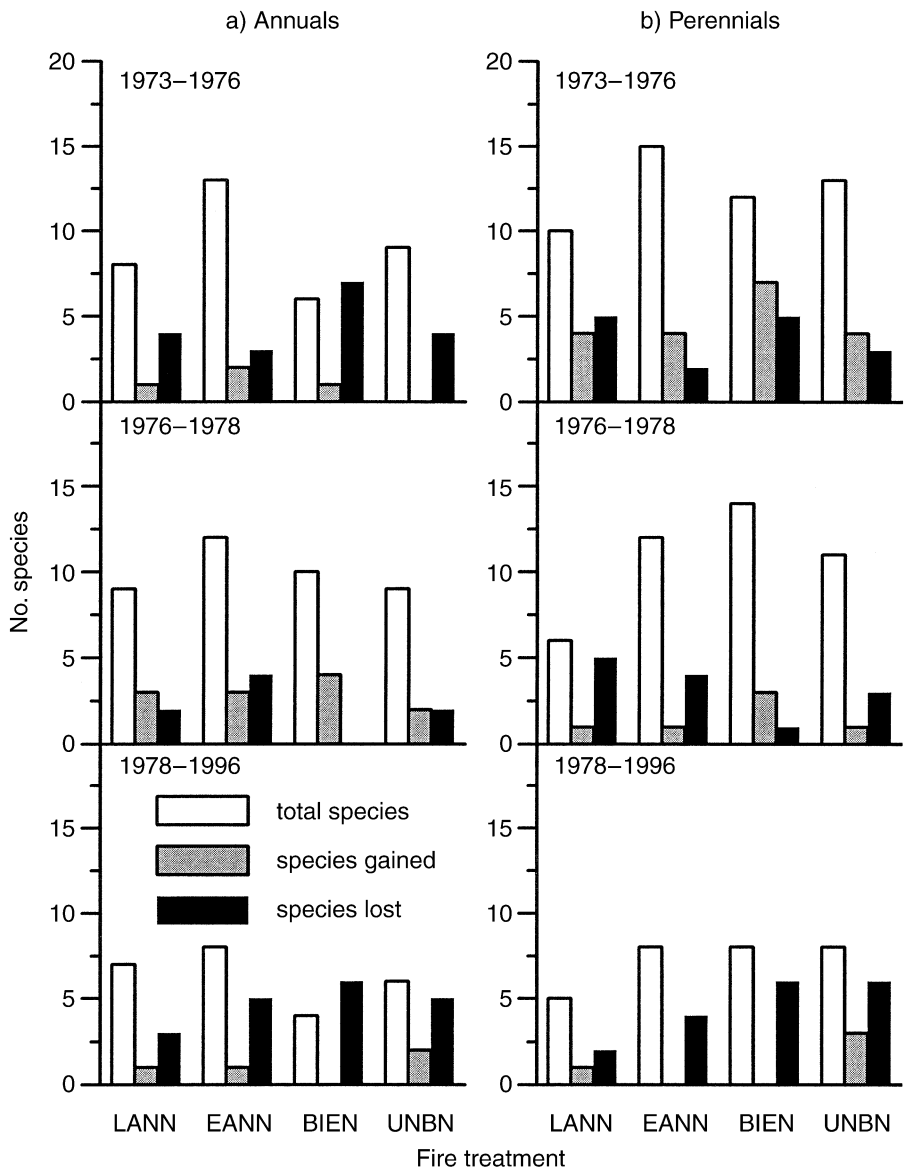

FIG. 8. Turnover of (a) annual and (b) perennial grass species on respective woodland treatment plots between 1973 and 1976, 1976 and 1978, and 1978 and 1996. Total species refers to the number of species remaining at the end of the assessment period. See Fig. 2 for treatment abbreviations.

of new stems to the midstory in all treatments (including LANN) and, hence, an increase in total stem density across all treatments and plots.

3. *Overstory*.—There was no significant change in the density of stems with time ($F_{1,8} = 0.77$, $P = 0.406$), nor were there significant treatment ($F_{3,8} = 0.88$, $P = 0.492$) or treatment by time effects ($F_{3,8} = 1.96$, $P = 0.198$; Table 4). The failure to record increases in the density of overstory stems despite substantially increased numbers of the smaller size classes is most likely attributable to the growth forms of the species that increased most (Table 4); many of these species rarely reach 8 m in height. In addition, it should be recognized that the total number of stems in the overstory is small and the power of statistical tests is accordingly weak. There was a significant increase in basal area ($F_{1,8} = 11.83$, $P = 0.009$). The increase was most marked in the UNBN treatments, which started from a very low base (Fig. 10d), but the treatment by time effect was not statistically significant ($F_{3,8} = 0.98$, $P = 0.447$) and there was no significant between-subjects treatment effect ($F_{3,8} = 0.28$, $P = 0.838$). Again it would appear that the increase in basal area is attributable to an increase in the average size of stems rather than to significant additions through new stems, despite the interval of 23 years between measurements.

TABLE 3. Changes in stem density and basal area of individual species in open forest in relation to time, fire treatment (Treat.), and time × fire treatment interaction (T × T).

Species (and family)	Growth form	Response											
		Overall change			Understory			Midstory			Overstory		
		U	M	O	Time	Treat.	T × T	Time	Treat.	T × T	Time	Treat.	T × T
Acacia aulacocarpa (Mimosaceae)	small tree	0	+	NA	NS	NS	NS	NS	*	NS	NA	NA	NA
Acacia dimidiata (Mimosaceae)	small tree	+	+	NA	****	NS	NS	**	***	*	NA	NA	NA
Acacia mimula (Mimosaceae)	small tree	0	+	NA	NS	NS	NS	****	NS	****	NA	NA	NA
Corynotheca lateriflora (Liliaceae)	shrub	+	NA	NA	*	NS	NS	NA	NA	NA	NA	NA	NA
Erythrophleum chlorostachys (Caesalpinaceae)	canopy tree	+	+	0	NS	***	*	****	****	****	NA	NA	NA
Eucalyptus miniata (Myrtaceae)	canopy tree	0	0	+	NS	NS	NS	NS	NS	NS	NS NS†	NS NS†	NS NS†
Eucalyptus porrecta (Myrtaceae)	canopy tree	0	0	0	NS	NS	NS	NS	NS	NS	NS *†	*** NS†	NS NS†
Eucalyptus tetrodonta (Myrtaceae)	canopy tree	0	0	−	NS	NS	NS	NS	NS	NS	NS NS†	NS NS†	* NS†
Gardenia megasperma (Rubiaceae)	small tree	+	0	NA	NS	NS	**	NS	NS	NS	NA	NA	NA
Gardenia suffruticosa (Rubiaceae)	shrub	+	NA	NA	*	NS	NS	NA	NA	NA	NA	NA	NA
Grevillea goodii (Proteaceae)	shrub	+	NA	NA	NS	NS	*	NA	NA	NA	NA	NA	NA
Pachynema complanatum (Dilleniaceae)	shrub	+	NA	NA	****	NS	NS	NA	NA	NA	NA	NA	NA
Petalostigma quadriloculare (Euphorbiaceae)	shrub	+	NA	NA	*	NS	NS	NA	NA	NA	NA	NA	NA
Planchonella pohlmanniana (Sapotaceae)	small tree	0	0	0	NS	*	NS	****	****	****	NA	NA	NA
All live stems													
Stem density		0	+	0	NS	NS	NS	****	****	****	NS	NS	NS
Basal area		NA	NA	+	NA	NA	NA	NA	NA	NA	**	NS	**

Notes: Only those species showing statistically significant responses in at least one size class are shown. Counts of stems were $\log_e$-transformed (after adding 1) prior to analysis. Repeated-measures analyses were applied throughout. Overall change (between first and last sampling) is denoted, respectively, for understory (U), midstory (M), and overstory (O), where: 0 = no significant change, + = significant increase, − = significant decrease, and NA = not applicable or insufficient data.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$; NS, not significant.

† This refers to a change in basal area.

Structural change in woody plants: individual species

In open forest, a number of woody species were sufficiently abundant to permit individual analysis of change and its relation to fire treatment in the same way as total stem density. For brevity, details are presented only for those species that showed significant change through time or clear treatment differences (Table 3). In the understory stratum, nine species showed statistically significant variation in stem density, with those species that showed any change more often increasing. Although variation was statistically related to treatment in a number of species, patterns are idiosyncratic and no strong and consistent trends are discernible across the range of species considered. In contrast, all five species exhibiting significant change in midstory stem density increased in density. Such increases were much more pronounced in UNBN or lower intensity/lower frequency fire treatments (BIEN, EANN). Three of these were *Acacia* species that are unlikely to reach the canopy. Only *Erythrophleum chlorostachys*, which increased in density in the midstory and showed strong responses to fire treatment, has the potential to reach the canopy in significant numbers. Responses of the dominant eucalypts through time were relatively small and only weakly related to fire treatment.

In woodland, understory stem densities for seven species varied significantly during the experiment and two of these also changed in the midstory (Table 4). Of the five species responding significantly solely in the understory, two (*Gardenia suffruticosa*, *Waltheria*

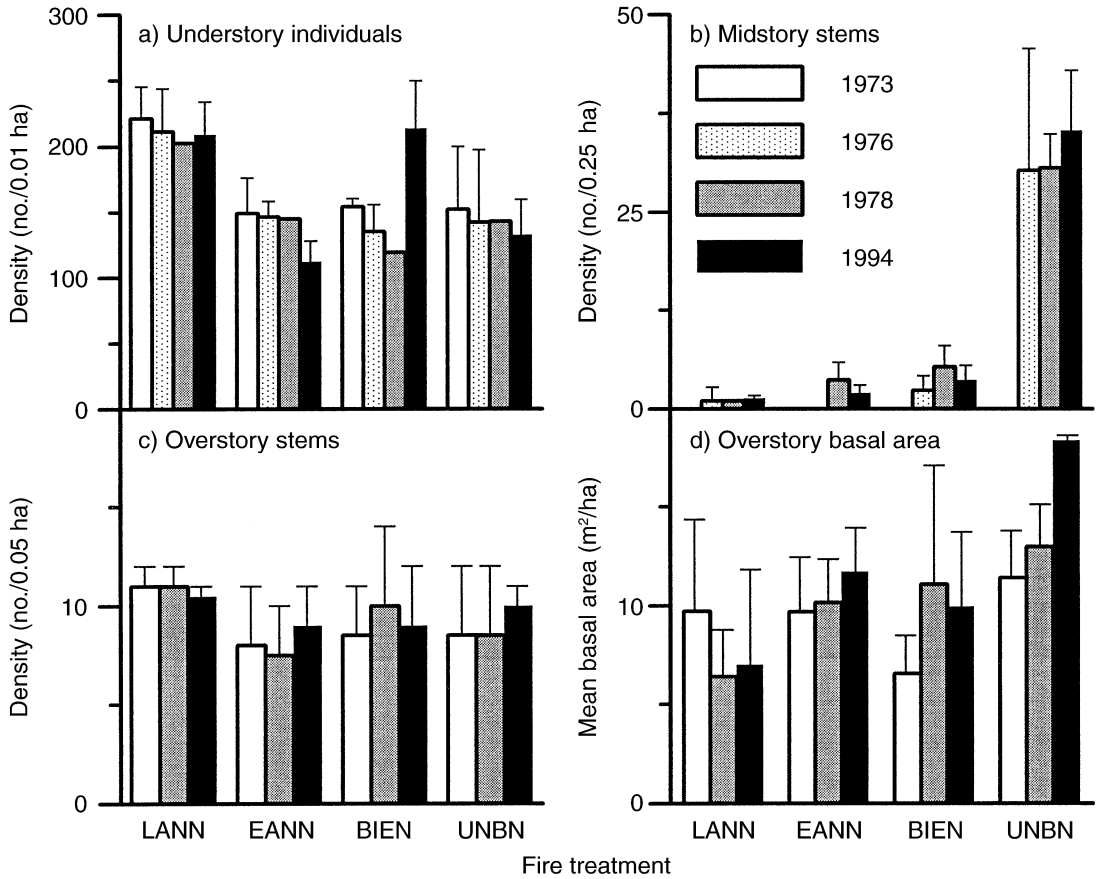

FIG. 9. Mean density (+1 SE) of (a) understory individuals, (b) midstory stems, (c) overstory stems, and (d) overstory basal area in respective open forest treatments (see Fig. 2).

indica) increased in density without evidence of fire treatment effects, one (*Parinari nonda*) declined in density without fire effects, and two (*Petalostigma pubescens*, *Planchonia careya*) generally increased in burned treatments relative to UNBN. In the midstory, six species changed in density, with four becoming more abundant and two declining. Two of the increasing species (*Acacia holosericea*, *Antidesma ghaesembilla*) showed strong responses to fire treatment, increasing in density particularly in UNBN treatments. None of these same species varied in the canopy, where two other species increased slightly in density and one decreased in density. None showed canopy responses to fire treatment.

Woody species turnover

In open forest, woody species turnover ranged between 30% and 40% in the various treatments, mostly reflecting the contribution of new species (Fig. 11a). Although there were no significant differences concerning total, new, or lost species between treatments ($P > 0.05$), more new species were recorded on UNBN and BIEN than on more frequently burned plots. Woody species turnover on woodland treatments ranged between 42% and 53%, with the major contribution consisting of new species, as for open forest (Fig. 11b). Similarly, although there were no significant differences concerning total, new, or lost species between treatments ($P > 0.05$), more new species were recorded on UNBN and BIEN than on more frequently burned plots. By contrast with open forest, however, there was substantial establishment of rain forest pioneer species on woodland plots (Fig. 12a): *Alstonia actinophylla*, *Antidesma ghaesembilla*, *Breynia cernua*, *Briedelia tomentosa*, *Ficus scobina*, *Fleuggea virosa*, *Grewia breviflora*, *Premna acuminata*, *Strychnos lucida*, *Trema tomentosa*, and *Vitex glabrata*.

Although establishment of rain forest pioneers occurred to some extent on all woodland treatments, it occurred particularly on UNBN plots, and also markedly on one LANN plot (Fig. 12b). We can only interpret this latter, enigmatic observation as reflecting the past effects of feral buffalo in selectively reducing fuel loads on this particular LANN plot, perhaps through the frequenting of a resting place, or ''buffalo camp.'' Additionally, buffalo activity favors the establishment of the relatively fire-retarding exotic herbaceous species, *Hyptis suaveolens*; as noted previously,

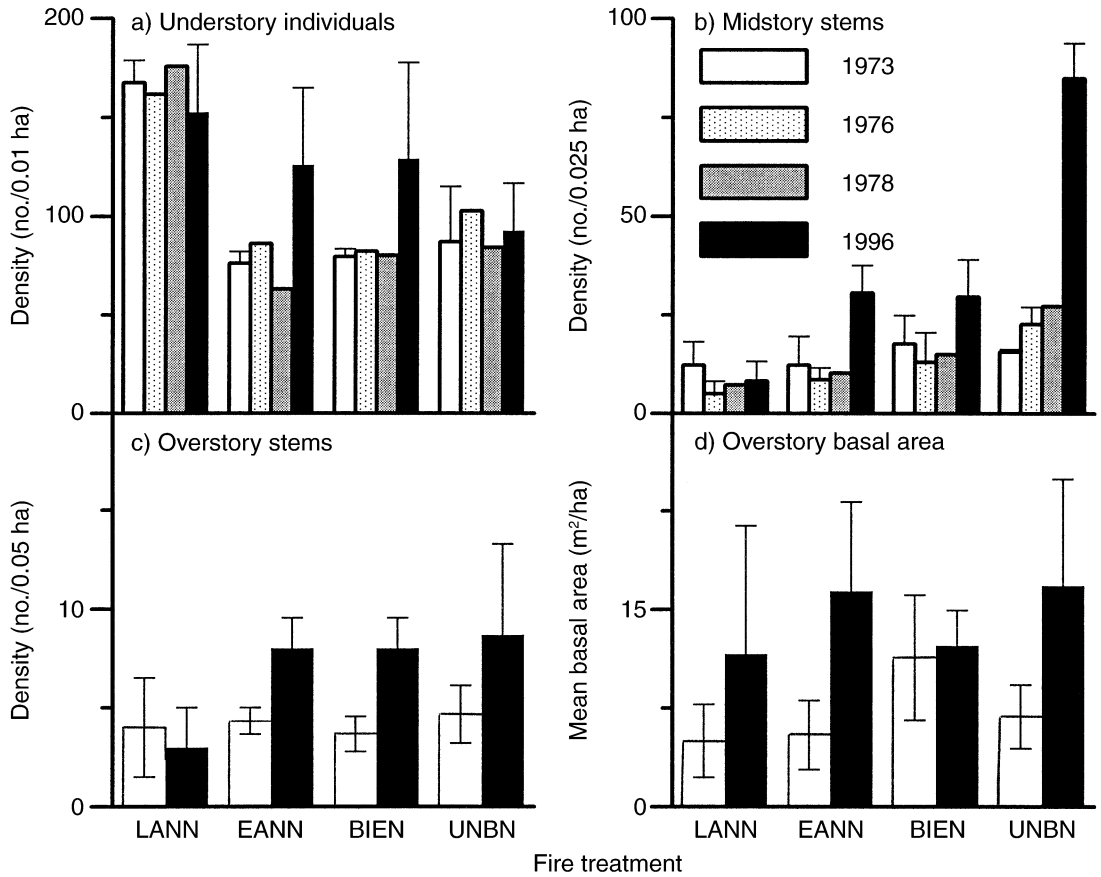

FIG. 10. Mean density (+1 SE) of (a) understory individuals, (b) midstory stems, (c) overstory stems, and (d) overstory basal area in respective woodland treatments (see Fig. 2). Note that, for 1978 midstory data, error bars are not given because only treatment means are available.

patches of trampled bare ground and dense stands of *Hyptis* were reported on the woodland experimental site until at least the mid-1980s.

DISCUSSION

Experimental fire regimes

Available data indicate that mean fire intensities varied significantly between treatments on both open forest and woodland sites; that fire intensities were generally greater in woodland; that LANN fire intensities were significantly greater than EANN, both in open forest and woodland; and that, with the exception of woodland LANN treatments (that frequently burned at high intensity, i.e., >2500 kW/m), burning treatments were typically of low or moderate intensity. Comparable quantitative data for savanna experimental sites are scarce. However, mean Byram fire intensities (I) achieved at the nearby Kapalga site (Williams et al. 1998), derived from perimeter burning of large, catchment-scale (15-km^2) plots, were substantially greater than for similar treatments at Munmarlary: EANN, 421 and 804 kW/m for open forest and woodland, respectively [Munmarlary] vs. 2100 kW/m [Kapalga]; LANN, 1177 and 2739 kW/m for open forest and woodland, respectively [Munmarlary] vs. 7700 kW/m [Kapalga]). Significantly, very high savanna fire intensities (>15 000 kW/m) were experienced on LANN treatments at Kapalga in one year (Williams et al. 1998). Such intensities contrast with extreme intensities of over 100 000 kW/m in canopy-borne temperate forest infernos (Gill and Catling 2002).

Although rates of spread in predominantly grassy savanna fuels have been shown to be independent of fuel load under experimental, open grassy conditions (Cheney et al. 1993, Cheney and Sullivan 1997), observations reported here under more wooded canopy conditions confirm that, as postulated by Lonsdale and Braithwaite (1991), the relatively small size of treatment plots at Munmarlary (and the very great majority of savanna experimental fire plots elsewhere) limits the assessment of fire impacts to low- to moderate-intensity fire regimes, in that they preclude the attainment of maximum forward rates of spread and, thus, maximum Byram fire intensities.

Particularly intense fires in northern Australian savannas are known to have significant differential spe-

TABLE 4. Changes in stem density and basal area of individual species in woodland in relation to time, fire treatment (Treat.) and time × fire treatment interaction (T × T).

Species (and family)	Growth form	Response											
		Overall change			Understory			Midstory			Overstory		
		U	M	O	Time	Treat.	T × T	Time	Treat.	T × T	Time	Treat.	T × T
Acacia holosericea (Mimosaceae)	shrub	0	+	NA	NS	NS	NS	*	**	**	NA	NA	NA
Antidesma ghaesembilla (Euphorbiaceae)	shrub	+	+	NA	*	NS	NS	**	**	**	NA	NA	NA
Brachychiton paradoxus (Sterculiaceae)	small tree	0	−	NA	NS	NS	NS	*	NS	NS	NA	NA	NA
Cochlospermum fraseri (Bixaceae)	small tree	0	+	NA	NS	NS	NS	*	NS	NS	NA	NA	NA
Erythrophleum chlorostachys (Caesalpinaceae)	canopy tree	0	0	+	NS	NS	NS	NS	NS	NS	* *†	NS NS†	NS NS†
Eucalyptus confertiflora (Myrtaceae)	canopy tree	0	+	0	NS	NS	NS	*	NS	NS	NS NS†	NS NS†	NS NS†
Eucalyptus tectifica (Myrtaceae)	canopy tree	0	0	−	NS	NS	NS	NS	NS	NS	* NS†	NS NS†	NS NS†
Gardenia suffruticosa (Rubiaceae)	shrub	+	NA	NA	*	NS	NS	NA	NA	NA	NA	NA	NA
Livistona humilis (Arecaceae)	shrub	0	−	NA	NS	NS	NS	*	NS	NS	NA	NA	NA
Parinari nonda (Chrysobalanaceae)	small tree	−	NA	NA	*	NS	NS	NA	NA	NA	NA	NA	NA
Petalostigma pubescens (Euphorbiaceae)	small tree	0	0	NA	NS	*	NS	NS	NS	NS	NA	NA	NA
Planchonia careya (Barringtoniaceae)	small tree	0	0	NA	NS	NS	*	NS	NS	NS	NA	NA	NA
Terminalia ferdinandiana (Combretaceae)	small tree	0	0	+	NS	NS	NS	NS	NS	NS	* *†	NS NS†	NS NS†
Waltheria indica (Sterculiaceae)	shrub	+	NA	NA	*	NS	NS	NA	NA	NA	NA	NA	NA
All live stems													
Stem density		+	0	0	*	NS	NS	NS	*	**	NS	NS	NS
Basal area		NA	NA	+	NA	NA	NA	NA	NA	NA	***	NS	NS

Notes: Only those species showing statistically significant responses in at least one size class are shown. Counts of stems were $\log_e$-transformed (after adding 1) prior to analysis. Repeated-measures analyses were applied throughout. Overall change (between first and last sampling) is denoted, respectively, for understory (U), midstory (M), and overstory (O), where 0 = no significant change, + = significant increase, − = significant decrease, and NA = not applicable or insufficient data.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$; NS, not significant.

† Refers to change in basal area.

cies effects on stem mortality (Lonsdale and Braithwaite 1991, Williams et al. 1999) and on floral and fruit production (Setterfield 1997). Although the occurrence (frequency, extent) of very intense fires in the regional landscape is not quantified, these are observed to correspond generally with peak weather conditions for fire in September/October (Gill et al. 1996). Fire history data for Kakadu National Park (which includes the Munmarlary site) for the period 1980–1994, indicate that an average 63% of eucalypt woodland and 47% of open forest was burned annually over this 15-year period, with most burning (60%) occurring in the early dry-season period before the end of July (Russell-Smith et al. 1997). Similar patterns, but with a general preponderance of late dry-season fire, are evident elsewhere for northern Australian mesic savannas (Williams et al. 2002). The regional potential for relatively frequent, intense fires under contemporary patterns of ignition (mostly anthropogenic) is thus high.

Feral buffalo may have affected experimental fires by reducing and fragmenting fuel loads and by encouraging the spread of less flammable herbaceous weedy species, particularly on the woodland site. For the first 10 years or so of the experiment, buffalo densities in the region are likely to have been regionally on the order of 15–30 animals/km^2 in favorable habitats, based on survey data from Kapalga (Ridpath et al. 1983). With the advent of a major feral animal control program in the 1980s, densities had been reduced to substantially <0.1 animal/km^2 by the early 1990s (Skeat et al. 1996). Changes in the abundance of large grazing and browsing animals that exercise preference for particular species or sites (Tulloch and Cellier 1986) have significant potential for affecting both vegetation composition and structure (Scholes and Archer 1997, Ash and McIvor 1998). However, despite this change in herbivore density, available fuel load (Russell-Smith et al. 2002*a*) and fire intensity data (Figs. 3 and 4)

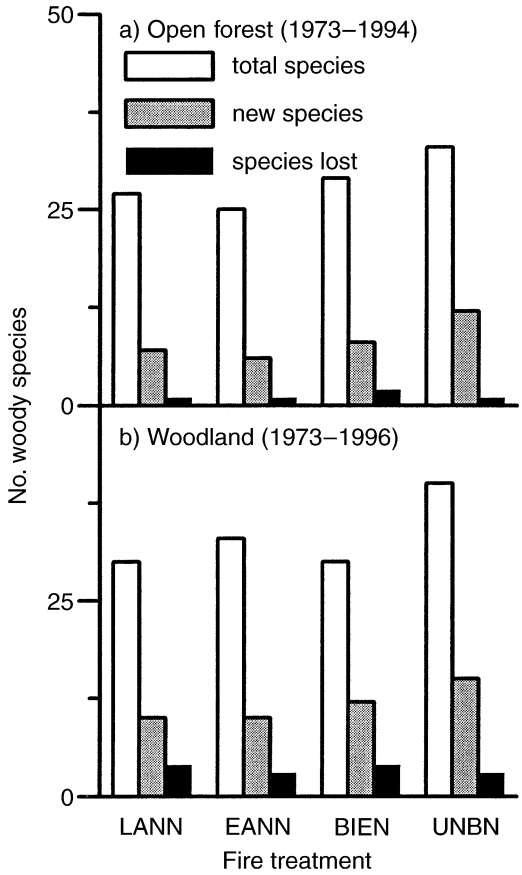

FIG. 11. Turnover of woody species on respective fire treatments (see Fig. 2) for (a) open forest (1973–1994) and (b) woodland (1973–1996). Woody species data are combined from the understory, midstory, and overstory.

indicate no consistent trends of increasing fuels or fire intensities from the mid-1980s.

Soil nutrients

The effects of fire regimes on savanna soils vary, with many studies showing little difference between unburned and frequently burned sites (Moore 1960, Trapnell et al. 1976, Cass et al. 1984, Schneider 1989, Martin et al. 1990, Scholes and Walker 1993), and others showing that fires are associated with decreasing or increasing soil nutrient availability in different parts of the soil profile (Coutinho 1990). Although there is no universal pattern, extremely severe fire regimes with frequent late dry-season fires often tend to reduce nutrient availability, although more benign regimes may increase availability compared with fire exclusion (Fagbenro 1982, Bird et al. 2000). Conversely, frequent substantial impacts of fires sometimes result in increasing nutrient availability (Materechera et al. 1998, Bird et al. 2000).

Often the greatest changes observed in soil properties occur at those sites where fire regimes also cause substantial changes in vegetation structure and floristic composition, typically the development of fire-sensitive forest flora in fire-excluded sites, and grassland with fire-tolerant trees on frequently burned sites (e.g., Garcia-Miragaya and Caceres 1990, Bowman and Fensham 1991). The direction of changes in soil properties varies. For example, some studies show an increase in pH and cation concentrations on frequently burned sites (Tester 1989, Materechera et al. 1998), and others show a decrease (Bowman and Fensham 1991). The role of surface runoff in removing deposited ash during rainstorms may be a significant factor in causing these differences in response to fire regimes (Kellman et al. 1985).

The greater concentration of nitrate-nitrogen in the soils of UNBN plots in both woodland and open forest at Munmarlary is consistent with suggestions that frequent burning in this region causes a net loss of nitrogen (Cook 1994) and a decline in nitrogen concentrations of plant tissues (Cook 2001). These changes are likely to result in decreased growth rates of plants and a decrease in their quality as food resources for fauna.

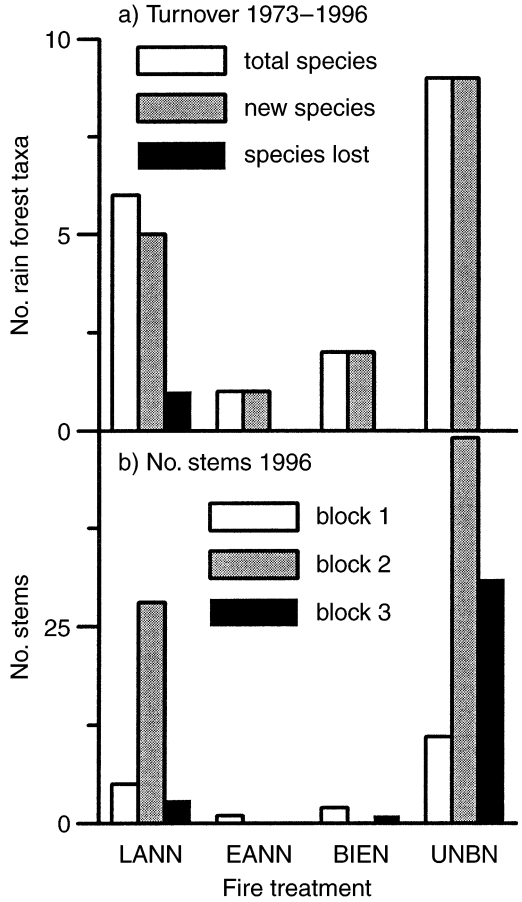

FIG. 12. Establishment of woody rain forest species in woodland: (a) species turnover between 1973 and 1996 for respective fire treatments (see Fig. 2) and (b) number of rain forest species stems sampled in respective treatment plots over the life of the experiment, by block.

Other changes observed in soil chemical properties were inconsistent between soil types and across fire treatments. The greater pH of burned relative to unburned sites observed in the woodland may be due to the increased exchangeable cation concentrations on the burned sites, but this pattern was not seen in the open forest soils. The lack of evidence of increased organic carbon concentrations in the absence of fire probably reflects very high rates of biological decomposition in the absence of fire, typical of hot tropical conditions. This is consistent with the results of 25 years of fire exclusion in savannas at Lamto, Cote d'Ivoire, where, despite a 52–70% turnover in soil carbon, rapid decomposition of organic matter in the absence of fire resulted in no significant changes in total soil carbon (Martin et al. 1990).

Grass species composition

A major, if unexpected, finding of this study was the overall decline in frequency of occurrence particularly of annual grasses, both in open forest and woodland, but also to a lesser extent of perennial grasses in woodland (Fig. 5). For most species, this occurred independently of treatment, particularly after 1978 in open forest (Fig. 7), and conspicuously between 1973 and 1976 and 1978 and 1996 for annual species in woodland (Fig. 8). Although trend data are presented only for those species exhibiting significant treatment effects on at least one site over the life of the experiment (Fig. 6), from assembled data it is apparent that decline in species frequencies was established generally within the first five years of the experiment. Similar responses have not been reported previously from northern Australian savanna fire-plot assessments undertaken at Munmarlary (Bowman et al. 1988), nor at Kapalga (R. J. Williams, *unpublished data*).

Given the limited variability in rain fall seasonal distribution and quantity over the study period (Fig. 1), observed declines in annual grasses on burning treatments might be attributed alternatively to effects of selective grazing, or the imposition of invariant, frequent fire regimes. With regard to selective grazing, it is notable that trends established in grass species compositional change under high buffalo densities were, if anything, amplified (Fig. 7a) following reduction of buffalo densities in the 1980s. Invariant fire regimes are known to have significant consequences for the maintenance of diverse species assemblages, e.g., heath communities (Morrison et al. 1995, Gill and McCarthy 1998). It is feasible, therefore, that the collapse of most annual grasses and the attendant increase in dominance of the vigorous annual *Sorghum stipoideum*, evident especially on open-forest burned treatments, was attributable to the imposition of invariant, frequent burning treatments. This hypothesis has significant management implications and should be tested. Nevertheless, such observations require qualification, given the considerable level of species turnover evident from one sample period to the next. Elsewhere, Russell-Smith et al. (2002*b*) describe the spread of another annual *Sorghum* species in response to frequent fire. The lack of change in grass species composition observed at Kapalga presumably might be explained by the fact that annual *Sorghum* was already widespread by 1990 in response to contemporary patterns of frequent, relatively intense burning.

Decline of annual grass species (including *Sorghum stipoideum*) and, conversely, an attendant increase in the fine-stemmed perennial grass species, *Eriachne triseta*, was observed on UNBN treatments both in open forest and woodland (Figs. 5 and 6). Decline in annual *Sorghum* in the absence of burning has been reported previously by Hoare et al. (1980) from Munmarlary, and elsewhere by Andrew and Mott (1983) and Russell-Smith et al. (1998). Such decline has been attributed both to shading from developing shrub regeneration, and to the development of seed barriers through litter accumulation (Hoare et al. 1980, Andrew and Mott 1983).

Comparable data from African fire plot studies afford varying results (O'Connor 1985). For example, for an experiment undertaken over two years involving six treatments incorporating grazing and burning in Kainji Lake National Park, Nigeria (rainfall 1200 mm per year, with five consecutive months with $\ll$50 mm rainfall), Afolayan (1978) found that the annual grass, *Hyparrhenia involucrata*, substantially dominated EDS (early dry-season) treatments (with and without grazing); the perennial grass, *Loudetia flavida*, substantially dominated LDS (late dry-season) treatments; and the aforementioned annual and perennial grasses co-dominated UNBN treatments. Conversely, for a long-term experiment in northeast Ghana (rainfall 1100 mm/yr, with 4–5 consecutive months with $<$50 mm rainfall), Brookman-Amissah et al. (1980) found that, after 26 years, weedy annuals (*Pennisetum pedicellatum*, *Chasmopodium caudatum*) were common in UNBN and the annual *Tripogon minimus* was common in LANN; the perennial *Loudetia flavida* remained dominant in EANN, LANN and UNBN, although having declined somewhat in the latter; and, ominously, the robust perennial *Andropogon gayanus* had increased in all treatments. This introduced species is now spreading in northern Australia. Savanna grass species, whether annual or perennial, evidently exhibit varying, presumably competitive, responses in different locations according to the species mix of life history attributes available at any one site, and extrinsic factors such as annual rainfall variability (O'Connor 1985, Scholes and Walker 1993, Williams et al. 2002).

A further feature of the assembled Munmarlary grass data is the high rate of species turnover evident from one sampling period to the next at permanently marked 1×1 m^2 permanent quadrats, particularly for both annual and perennial grasses in woodland treatments between 1973 and 1976, and 1976 and 1978 (Fig. 8).

Similar high rates of species turnover in respective treatments are evident for herbaceous species data in general, presented in detail in Hoare et al. (1980:Appendices D, E). We are aware of no other comparable turnover data for savanna herbaceous species.

Woody vegetation changes

Pooled stems.—Under the low- to moderate-intensity fire regimes imposed in this experiment, only relatively minor vegetation structural changes were attributable to burning of any sort, both in open forest and in woodland. Significant change was observed, however, between burned and UNBN treatments; specifically, the development of a denser midstory in both open-forest and woodland UNBN treatments. Release of understory stems into the midstory occurred within 5 years in open forest (Fig. 9b), and at some time later than this in woodland (Fig. 10b). Over the duration of the experiment there were evident trends of generally increasing midstory stem density and basal area of canopy stems (on UNBN treatments especially) in open forest, and understory density and basal area of canopy stems in woodland. Data for dead stems were too few for meaningful analysis in open forest, and showed an enigmatic increase with time, independent of treatment, in woodland; possibly buffalo impact was involved.

Such relatively subtle structural changes contrast markedly with the impacts of more intense fires recorded at Kapalga (Williams et al. 1999). There, basal area increased marginally in UNBN (3.5%) and EANN (0.5%) treatments, but declined substantially in LANN (−27%), and in an unplanned, very high intensity fire (−42%). Stem survival in an unplanned fire, both of dominant eucalypt and larger deciduous non-eucalypt species, increased sharply over the range 2–20 cm dbh and fell sharply in stems > 40 cm dbh. Although whole-plant survival was 84% over all species (but 36% in *Livistona* palms), stem survival was just 34% overall; stem survival was greatest in eucalypts and lowest in other deciduous species. These responses to a high-intensity unplanned fire were broadly similar to those obtained from the undertaking of the relatively high-intensity LANN treatment at Kapalga, 1990–1994, with the exception that *Livistona* survival was 99% in the experimental LANN fires. For UNBN and EANN treatments, whole-plant survival was 97% and 87% and stem survival was 96% and 72%, respectively (Williams et al. 1999).

These observations concerning the relatively severe impacts of LANN treatments on woody stem density and basal area are congruent with the results from African savanna experimental fire plot studies (e.g., Trapnell 1959, Mensbruge and Bergeroo-Campagne 1961; but see Geldenhuys 1977), including designs that involved clear-felling at establishment (e.g., Charter and Keay 1960, Ramsay and Rose Innes 1963, Brookman-Amissah et al. 1980, Chidumayo 1988). In contrast to northern Australian studies at Munmarlary and Kapalga, however, African studies generally report substantial increases in stem density from EANN and UNBN treatments (Rose Innes 1972). Unfortunately, directly comparable data for sites that were not clear-felled at establishment are scarce.

For 2-ha unreplicated plots established in derived savanna at Kokonedekro, Ivory Coast, after 24 years, densities of stems ≥5 cm dbh had increased by more than 190% on both EANN and UNBN treatments, but had declined to just 27% on LANN (Mensbruge and Bergeroo-Campagne 1961). Equivalent data for stems ≥10 cm dbh, however, indicate that stem densities increased on all treatments as follows: UNBN, 690%; EANN, 800%; and LANN, 150%. The major impact of LANN burning was thus on smaller stem size classes.

Although a comparable design also was undertaken on 0.4-ha unreplicated plots at Ndola in present-day Zimbabwe (Trapnell 1959), the data do not allow for a strict comparison between initial (1933) and next available (1944) assessments because of differences in units of measurement. However, it is apparent from the discussion and various data presented that mortalities of adults and (particularly) juveniles of typical savanna species were greatest in LANN and less in EANN, whereas there was a marked increase of at least juvenile size classes, both of savanna and closed-forest species, in UNBN. The most detailed comparable African fire plot assessment is provided by Geldenhuys (1977) for a replicated design involving five treatments, each with five plots (33.5 × 33.5 m), and two sites from low-rainfall (600 mm/yr) Kavango, in present-day Namibia. Geldenhuys reports the results of an assessment of basal area increment for certain species between 1959 and 1975 and a one-off survey in 1975 of stem heights and diameters for all species in new subplots. No significant effect of treatment on increment was found for the two species examined. In comparison with the four burning treatments, UNBN treatments resulted in greater height and volume of undergrowth, and larger numbers of tree stems <5 cm dbh, and significantly favored the regeneration of fire-sensitive species.

From limited comparable African fire plot data, therefore, it would appear that, under experimental time frames of the order of 1–2 decades, LANN treatments usually result in significant declines of at least juvenile size classes, UNBN treatments result in significant increases of at least juvenile size classes, and EANN treatments result in at least neutral-to-significant increase of juveniles, and sometimes significant increase in adults also. It should be noted that plot sizes in all of these African studies are small in comparison to those at Kapalga.

A further aspect noted in various African studies is the establishment of rain forest species on EANN and particularly UNBN treatments, especially where plots lie in relatively close proximity to rain forest sources. Conversely, at more remote savanna experimental sites,

usually at lower rainfall, vegetation thickening on unburned sites results from a greater abundance of savanna species (Swaine et al. 1992). Earlier vegetation studies at Munmarlary did not mention (Hoare et al. 1980) or, using different sampling methods, did not find evidence for establishment of rain forest species (Bowman et al. 1988, Bowman and Panton 1995). Rain forest species were not reported from five-year-old Kapalga UNBN treatment plots. At Munmarlary, establishment of rain forest pioneer species occurred only in woodland, mostly on UNBN, but significantly also on one LANN plot, mostly between 1978 and the final assessment in 1996.

We have attributed the somewhat paradoxical establishment of rain forest species on one LANN plot to the possible effects of buffalo impact. All rain forest species entering the fire treatments and UNBN plots, with the exception of one potentially tall tree (*Alstonia actinophylla*), are small trees or shrubs. All possess small, fleshy fruits amenable for dispersal by birds, with the exception of *Alstonia*, which possesses wind-dispersed, plumed propagules. Assessment of aerial photographs shows that the nearest closed-canopy rain forest patch is ~4 km from the woodland site and ~3.5 km from the open forest site. Although a seasonal creek containing scattered populations of rain forest taxa is <250 m from most woodland plots, no similar drainage line occurs in close proximity to the open forest site, which is situated in a featureless, extensive, colluvial mantle of deep sandy loam sediment.

The former absence of records of rain forest species from Munmarlary UNBN plots has been used, along with various other data illustrating the slow rate of rain forest species' establishment in eucalypt savanna (e.g., Fensham 1990, Bowman and Fensham 1991), to argue that ''a succession model describing the broad-scale transformation of eucalypt open-forest to closed monsoon forest is not tenable'' (Fensham 1990:261). Certainly, such succession is improbable, considering the fire regimes current over much of northern and northwestern Australia, as well as experimental studies (Stocker 1971, Bowman and Panton 1993) that suggest that mycorrhizas, soil fertility, and soil moisture are all important factors in regulating monsoon rain forest seedling establishment and growth. Nevertheless, in northeastern Australia, considerable expansion of rain forest is currently occurring under conditions of limited seasonal water deficit and limited burning (Harrington and Sanderson 1994, Russell-Smith and Stanton 2002).

Individual species.—As for northern Australian savanna formations in general, a characteristic feature both of open-forest and woodland woody species complements sampled in this experiment is the high proportion of species that resprout following fire disturbance. Only two of the species sampled, both relatively fast-growing, short-lived acacias (*Acacia holosericea*, *A. oncinocarpa*), are obligate seeders (sensu Gill 1981), i.e., fire-sensitive species that regenerate from seed alone. By contrast, obligate seeders comprise 50% of the woody species occupying rugged regional sandstone substrates (Russell-Smith et al. 1998).

Few species exhibited significant responses to fire regime treatment over the experimental period, in stark contrast to the magnitude of responses observed for single, very intense fires by Lonsdale and Braithwaite (1991) and Williams et al. (1999). In total, statistically significant treatment responses were observed at Munmarlary for 10 species in open forest and four in woodland. Although small sample plots and associated high variances no doubt contributed to this result, many species, including the dominant eucalypts, were sufficiently abundant in various height classes from the commencement of the experiment for detection of substantial population change over two decades, should this occur. The fact that change was, in the main, muted over the range of applied fire treatments confirms the relative stability of eucalypt open forest and woodland under low- to moderate-intensity, frequent burning (e.g., Hoare et al. 1980, Stocker and Mott 1981, Bowman et al. 1988, Williams et al. 2002). Against this background, a number of significant individual species responses warrant comment.

1. *Species population increases in BIEN and particularly UNBN treatments*.—Eight species exhibited increases, six in open forest and two in woodland. Significant accessions into the midstory included the rain forest pioneer *Antidesma ghaesembilla* in woodland (which also increased anomalously on one LANN plot, as described previously); the small tree *Planchonella pohlmanniana* in open forest; *Erythrophleum chlorostachys*, which showed a marked release in open forest; and four relatively short-lived *Acacia* species (three species in open forest, one in woodland), which tended also to show episodic recruitment followed by decline. Given the duration of the experiment, it is surprising that significant release of other non-eucalypt species into the midstory was not detected, although weak trends in this direction were apparent, if slight, for the small trees *Terminalia ferdinandiana* and *Gardenia megasperma* in woodland. Development of mixed-species (non-eucalypt) midstories has been reported previously for unburned woodland at Munmarlary after 15 years of fire protection (Bowman et al. 1988), and also from near Darwin after 10 years of fire protection (Fensham 1990). As described by Braithwaite and Estbergs (1985), frequent fires evidently suppress the development of slower growing, non-eucalypt savanna species.

2. *Species population increases in burned treatments*.—Five species clearly exhibited a pattern of increase, but only in the understory size class: three in open forest (*Erythrophleum*, *Grevillea goodii*, *Planchonella pohlmanniana*) and two in woodland (*Petalostigma quadriloculare*, *Planchonia careya*); a further species, *Gardenia megasperma*, exhibited a somewhat idiosyncratic response in open forest. With the possible

exception of *Grevillea goodii*, such increases in stem density presumably reflect the capacity of these species to regenerate vegetatively following burning. Vegetative aerial stem production may be relatively spatially restricted when arising from lignotuberous shoots (e.g., the previously noted species of *Gardenia*, *Petalostigma*, *Planchonella*, *Planchonia*), or may occur over an extensive area when from root suckers (*Erythrophleum*) and rhizomes, as documented for a large number of northern Australian woody savanna taxa (Lacey and Whelan 1976). Although *Grevillea goodii* also resprouts from lignotubers, observations suggest that this is limited to a single, nonspreading rootstock; hence, observed population increases in this species presumably reflect the establishment of new individuals from seed.

3. *Lack of response in Eucalyptus*.—Although slight, but significant, treatment effects were observed for canopy trees in three eucalypt species on open-forest plots, no significant treatment-related responses were observed for eucalypts in understory and midstory size classes, either in open forest or woodland. This apparent insensitivity to fire regime, in combination with consistently low midstory stem densities of dominant eucalypts, has significant implications for population dynamics and maintenance of canopy populations. Vegetative regeneration is universal in tropical savanna eucalypts, mostly from lignotubers, but also rhizomes in some species (Lacey 1974, Lacey and Whelan 1976). Production of eucalypt seedlings is observed rarely, dependent on seedfall being coincident with highly localized early wet-season rains (Setterfield and Williams 1996).

Similar observations concerning the lack of eucalypt midstory development in northern Australian savanna systems have been reported previously from studies undertaken at Munmarlary (Hoare et al. 1980, Bowman et al. 1988) and elsewhere (Braithwaite and Estbergs 1985, Wilson and Bowman 1987, Fensham 1990, Fensham and Bowman 1992). Although frequent fires have been implicated in the midstory recruitment bottleneck in some past studies (Hoare et al. 1980, Braithwaite and Estbergs 1985), experimental canopy removal studies undertaken by Fensham and Bowman (1992) indicate that eucalypt overstory root competition plays a significant role in the suppression of smaller size classes. It is thus notable that basal area generally increased with time at Munmarlary, both in open forest and woodland, probably attributable mostly to the increasing size of stems already present rather than to accessions into the overstory; in other words, mature canopy conditions prevailed over the duration of this 23-year experiment.

Management implications

In conclusion, we address two issues raised by the Munmarlary fire experiment: (1) implications of the assembled data for fire management of eucalypt-dominated savanna systems; and (2) the wider role of long-term fire experiments, especially given the very considerable resource issues involved.

Given ample anthropogenic and natural ignition sources and a vast flat-to-undulating terrain, fire exclusion at landscape scales is not a viable option for managing northern Australian savannas because it results in frequent, extensive, late dry-season fires (e.g., Jacklyn and Russell-Smith 1998, Williams et al. 2002). Rather, assembled data suggest the following.

1) Under regimes of low-to-moderate fire intensity, particularly those involving regular burning at relatively fine spatial scales, changes associated with frequent fires are not acute.

2) Some long-term changes appear to be associated with invariant regular burning, including increased dominance of flammable annual *Sorghum* spp. and the prospect of slow changes in population structure of the dominant eucalypts, may lead to long-term changes in the character of these singular communities. Other invariant regimes, including complete exclusion of fire, are likely to lead to change that disadvantages some elements of the fauna (e.g., Garnett 1992, Franklin 1999).

3) These concerns appear most likely to be realized if particular active burning regimes dominate large areas for sustained periods. Under prevailing social and economic circumstances in northern Australia, the regime most likely to be achievable at a significant scale close to larger population centers is a comprehensive regime of annual burning with a mix of early (much of the area) and late (in those areas not burned early) fires. Such a regime will probably lead to change that is adverse for the maintenance of biological diversity by impacting on various fire-sensitive flora and susceptible fauna; enhancing fuel loads through the increased dominance of *Sorghum* species (which will provide fuel loads needed to sustain comprehensive burns, even in an environment where fine and coarse woody fuels are less available); eliminating woody debris that provides shelter and food for many fauna; and reducing survivorship of older standing trees that have a high probability of containing hollows large enough to support populations of hollow-dependent mammalian, reptilian, amphibian, and avian fauna.

4) In areas where human population density and other infrastructure is too limited to intervene in this intensive way, the regime is likely to include spatially limited, frequently burned ''sacrifice'' areas ignited early in the year to inhibit the spread of large wildfires later in the year. These preventative measures often fail, such that other large areas will continue to be frequently burned by intense late dry-season fires (Dyer et al. 2002), which will experience more rapid and widespread deterioration of the type just outlined.

5) Although examples of fine-scale fire management exist, notably in increasingly rare situations under traditional Aboriginal stewardship (Yibarbuk et al. 2001),

such intensive practices are not readily transferable to wider landscapes and contemporary patterns of land use and occupancy.

In all likelihood, reactive fire regimes will continue to result in the loss of biodiversity from flammable northern Australia systems (Kerle 1985, 1998, Friend 1987, McKenzie and Belbin 1991, Russell-Smith and Bowman 1992, Woinarski and Fisher 1995, Andersen et al. 1998, Russell-Smith et al. 2002*b*, Williams et al. 2002). As is widely recognized elsewhere (e.g., Hansson 1997), the development of patchy, heterogeneous fire regimes is essential for maintaining regional habitat and faunal biodiversity (Woinarski 1990, Andersen 1991, Trainor and Woinarski 1994, Braithwaite 1995, Dostine et al. 2001).

Despite evident limitations, Munmarlary clearly provides some useful management information. However, application of these findings continues to be limited, given that the experiment was designed and executed without active participation of land owners and managers. Indeed, precisely timed, uniform fire treatments are perhaps the last approach that a manager is likely to seek or is able to apply. Active participation of land managers in the design and implementation of the experiment probably would have resulted in substantial practical modifications, including assessment of more intense fire regimes (using larger plot sizes as undertaken at Kapalga), and application of wet-season burning for reducing annual grass fuels (Stocker and Sturtz 1966). Today's managers would almost certainly seek to address looming ecological crises such as the contemporary invasion of north Australian savannas by escaped vigorous perennial pasture grasses (Lonsdale 1994) such as gamba grass (*Andropogon gayanus*) and mission grass (*Pennisetum polystachion*). These species provide substantially larger fuel loads than native grass species (Panton 1993) and have the potential to transform fire regimes in northern Australian savannas as they have elsewhere (D'Antonio and Vitousek 1992).

There are at least two plausible directions for, and approaches to, future management-focused research to ensure that it meets the existing and emerging needs of fire managers. The first relies on development of comprehensive simulation models that, subject to a range of assumptions about impacts of different sequences of fire treatment on individual sites and abiotic and biotic interactions among different sites, seek to predict larger scale, longer term outcomes. None of the long-term fire experiments to which we have referred generates the insights or parameter values needed to derive mechanistic or empirically based models. A new set of more relevant experiments would be required. This leads to the second response, which has been to call on managers to engage with researchers in adaptive management experiments (sensu Walters 1986, Andersen 1999). Active adaptive management experiments would involve careful choice and implementation of a range of management options, designed with reference to different, and preferably competing, models of likely outcomes (Walters 1986). Adaptive management experiments will, by definition, keep pace with changing issues and give researchers and managers a common experience base.

If carefully designed, initially modest projects not only will provide a crucial first step toward larger scale, higher risk, and hence more informative management experiments, but also will provide additional useful information by encompassing a greater range of temporal variation in fire treatments than has been examined hitherto. Most important, participants in these processes will have an opportunity to debate and identify common objectives for wider application and to design acceptable ways of testing options. The experience of testing options will be accompanied by review of the desirable and achievable, and hence some shift of aims, which researchers will be expected to accommodate (Whitehead 1999). Clearly, such a vision requires the development of close relationships between researchers and managers, maintained over long periods. Achieving such integration is one of the major challenges confronting improved fire management in northern Australia, and arguably in savannas generally.

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