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Abstract

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Disciplines

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Managing the matrix: decadal responses of eucalypt-dominated savanna to ambient fire regimes

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Abstract. Much of our understanding of the response of savanna systems to fire disturbance relies on observations derived from manipulative fire plot studies. Equivocal findings from both recent Australian and African savanna fire plot assessments have significant implications for informing conservation management and reliable estimation of biomass stocks and dynamics. Influential northern Australian replicated fire plot studies include the 24-year plot-scale Munmarlary and the five-year catchment-scale Kapalga, mesic savanna (>1000 mm/yr of rainfall) experiments in present-day Kakadu National Park. At Munmarlary, under low-to-moderate-intensity fire treatments, woody vegetation dominated by mature eucalypts was found to be structurally stable. At Kapalga, substantial declines in woody biomass were observed under more intense fire treatments, and modeling assessments implicate early-season fires as having adverse effects on longer-term tree recruitment. Given these contrasting perspectives, here we take advantage of a landscape-scale fire response monitoring program established on three major northern Australian conservation reserves (Kakadu, Litchfield, and Nitmiluk National Parks). Using statistical modeling we assess the decadal effects of ambient fire regime parameters (fire frequency, severity, seasonality, time since fire) on 32 vegetation structure components and abundance of 21 tree and 16 grass species from 122 monitoring plots. Over the study period the mean annual frequency of burning of plots was 0.53, comprising mostly early-dry-season, low-severity fires. Structural and species responses were variable but often substantial, notably resulting in stem recruitment and declines in juveniles, but only weakly explained by fire regime and habitat variables. Modeling of these observations under three realistic scenarios (increased fire severity under projected worsening climate change; modest and significant reductions in fire frequency to meet conservation criteria) indicates that all scenarios have positive and negative structural implications. Effecting significant regional fire regime change (e.g., reduction in frequency and size of severe fires) is demonstrably feasible, but it incurs risks and potentially some undesirable structural consequences. Given recent Australian and African experience, the generality and application of landscape-scale implications derived from manipulative fire assessments (including variable grazing and browsing regimes) in savanna require more critical assessment.

Key words: *Australia; biodiversity; Eucalyptus spp.; fire management; long-term fire regimes; monsoon tropics; tropical mesic savanna.*

INTRODUCTION

Recent decades have seen substantial advances in our understanding of the role of fire regimes in regulating the composition, structure, and dynamics of savanna systems. It is now widely recognized that while water availability strongly influences savanna woody biomass at landscape and continental scales (Williams et al. 1996, Sankaran et al. 2005, Bucini and Hanan 2007), fire regimes, grazing, browsing, and other disturbance act as important modifiers of tree–grass and woody biomass

relationships at local and site-specific scales (Scholes and Archer 1997, Higgins et al. 2000, Sankaran et al. 2004, Holdo et al. 2009). Under savanna fire regimes dominated by frequent, especially intense fires, typically grasses are promoted, woody fire-sensitive species are at risk, vegetative resprouts proliferate, and upper strata are depleted (Trapnell 1959, Rose Innes 1972, Bond and van Wilgen 1996, Hoffmann 1999). These principles generally hold true also for northern Australian savanna vegetation components (Williams et al. 2002), although population responses of the dominant eucalypts (including *Corymbia*) are less well understood based on evidence from two influential replicated fire plot experimental treatments. Recent African experience also

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highlights variable responses and insights derived from a long tradition of manipulative fire treatments (Higgins et al. 2007). Such uncertainties have significant implications for informing conservation management and reliable estimation of biomass stocks and dynamics in savanna systems.

Medium- to long-term manipulative fire experiments have been a feature of fire research in the savannas of northern Australia (Williams et al. 2003b). These include notably the 24-year hectare-scale experiment at Munmarlary (Russell-Smith et al. 2003a) and the five-year catchment-scale experiment at Kapalga (Andersen et al. 2003), both in present-day World Heritage Kakadu National Park. At each site a small set of consistently applied treatments (e.g., annual early-dry-season [EDS] fires, late-dry-season [LDS] fires, unburned controls) was applied to a restricted set of eucalypt-dominated, mesic (>1000 mm/yr of rainfall) savanna vegetation types. Fire intensities and severities experienced at Munmarlary are more representative of contemporary regional prescribed fire regimes than those generally experienced at Kapalga (Russell-Smith and Edwards 2006). At Munmarlary, unrestricted grazing and browsing by feral Asian buffalo occurred over much of the experimental period. At Kapalga, buffalo were removed prior to imposition of fire treatments; however, observations concerning buffalo and fire impacts on eucalypt adults and juveniles were obtained from an adjoining site (Werner 2005, Werner et al. 2006).

At Munmarlary, under low-to-moderate intensity (EDS, 420–800 kW/m; LDS, 1200–2700 kW/m, for open-forest and woodland vegetation, respectively) frequent burning, woody vegetation dominated by mature eucalypts was found to be structurally stable, whereas, in the absence of burning for at least five years, there was release of the non-eucalypt, woody component into the midstory. For grasses, invariant frequent burning led to the dominance of a small number of annual species, notably the regional dominant *Sarga* (formerly *Sorghum*; following Spangler 2003). In the absence of burning, annual grass species declined generally, while some perennials increased and most decreased (Russell-Smith et al. 2003a).

At Kapalga, “ring-burning” of large catchment-scale (15–20 km²) compartments resulted in mean fire intensities 2.5–6 times greater than those at Munmarlary (Williams et al. 2003a). In contrast to relatively subtle changes in woody biomass and density at Munmarlary, the more intense fires at Kapalga resulted in substantial declines of basal area in LDS treatments (–27%) and following an unplanned, very-high-intensity fire (–42%). While little change was recorded for grass species composition at Kapalga over the course of the experiment (Williams et al. 2003a), this observation might be explained by the fact that annual *Sarga* was already widespread in response to contemporary patterns of frequent, relatively intense burning. Combining available tree growth, mortality, and re-

ruitment data from two Kapalga data sets (Williams et al. 2003a, Werner 2005), Prior et al. (2006) reported differential effects of fire seasonality (EDS vs. LDS fires) on three different size class categories of woody trees. These authors concluded that the current regional regime of frequent (especially EDS) fires was likely to have adverse effects on longer-term recruitment of trees in northern Australian savannas.

The equivocal findings and perspectives provided by Munmarlary and Kapalga fire experiments have significant implications for conservation management of savanna systems in northern Australian reserves and, while many management objectives find support (e.g., reducing fire frequency and intensity for relatively fire-sensitive taxa and communities), issues relating to the desired frequency, severity, and seasonality of prescribed burning regimes in more fire-tolerant savannas remain contested (Andersen et al. 2005, Woinarski et al. 2005, Prior et al. 2006). With reference to an extensive independent, decadal (1995–2004) data set assembled in conjunction with a long-term vegetation and fire effects monitoring program established on three major northern Australian reserves (Kakadu, Litchfield, and Nitmiluk National Parks), our purpose here is to explore several related questions. What has been the decadal response of savanna vegetation structure and common tree and grass species composition to ambient fire regimes in these reserves? How do responses observed under the ambient regime compare with those observed under Munmarlary and Kapalga manipulative treatments? And what regimes, should it be feasible to deliver them at landscape scales, are more likely to afford ecologically sustainable outcomes? We undertake this assessment through statistical modeling of data sets assembled from 122 savanna open-forest and woodland (hereafter referred to as savanna) permanent monitoring plots, each sampled on three occasions (at establishment, at five years, and at 10 years), annual observations of fire incidence and severity, and ancillary biophysical data. Buffalo densities were very low on all three reserves throughout the assessment period.

MATERIALS AND METHODS

Regional context

The three parks are located in the northwestern “Top End” of the Northern Territory, Australia; Kakadu is 19 092 km² in area, Litchfield is 1464 km², and Nitmiluk is 2924 km² (Fig. 1). The entire region shares a broadly similar monsoonal climate, with annual rainfall declining from ~1500 mm in the vicinity of Litchfield and the northern sub-coastal portions of Kakadu to ~1000 mm in Nitmiluk in the southeast (Fig. 1). While annually highly variable in quantity, the wet season (predominantly November–March) is very reliable.

The parks also share various physiographic features in common, notably extensive tracts of infertile, typically rugged sandstone uplands and associated plateau surfaces surrounded by typically laterized undulating

lowlands and plains. Kakadu is famous also for its extensive estuarine and freshwater wetland floodplain systems. By park, Kakadu encompasses mostly lowland formations (67%), then sandstone uplands (22%), and floodplains (11%). Conversely, Litchfield and Nitmiluk comprise mostly sandstone uplands (63% and 71%, respectively). Apart from floodplain systems, vegetation types are broadly similar across the three parks and are dominated by extensive eucalypt-dominated savanna, with lesser components of sandstone heaths, monsoon rain forest and, in Nitmiluk, small patches of closed-canopy lancewood (*Acacia shirleyi*) thicket.

Prevailing climatic conditions are conducive to rapid development of grassy fuels following fire, such that fires may recur at any one site on an annual–biennial basis (Williams et al. 2002). Even in rugged sandstone formations, accumulation of fine grass and litter fuels is sufficient to support intense fires (>5000 kW/m) in all but exposed rock situations under late-dry-season climatic conditions within 1–3 years of having been burned previously (Russell-Smith et al. 1998). Fires in the region are almost invariably anthropogenic in origin and ground-borne.

Over the assessment period 1995–2004, an annual mean of 66% of Litchfield, 51% of Nitmiluk, and 42% of Kakadu was burned (Russell-Smith et al. 2009). In all parks, fire extent was most frequent in the EDS (~April–July), by a factor of 3.1 in Litchfield, 2.2 in Kakadu, and 1.4 in Nitmiluk. Approximately 50% of lowland landform units were burned in all parks, particularly fire-prone savannas. By contrast, burning of sandstone uplands varied markedly between parks; 70% of sandstone savanna was burned on average in Litchfield, 51% in Nitmiluk, and 29% in Kakadu. The assessment period also coincided with low densities of feral Asian water buffalo and cattle (hence higher grassy fuel loads) following very substantial population reductions through the late 1980s and early 1990s associated with a national bovine disease eradication program (Skeat et al. 1996, Petty et al. 2007).

Monitoring plots

Some 220 permanent monitoring plots (each 40×20 m) were established on the three parks in 1994–1995. Of these, 133 plots are located in Kakadu, with 41 and 46 in Litchfield and Nitmiluk, respectively (Fig. 1), sampling a variety of landform and vegetation types. All plots were resampled in 1999–2000 and 2004–2005. All sampling was conducted at the end of the wet season to facilitate flora identification (i.e., before herbaceous plants wither or vegetation is burned).

A variety of vegetation and environmental information was recorded at each plot. For adult trees (woody stems ≥ 5 cm dbh; measured at 1.3 m above the ground surface), all individuals in the plot were counted and tagged; for taller shrubs (>0.5 m), all individuals were counted within a fixed 40×10 m subplot; counts of

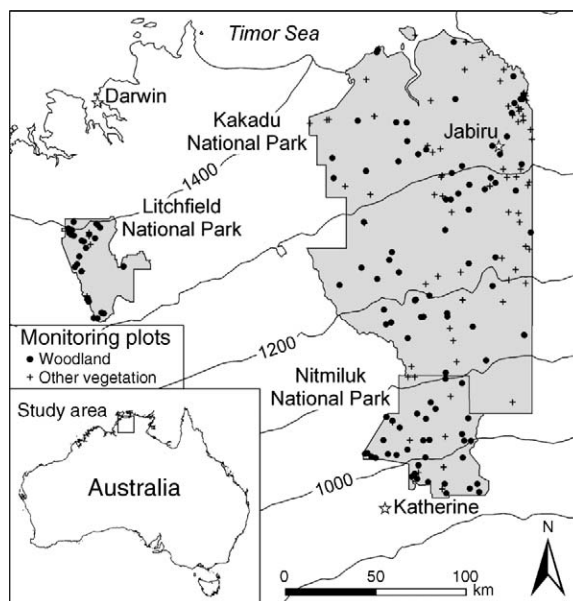


FIG. 1. Map of the study location in Northern Territory, Australia, with rainfall isohyets (mm) and distribution of the monitoring plots within three national parks (in gray).

small shrubs (≤ 0.5 m) were recorded in two fixed 40×1 m transects; and for herbaceous ground-layer species, cover was recorded in each of 40 fixed 1×1 m quadrats. All species occurring within each of three height strata (trees, shrubs, and ground layer) were recorded such that any species may be recorded in more than one class. Full details of the vegetation sampling design are given in Edwards et al. (2003).

Fire incidence and severity have been determined similarly for plots in each park, following the methodology described previously for Kakadu and Nitmiluk by Russell-Smith and Edwards (2006). Where possible, monitoring plots have been photographed once or twice each year throughout the 10-year monitoring period. Using the photos, plots were scored as recently burned or unburned. Fire severity at burned plots was categorized as mild, moderate, or severe, using the severity index developed by Russell-Smith and Edwards (2006), based largely on the scorch height of leaves. Leaf scorch height has been shown to be closely related to measured Byram fire line intensity in these savannas ($R^2 = 0.85$; Williams et al. 1998). Mild fires were those with scorch heights of ≤ 2 m, suggesting Byram fire line intensities of <1000 kW/m. Moderate fires were those in which the canopy was scorched to mid-height, suggesting intensities of 1000–2000 kW/m. Severe fires were those in which the canopy was scorched to its full height, suggesting intensities of >2000 kW/m. The season of each fire was also estimated as either early or late. Fires in the wet season and early dry season (EDS) were described as early, and fires occurring later in the dry season (LDS, ca. August–November) were described as late.

TABLE 1. Variables used in analysis and mean values for continuous response and explanatory variables in long-term response of Australian eucalypt savanna to fire regimes.

Variable description	Name	Mean†	Mean change ($t_3 - t_1$)‡	Mean change (%)
a) Change (response) variables				
Tree basal area (m ² /ha)				
All trees	BA	7.6	-0.3 ± 0.2	-3.5
Eucalypts (including <i>Corymbia</i>)	Euc BA	4.7	-0.2 ± 0.1	-3.9
Live tree (≥5 cm dbh) stem density (stems/ha)				
Small trees (<10 cm dbh)	Small Trees	158	2.5 ± 9.5	1.6
Medium trees (10–30 cm dbh)	Medium Trees	162	-15.6 ± 4.3	-9.6
Large trees (>30 cm dbh)	Large Trees	22.7	1.5 ± 1.2	6.5
All trees	All Trees	342	-11.6 ± 7.3	-4.4
Small eucalypts (<10 cm dbh)	Small Eucs	53.9	1.2 ± 5.3	2.2
Medium eucalypts (10–30 cm dbh)	Medium Eucs	88.2	-10.9 ± 2.4	-12.4
Large eucalypts (>30 cm dbh)	Large Eucs	27.7	2.2 ± 1.3	7.9
All eucalypts	All Eucs	170	-7.6 ± 4.9	-4.4
Shrub (<5 dbh) density (stems/ha)				
Small juvenile trees (<50 cm tall)	Small Juv Trees	6064	-334.0 ± 1348	-5.5
Medium juvenile trees (50 cm to 2 m tall)	Medium Juv Trees	1061	-257.7 ± 136	-24.3
Tall juvenile trees (>2 m tall, <5 cm dbh)	Tall Juv Trees	257	67.4 ± 30.3	26.3
Small eucalypts (<50 cm tall)	Small Juv Eucs	1071	-456.2 ± 145	-42.6
Medium eucalypts (50 cm to 2 m tall)	Med Juv Eucs	439	-134.9 ± 49.5	-30.8
Tall eucalypts (>2 m tall, <5 cm dbh)	Tall Juv Eucs	89.5	7.1 ± 10.2	8.0
Small shrubs (<50 cm tall)	Small Shrubs	2638	218.4 ± 369	8.3
Medium shrubs (50 cm to 2 m tall)	Medium Shrubs	906	-108.5 ± 109	-12.0
Tall shrubs (>2 m tall, <5 cm dbh)	Tall Shrubs	200	-20.5 ± 27.0	-10.3
Species richness (no. species/plot)				
Fruit tree species	Fruit Tree Richness	2.2	0.04 ± 0.10	2.3
Deciduous trees	Deciduous Tree Richness	2.5	0.03 ± 0.10	1.9
Evergreen trees	Evergreen Tree Richness	4.3	-0.2 ± 0.1	-1.3
All tree species	Tree Species Richness	6.9	-0.2 ± 0.2	-4.4
Small shrubs (<50 cm tall)	Small Shrub Richness	7.8	0.2 ± 0.4	1.9
Medium shrubs (50 cm to 2 m tall)	Medium Shrub Richness	10.3	-0.2 ± 0.4	-1.7
Tall shrubs (>2 m tall, <5 cm dbh)	Tall Shrub Richness	3.4	0.5 ± 0.3	15.7
Annual forbs	Annual Forb Richness	6.2	1.5 ± 0.4	23.9
Perennial forbs	Perennial Forb Richness	8.2	0.1 ± 0.3	0.7
All forbs	Forb Species Richness	15.6	1.4 ± 0.6	8.7
Annual graminoids	Annual Graminoid Richness	3.8	1.4 ± 0.3	38.1
Perennial graminoids	Perennial Graminoid Richness	3.9	0.5 ± 0.2	12.7
All graminoids	Graminoid Species Richness	7.8	1.7 ± 0.3	22.4
b) Explanatory variables				
Environmental				
Kakadu, Litchfield, Nitmiluk National Parks	Park			
Sandstone or lowland habitat	Habitat			
Site productivity index§	PI			
Soil depth¶	Soil Depth			
Soil texture: five classes from sand to clay	Soil Type			
Topographic position#	Topo			
Inundation: three classes from dry to perennially moist	Inundation			
Mean annual rainfall (mm)	Rainfall	1245 ± 12.9		
Rock cover (%)	Rock	10.2 ± 1.9		
Canopy height (m), mean of three tallest stems	Canopy Height	14.2 ± 0.4		
Fire				
Fire frequency (no. fires/yr)	Fires	0.53 ± 0.02		
Early-season fire frequency (no. fires/yr)		0.40 ± 0.02		
Late-season fire frequency (no. fires/yr)		0.13 ± 0.01		
Mild-fire frequency (no. fires/yr)	Mild Fires	0.35 ± 0.02		
Moderate-fire frequency (no. fires/yr)	Mod Fires	0.13 ± 0.12		
Severe-fire frequency (no. fires/yr)	Severe Fires	0.05 ± 0.01		
Time since last moderate or severe fire (yr)	TS Mod/Sev Fire	4.7 ± 0.3		
Time since last severe fire (yr)	TS Sev Fire	8.0 ± 0.3		
Longest fire-free period (yr)	Fire Free Period	2.9 ± 0.1		

Notes: Values are given as mean ± SE. Diameter at breast height was measured at 1.3 m above the ground surface. Frequency of early- and late-dry-season fires is included for comparison only. Three assessments were made: t_1 , t_2 , and t_3 , in three parks located in the northwestern "Top End" of the Northern Territory, Australia.

† For response and explanatory variables, means are given for t_1 . For fire variables, means are given for t_1 – t_3 .

Analysis

Change in vegetation structure.—Using data for 122 eucalypt savanna woodland and open-forest plots for which complete decadal fire histories were available, changes in 32 vegetation structure variables describing tree, shrub, and ground layer components (Table 1) were analyzed with reference to the absolute magnitude of change over the full 10-year period. Absolute, rather than proportional, change was used given that values of the latter are not normally distributed and have unrealistically large values for variables with low values at the first sample. Juvenile tree and juvenile eucalypt variables incorporate juvenile size classes, respectively, of tree species (including eucalypts) and eucalypts only. Shrub variables include all erect woody taxa that typically do not develop a tree habit (defined here as stems ≥ 5 cm dbh).

Ten environmental or habitat variables and seven fire regime explanatory variables were used for preliminary exploratory assessments (Table 1). Estimates of mean annual rainfall (MAR) were derived using the software ANUclim (version 5.1; Centre for Resource and Environmental Studies, Australian National University, Canberra, ACT, Australia). This software provides interpolated long-term climatic averages for respective plot locations for the period 1921–1995. Fire regime variables were assembled from plot records. For modeling purposes, fire severity (as opposed to fire seasonality) variables were used given that initial assessment indicated that fire severity was more strongly correlated with most vegetation structural responses. Nevertheless, it is well recognized that fire severity and fire seasonality are closely related in northern Australian savannas (Russell-Smith et al. 2003a, Williams et al. 2003a). In this study, the correlation between EDS fire frequency and mild-fire frequency was 0.82 and that between LDS fires and severe fires was 0.37.

Relationships between structural change and explanatory variables were analyzed using generalized linear modeling (McCullagh and Nelder 1983), using Akaike's information criterion (AIC) to select "best" models (Burnham and Anderson 2002). For analysis, the assembled data set was not separated into component five-year periods because preliminary analyses indicated that the increase in sample size did not result in increased explanatory power. All analyses assumed a normal error distribution. The distribution of each response variable was checked visually for conformity

to the normal distribution. The potential set of 17 explanatory variables (seven fire, 10 covariates) was reduced to eight (four fire, four covariates) by choosing those with the largest number of significant relationships with response variables when fitted individually. From this set, all model combinations subject to a maximum of two fire variables and one covariate were compared to identify the best model and any alternative models with $\Delta\text{AIC} < 2$ (Burnham and Anderson 2002). All two-way interactions between fire and environmental/habitat variables in the best model were tested and included in the final model if they reduced AIC and were statistically significant. The percentage of null deviance captured was used to measure the goodness of fit of the best model and of the fire terms in the model (without interactions present). Standard diagnostic graphics (fitted vs. residuals and quantile-quantile [q-q] plot) were used to test regression assumptions.

Additionally, to assess whether structural responses to fire regime variables were similar across the three parks, we added the variable "Park" to the best model for each structural variable. Improvement to the best model was gauged by reduction in AIC; if there was no improvement then Park was assessed on its own.

We also used the model equations to predict, for each vegetation structure variable at time 1 (t_1), what the consequences of changing the fire regime would be under three scenarios: (1) increasing the frequency of severe fires from current (0.05 fires/yr; Table 1) to 0.1 fires/yr (with an associated decrease in mean time since moderate or severe fires from 4.7 to 3.9 years); (2) reducing fire frequency from 0.53 fires/yr (Table 1) to 0.4 fires/yr for all fires, maintaining mild-fire frequency at 0.35 fires/yr and reducing both moderate and severe-fire frequencies to 0.025 fires/yr; and (3) reducing fire frequency to 0.25 fires/yr for all fires, comprising annual frequencies of 0.05 fires/yr for mild fires, 0.10 fires/yr for moderate fires, and increasing severe fires to 0.1 fires/yr as a consequence of the reduction in overall fire area. Each scenario was expressed as the change in each variable compared to the change predicted under the current fire regime (i.e., with current mean values of the fire variables).

Species.—Response data were assembled for 37 of the most commonly sampled individual species, comprising 16 grasses including seven annuals (Fig. 2) and 21 trees (Fig. 3). For each tree species, separate analyses were undertaken for changes in basal area, stem density, and

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‡ For response variables, note that means describe the net change over the 10-year observation period, where t_1 refers to the initial assessment and t_3 to the third assessment.

§ Site productivity index is composed of three equal classes based on initial plot basal area: 1, < 5.25 m²/ha; 2, 5.25–9 m²/ha; 3, > 9 m²/ha.

¶ Soil depth is composed of three classes: 1, < 20 cm, skeletal; 2, < 100 cm, shallow; 3, > 100 cm, deep.

Topographic position is composed of five classes from valley flat to hilltop/plateau.

|| Derived from interpolated climate surface (ANUclim; see *Materials and methods: Analysis*).

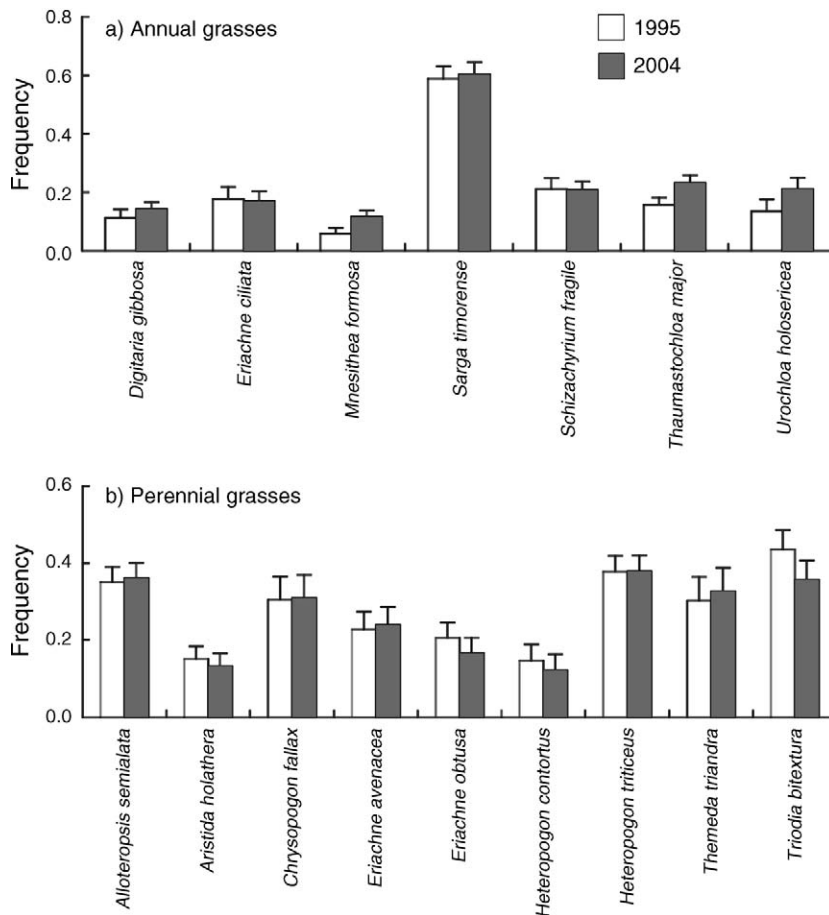


FIG. 2. Change in sampled frequency (mean + SE) of (a) annual and (b) perennial grass species.

density of small, medium, and tall juveniles, per plot. For grass species, analyses were undertaken for changes in sampled frequency per plot. While mean cover change data for grass species are also presented in *Results*, these were not used in statistical modeling given inherent subjectivity in field cover estimates.

To increase sample size, the effect of fire regimes on changes in species response variables was examined using data for the two sample periods (t_1-t_2 , t_2-t_3) using generalized mixed modeling. Initially, correlation coefficients were calculated between all species response variables and the same 17 fire and environmental explanatory variables used for assessment of vegetation structure change. Three fire variables (“fire frequency,” “severe-fire frequency,” “time since moderate or severe fire”), and one habitat variable (“basal area”) with the highest average correlation with species variables were retained for modeling. For each species response variable, eight models were fitted: the null model (no terms), basal area, fire count, severe fire count, time since moderate/severe fires, basal area + fire count, basal area + severe fire count, and basal area + time since moderate/severe fires. Plot was included in each model

as the random variable to account for the fact that values for two separate periods were included for each plot.

Models were compared using AIC. If the basal area model had a lower AIC than the null model then this was taken as the base model, and the effect of each fire variable was judged against it (e.g., $\Delta\text{AIC} = [\text{basal area} + \text{fire term AIC}] - [\text{basal area AIC}]$). Otherwise ΔAIC was calculated against the null model.

We report the estimate of the fire term relationship and statistical significance (P) for those species response variables with supported models. These were discriminated by those in which ΔAIC was >2 and those in which it was <2 (and thus for which the model without a fire term was a supported alternative model). Generally, but not always, models with $\Delta\text{AIC} > 2$ also had a significant fire term ($P < 0.05$). We refer to these models with $\Delta\text{AIC} > 2$ as “adequate models.” We also calculated a measure of the goodness of fit of the model as developed for mixed models; this is a pseudo- R^2 calculated from the difference in log-likelihood between the model and the null model (Magee 1990). To assist interpretation of the large number of models, here we

report on the number of models from different groupings of response variables that showed relationships with each of the three fire variables. This focus also partly overcomes the statistical problem associated with analysis of so many models resulting in spurious significant relationships.

RESULTS

Fire regime

Over the 10 years of observations, the average annual fire frequency experienced on plots was 0.53, of which 0.35 was for mild severity fires, 0.13 for moderately severe fires, and 0.05 for severe fires. The average fire frequency was 0.40 for EDS fires and 0.13 for LDS fires. Where observed, average return periods for moderate or severe fires was 4.7 years and 8 years for severe fires only (Table 1).

Vegetation structure change

Overall, tree basal area and stem density declined slightly (<5%), with the decline attributable to the medium-sized (10–30 cm dbh) stem class. Small and medium-sized juvenile tree density classes declined, whereas densities of tall recruits increased. While eucalypts followed these general patterns, they exhibited substantial and disproportionately larger declines in smaller recruit classes. At the start of the study eucalypts comprised 62% of basal area and just under half of total tree stem density. Small-shrub (non-tree) densities increased, whereas substantial declines occurred in medium and tall size classes. Species richness increased in 10 of 14 assessed structural classes, but declined slightly in evergreen trees and trees overall and medium-sized shrubs (Table 1).

The best models for 24 structural variables exhibited a fire response, with time since moderate or severe fire occurring in 11 models, fire frequency in 10, severe-fire frequency in nine, and mild-fire frequency in four. In general, explanatory models for the 32 structural variables were weak, with only one model (for tall shrubs) describing more than 20% of null deviance and nine others describing between 10% and 20%; collectively fire terms contributed a mean 4.2% of null deviance of the best models (Table 2).

Time since moderate or severe fire was significantly positively associated with tall shrub density and species richness and tall juvenile tree (including eucalypt) stem density and significantly negatively associated with densities of large trees and medium-sized eucalypt juveniles. Both fire frequency and severe-fire frequency were associated mostly with negative structural responses (Table 2). Fire frequency was significantly negatively associated with small tree and total tree stem density and evergreen and total tree species richness and significantly positively associated with medium-sized shrubs. Severe-fire frequency was significantly negatively associated with large tree density, evergreen and total tree species

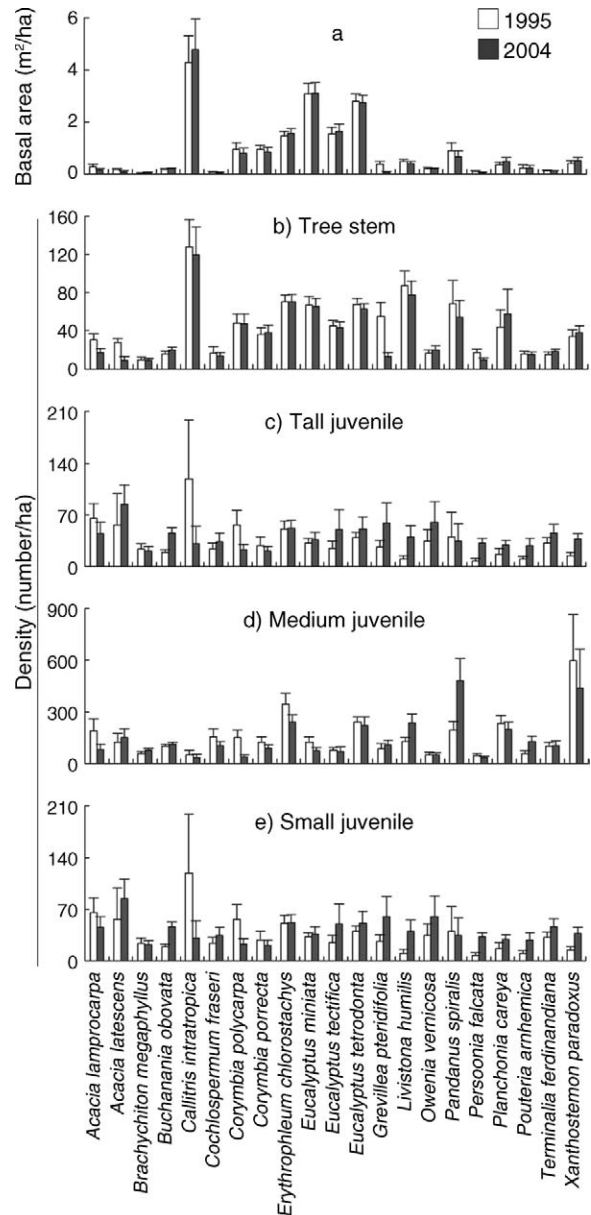


FIG. 3. Change in sampled population structure parameters (mean + SE) for 21 common tree species: (a) basal area and (b–e) densities of (b) tree stems (≥ 5 cm dbh), (c) tall juveniles (> 2 m tall, < 5 cm dbh), (d) medium juveniles (50–200 cm tall), and (e) small juveniles (50 cm tall).

richness, annual and total forb species richness, and perennial graminoid species richness.

With the addition of the variable park, explanatory best models were improved for 14 of the 32 structural variables and, by itself, was found to be significant in another four. Of the 14 best models, the negative influence of Litchfield NP alone was observed in 10 (medium tree density, all juvenile eucalypt density classes, large eucalypt density, and evergreen tree, tall

TABLE 2. Explanatory models for assessing change in vegetation structure attributes from woodland plot data ($n = 122$ plots).

Variable	Best model	Fire terms P
Trees		
Small juv trees	Habitat	
Medium juv trees	+Soil Depth – TS Mod/sev Fire	NS
Tall juv trees	+TS Mod/sev Fire	*
Small trees	Habitat – Fires + Mild Fires	** (Fires), NS (Mild Fires)
Medium trees	Habitat	
Large trees	–Severe Fires – TS Mod/sev Fire	*(Severe Fires), **(TS Mod/sev Fire)
All trees	Habitat – Fires + Mild Fires	** (Fires), NS (Mild Fires)
Tree basal area	PI	
Small juv eucs	Habitat – TS Mod/sev Fire	NS
Med juv eucs	–TS Mod/sev Fire	*
Tall juv eucs	+TS Mod/sev Fire	NS
Small eucs	Habitat + TS Mod/sev Fire	NS
Medium eucs	Prod	
Large eucs	–TS Mod/sev Fire	NS
All eucs	PI	
Euc basal area	PI + TS Mod/sev Fire	NS
Tree species richness	Habitat – Fires – Severe Fires + Fires × Severe Fires	** (Fires), ** (Severe Fires) *(Fires*Severe Fires)
Fruit tree richness	Habitat – Fires + Habitat × Fires	NS (Fires), ** (Habitat*Fires)
Deciduous tree richness	–Fires	NS
Evergreen tree richness	Habitat – Fires – Severe Fires	*(Fires), *(Severe Fires)
Shrubs		
Small shrubs	PI + Severe Fires + Mild Fires	NS (Severe Fires), NS (Mild Fires)
Medium shrubs	Habitat + Fires	**
Tall shrubs	+Severe Fires + TS Mod/sev Fire	NS (Severe Fires), *(TS Mod/sev Fire)
Small shrub richness	no model	
Medium shrub richness	Habitat	
Tall shrub richness	–Fires + TS Mod/sev Fire	** (TS Mod/sev Fire), NS (Fires)
Ground layer		
Forb species richness	Canopy height + Fires – Severe Fires	*(Severe Fires), NS (Fires)
Annual forb richness	PI – Severe Fires	*
Perennial forb richness	Habitat + Fires	NS
Graminoid species richness	PI – Severe Fires	NS
Annual graminoid richness	PI	
Perennial graminoid richness	Habitat – Severe Fires – Mild Fires	*(Severe Fires), NS (Mild Fires)

Notes: P (fire term) gives the significance level of the estimate for the fire terms in each model (NS, not significant; * $P < 0.05$; ** $P < 0.01$). The column for “Alternative fire terms” lists fire terms that are substitutable for those in the final model (where the difference in the Akaike information criterion [ΔAIC] is < 2 as given in parentheses). The “Fire terms deviance” column gives the change in deviance after removing the fire term(s) from the model (without interactions present) expressed as a percentage of the null deviance.

shrub, forb, graminoid, annual graminoid species richness) and, together with Nitmiluk NP, in a further two models (small shrub and annual forb species richness); positive influences were contributed by these respective parks in a further two models (medium shrub, annual forb species richness).

If severe-fire frequency is increased relative to the prevailing regime (scenario 1; Table 3), 17 measures are predicted to mostly moderately ($\leq 10\%$) decline and five to moderately increase. Components predicted to increase include four measures for smaller juvenile tree, eucalypt, and shrub classes, and a slight increase in large eucalypt stem density is predicted. With a modest reduction in fire frequency and severity (scenario 2), eight structural components are predicted to decline and 17 to increase. Mostly substantial declines are predicted to occur in five measures for smaller juvenile tree, eucalypt, and shrub classes, as well as large eucalypt stem density (37%) and perennial forbs (5%). Where fire frequency is markedly

reduced but severe-fire frequency increased as a result (scenario 3), 10 variables are predicted to increase and 15 to decrease. Under this scenario, we predict slight to moderate declines in eucalypt basal area, four stem density categories, tall juvenile trees, and four categories of ground cover species richness and mostly substantial declines in all three shrub classes.

Species

Species responses varied markedly over the 10-year observation period. For grasses, the mean sampled frequency of five of seven annual species increased, including three species by $> 10\%$; the frequency of five perennial grasses increased and four decreased, but none by $> 10\%$ (Table 4, Fig. 2). By contrast, changes in mean cover were of a different sign for five regionally significant taxa (Table 4). For 21 common tree species, most exhibited declines in basal area, stem density, and small and medium-sized juveniles and increases in tall

TABLE 2. Extended.

Alternative fire terms	Deviance (%)	Fire terms deviance (%)
	2.1	0
	4.7	2.4
+TS Mod/sev Fire – Fires (0.84), + TS Mod/sev Fire – Mild Fires (1.30)	5.4	5.4
– Fires (0.10)	15.8	5.5
+TS Mod/sev Fire (0.85)	2.7	0
	8.2	8.2
–Fires (0.49)	16.8	5.2
+Severe Fires (1.43)	5.5	0
no fire term (0.51), + Severe Fires (1.10), – Mild Fires (1.77)	6.3	2.5
–TS Mod/sev Fire + Mild Fires (1.28)	5.5	5.5
no fire term (0.19), – Fires + Mild Fires (0.64), – Fires (1.52),	3.1	3.1
	5.9	2.7
	5.4	0
–TS Mod/sev Fire – Severe Fires (0.26)	4.1	4.1
+TS Mod/sev Fire (0.70), – Severe Fires (0.93)	4.4	0
no fire term (0.03)	6.6	1.6
	17.6	11.3
+TS Mod/sev Fire (0.87), – Severe Fires (1.00)	12.7	8
no fire term (0.24), – Fires – Severe Fires (0.91)	1.8	0
	17.5	7.9
+Fires (0.67), + Mild Fires (1.03), + Severe Fires + Fires (1.29), + Severe Fires (1.32)	10.8	5
+Fires + TS Mod/sev Fire (1.08)	11.4	6.2
+TS Mod/sev Fire (0.63)	24.4	24.4
+TS Mod/sev Fire (1.26)	0	0
+Mild Fires (1.70)	4.4	0
+TS Mod/sev Fire (0.16)	10.6	10.6
+Mild Fires (0.46), – Severe Fires (0.58), – Severe Fires + Mild Fires (0.18)	6.6	6
+Fires – Severe Fires (0.95)	6.6	2.2
+Mild Fires (0.75), + Fires – Severe Fires (0.72), + Fires + TS Mod/sev Fires (0.82)	4.9	2.7
	8.3	2.8
–Severe Fires (0.97), + TS Mod/sev Fires (1.49)	8.3	0
–Severe Fires (0.65), – Severe Fires – Fires (0.61)	6	1.7

juveniles. These observations are consistent generally also with the responses of eucalypts and two obligate seeder taxa (*Callitris intratropica*, *Grevillea pteridifolia*; Table 5, Fig. 3).

Of the 16 species of grasses examined, eight exhibited a fire regime effect, although only four models were adequate ($\Delta AIC > 2$; Table 6). Of the perennials, *Alloteropsis semialata* exhibited a positive relationship and *Chrysopogon fallax* a negative relationship with fire frequency; *Eriachne avenacea* declined with time since moderate or severe fire. Of the annuals, three species (*Digitaria gibbosa*, *Mnesithea formosa*, *Thaumastochloa major*) exhibited declines with increasing fire or severe-fire frequency and two others (*Sarga timorensis*, *Schizachyrium fragile*) declined with time since moderate or severe fire.

All 21 tree species exhibited fire effects for at least one structural variable; 52 models contained a fire term, although only 29 of these were adequate (Table 6). Models were mostly weak (only 16 with $R^2 > 0.2$) and, of 58 individual species' population structure components that exhibited $>10\%$ positive or negative change

over the decadal study period (Table 4), explanatory models containing a fire term were identified for just 30 (52%). Where fire terms were included in tree species' response models, 24 (46%) conveyed negative effects of fire frequency or severe-fire frequency, 10 (19%) conversely reflected positive effects of these same frequency variables, and 12 (23%) and six (12%) models, respectively, reflected negative and positive effects of time since moderate or severe fire (Table 6).

DISCUSSION

Fire regimes and woody structure dynamics

In contrast to experimental fire response studies undertaken at Munmarlary and Kapalga in Kakadu NP, here we report the effects of ambient fire regimes experienced over a large expanse of mesic savanna in northern Australia based on an exceptionally large spatial, decadal-scale data set. Ambient fire regimes over the study period were generally EDS-dominated, mostly of mild fire intensity, and contrasted substantially with more intense treatments at Kapalga, and mostly at lesser frequencies than at both Munmarlary and Kapalga

TABLE 3. Model predictions of the decadal change in all vegetation response variables under three fire regime scenarios.

Variable	Scenario 1	Scenario 2	Scenario 3
Tree basal area (m ² /ha)			
All trees	0	0	0
Eucalypts (including <i>Corymbia</i>)	-0.06 (1.3)	0.72 (15.3)	-0.03 (0.6)
Live tree (≥ 5 cm dbh) stem density (stems/ha)			
Small trees	-6.0 (3.8)	95.4 (60.5)	46.2 (29.3)
Medium trees	0	0	0
Large trees	-3.1 (13.5)	13.5 (59.5)	-2.49 (11.0)
All trees	-6.2 (1.8)	2.8 (0.8)	-31.1 (9.1)
Small eucalypts	-3.0 (5.6)	36.0 (66.8)	-1.4 (2.6)
Medium eucalypts	0	0	0
Large eucalypts	0.8 (3.0)	-9.9 (35.7)	0.4 (1.4)
All eucalypts	-17.7 (10.4)	209 (123.2)	-8.1 (4.7)
Shrub (<5 dbh) density (stems/ha)			
Small juvenile trees	0	0	0
Medium juvenile trees	72.6 (6.8)	-857 (80.8)	33.0 (3.1)
Tall juvenile trees	-24.1 (9.4)	284 (110.7)	-10.9 (4.2)
Small eucalypts	81.9 (7.6)	-967 (90.3)	37.2 (3.5)
Medium eucalypts	40.2 (9.2)	-475 (108.3)	18.3 (4.2)
Tall eucalypts	-6.0 (6.7)	71.3 (79.7)	-2.7 (3.1)
Small shrubs	271 (10.3)	-230 (8.7)	-641 (24.3)
Medium shrubs	<-0.01 (0.0)	-200 (22.1)	-406 (44.8)
Tall shrubs	-52.7 (26.4)	462 (231)	-352 (176)
Species richness (no. species/plot)			
Fruit tree species	0	0.12 (5.3)	0.24 (10.8)
Deciduous trees	0	0.1 (3.9)	0.2 (7.9)
Evergreen trees	-0.18 (4.2)	0.25 (5.8)	0.15 (3.4)
All tree species	-0.24 (3.5)	0.38 (5.6)	0.29 (4.2)
Small shrubs	0	0	0
Medium shrubs	0	0	0
Tall shrubs	-0.25 (7.6)	3.0 (89.6)	-0.12 (3.5)
Annual forbs	-0.5 (7.9)	0.25 (4.0)	-0.5 (-7.9)
Perennial forbs	0	-0.37 (4.5)	-0.75 (9.1)
All forbs	-0.9 (5.8)	-0.18 (1.2)	-2.2 (14.0)
Annual graminoids	0	0	0
Perennial graminoids	-0.17 (4.4)	0.12 (3.1)	0.19 (5.0)
All graminoids	-0.4 (5.1)	0.2 (2.5)	-0.4 (5.1)

Notes: Each value describes the change relative to the current regime, with the percentage change given in parentheses: scenario 1, severe-fire frequency increased to 0.1; scenario 2, fire frequency reduced to 0.4, with mild-fire frequency maintained at 0.35, and moderate- and severe-fire frequencies each reduced to 0.025; scenario 3, fire frequency reduced to 0.25, mild-fire frequency reduced to 0.05, and moderate- and severe-fire frequency set at 0.1. Variables with zero in all three scenarios did not have a fire term in their model.

(Russell-Smith and Edwards 2006, Murphy et al. 2010). Rainfall over the decadal period was the highest recorded (Bureau of Meteorology 2008), major cyclonic episodes were regionally absent (Cook and Goyens 2008), and grazing and browsing by feral ungulates was slight (Petty et al. 2007).

In response, structural and species changes were variable but often substantial, notably resulting in recruitment of relatively fire-sensitive tall-tree juveniles and small trees, but declines in smaller-sized juveniles. These responses were only weakly explained by fire regime and habitat variables, suggestive that other, especially competitive factors are likely to have been contributory. Relatively small changes observed in tree structural attributes accord with observations that living biomass showed no net change based on the same data set (Murphy et al. 2009) and a 5% increase (equivalent to 1.5 m²/ha increase in basal area) in canopy cover change at 50 *Eucalyptus tetradonta*-dominated savanna sites in

Kakadu NP over the period 1964–2004, but especially in the first 20-year period (Lehmann et al. 2009). Other recent multi-decadal aerial photograph assessments also report increases in localized savanna canopy cover (Bowman et al. 2001) and rain forest cover (Banfai and Bowman 2006, Bowman and Dingle 2006) from Litchfield and Kakadu NPs, respectively.

For tree size classes, it is well documented from northern Australian studies that stem mortality and growth increment characteristics are strongly related to fire regime characteristics, fire severity especially. At Kapalga, Williams et al. (1999) found that stem survival was highest in the unburned regime (96%), 72% in the moderately severe, early-dry-season regime, and 30% in the relatively severe, late-dry-season regime; very severe fires differentially affected both smaller (<10 cm dbh) and larger (>40 cm dbh) stems. Stem survival was higher in evergreen eucalypts than in both eucalypt and non-eucalypt deciduous species. Using the present data

TABLE 4. Change in common grass species' mean sampled frequency and mean cover per plot in 1995–2004.

Species	Frequency	Cover (%)
Annuals		
<i>Digitaria gibbosa</i>	+ (109)	– (90)
<i>Eriachne ciliata</i>	– (78)	-- (69)
<i>Mnesithea formosa</i>	++ (97)	++ (80)
<i>Sarga timorensis</i>	+ (154)	-- (152)
<i>Schizachyrium fragile</i>	– (138)	-- (122)
<i>Thaumastochloa major</i>	++ (146)	++ (137)
<i>Urochloa holosericea</i>	++ (81)	++ (70)
Perennials		
<i>Alloteropsis semialata</i>	+ (149)	– (145)
<i>Aristida holathera</i>	– (82)	– (78)
<i>Chrysopogon fallax</i>	+ (67)	+ (65)
<i>Eriachne avenacea</i>	+ (66)	– (56)
<i>Eriachne obtusa</i>	– (60)	– (56)
<i>Heteropogon contortus</i>	– (47)	++ (45)
<i>Heteropogon triticeus</i>	+ (104)	++ (100)
<i>Themeda triandra</i>	+ (59)	++ (54)
<i>Triodia bitextura</i>	– (71)	– (69)

Notes: Key to symbols: --, decline >10%; –, decline <10%; +, increase <10%; ++, increase >10%. Numbers in parentheses represent *n*, where *n* = (total no. plots in which species *x* was sampled in interval *t*₁, *t*₂) + (total no. plots in which species *x* was sampled in interval *t*₂, *t*₃).

set, similar differential effects of severe fires on mortality of smaller and larger stems are reported by Prior et al. (2009). Tree stem growth (dbh increment) has been shown, using Kapalga data, to be strongly negatively

affected by intense LDS fires while promoted by less intense (but still moderately severe) EDS fires (Prior et al. 2006), whereas, based on a slightly expanded data set to that used here, Murphy et al. (2010) found that the highest observed frequencies of mild, moderate, and severe fires (1.0, 0.8, and 0.4 fires/yr, respectively) reduced tree growth by 24%, 40%, and 66%, respectively, relative to unburned sites.

In this study, fire effects were found to be relatively weak both for tree stem density and tree species richness categories, reinforcing the observation that the ambient regime experienced in this study was substantially less severe than that experienced at Kapalga. For tree density classes, the greatest fire effect (explaining only 8% of null deviance) concerned severe fires on large-sized trees, supporting similar observations concerning effects of severe fires made in other studies (Williams et al. 1999, Prior et al. 2009). Fire frequency per se (integrating mild, moderate, and severe fires) was observed to have negative effects on all four tree species richness components, as well as densities of small tree stems and tree stems generally. Conversely, four of five eucalypt tree structure classes were more strongly influenced by time since moderate or severe fire, three positively (small eucalypt density, all eucalypt stem density, eucalypt basal area) and one negatively (large eucalypt stem density). While increasing time since fire encapsulates the notion of increased opportunity for

TABLE 5. Change in common tree species structure components, 1995–2004.

Species	Stem density (individuals/ha)				Basal area (m ² /ha)
	Small juveniles	Medium juveniles	Tall juveniles	Stems	
<i>Acacia lamprocarpa</i>	-- (45)	-- (52)	-- (32)	-- (45)	-- (45)
<i>Acacia latescens</i>	-- (28)	++ (25)	++ (19)	-- (18)	-- (18)
<i>Brachychiton megaphyllus</i>	– (63)	++ (74)	– (26)	– (16)	++ (16)
<i>Buchanania obovata</i>	– (140)	+ (154)	++ (69)	++ (86)	+ (86)
<i>Callitris intratropica</i>	-- (22)	– (14)	-- (8)	– (29)	+ (29)
<i>Cochlospermum fraseri</i>	-- (37)	-- (47)	++ (38)	– (17)	– (17)
<i>Corymbia polycarpa</i>	-- (42)	-- (41)	-- (23)	– (46)	– (46)
<i>Corymbia porrecta</i>	-- (34)	-- (37)	– (21)	+ (43)	– (43)
<i>Erythrophleum chlorostachys</i>	+ (129)	-- (144)	+ (92)	– (152)	+ (152)
<i>Eucalyptus miniata</i>	-- (72)	-- (74)	+ (31)	– (96)	+ (96)
<i>Eucalyptus tectifera</i>	-- (21)	– (23)	++ (10)	– (38)	+ (38)
<i>Eucalyptus tetradonta</i>	-- (100)	– (104)	++ (52)	– (134)	– (134)
<i>Grevillea pteridifolia</i>	– (31)	+ (32)	++ (27)	-- (36)	-- (36)
<i>Livistona humilis</i>	+ (83)	++ (86)	++ (26)	– (63)	– (63)
<i>Owenia venticosa</i>	+ (35)	– (45)	++ (16)	++ (27)	+ (27)
<i>Pandanus spiralis</i>	-- (36)	++ (55)	– (7)	-- (35)	-- (35)
<i>Persoonia falcata</i>	-- (73)	– (72)	++ (33)	-- (25)	-- (25)
<i>Planchonia careya</i>	-- (87)	– (98)	++ (30)	++ (25)	++ (25)
<i>Pouteria arnhemica</i>	-- (33)	++ (48)	++ (17)	– (21)	– (21)
<i>Terminalia ferdinandiana</i>	+ (52)	+ (80)	++ (50)	++ (57)	– (57)
<i>Xanthostemon paradoxus</i>	-- (43)	-- (36)	++ (27)	+ (31)	+ (31)
Summary					
Decline >10%, --	14	7	3	5	5
Decline <10%, –	3	6	3	10	7
Increase <10%, +	4	3	2	2	7
Increase >10%, ++	0	5	13	4	2

Notes: Key to symbols: --, decline >10%; –, decline <10%; +, increase <10%; ++, increase >10%. Stem density size classes were: small juveniles, <50 cm; medium juveniles, 50–200 cm; tall juveniles, >200 cm but <5 cm dbh; stems, ≥5 cm dbh. Numbers in parentheses represent *n*, where *n* = (total no. plots in which species *x* was sampled in interval *t*₁, *t*₂) + (total no. plots in which species *x* was sampled in interval *t*₂, *t*₃).

TABLE 6. Individual species variables with supported fire models.

Species	Variable type	Model	Δ AIC	Fire estimate	<i>n</i>	<i>P</i>	<i>R</i> ²
Grasses							
<i>Alloteroopsis semialata</i>	frequency	Fires	3.93	0.17	149	0.017	0.06
<i>Chrysopogon fallax</i>	frequency	Fires	0.81	-0.26	67	0.106	0.04
<i>Digitaria gibbosa</i> †	frequency	Severe Fires	1.02	-0.35	109	0.090	0.03
<i>Eriachne avenacea</i>	frequency	TS Mod/sev Fire	1.42	0.01	66	0.075	0.05
<i>Mnesithea formosa</i> †	frequency	Fires	5.96	-0.29	97	0.007	0.08
<i>Sarga intrans</i> †	frequency	TS Mod/sev Fire	0.08	-0.02	154	0.155	0.01
<i>Schizachyrium fragile</i> †	frequency	BA + TS Mod/sev Fire	2.83	-0.03	138	0.088	0.05
<i>Thaumastochloa major</i> †	frequency	Severe Fires	2.61	-0.51	146	0.035	0.03
Trees							
<i>Acacia lamprocarpa</i>	basal area	Severe Fires	9.05	-2.41	45	0.002	0.22
	stem density	Severe Fires	6.46	-161.6	45	0.007	0.17
	small juv density	TS Mod/sev Fire	0.18	77.5	45	0.157	0.05
<i>Acacia latescens</i>	basal area	BA + TS Mod/sev Fire	5.59	0.07	18	0.038	0.36
	stem density	BA + TS Mod/sev Fire	1.46	5.21	18	0.135	0.21
	tall juv density	Severe Fires	9.43	-1306	19	0.007	0.45
	small juv density	Fires	0.12	-134.1	28	0.178	0.07
<i>Brachychiton megaphyllus</i>	basal area	Severe Fires	4.26	0.10	16	0.040	0.32
	stem density	Severe Fires	4.87	-69.4	16	0.034	0.35
	small juv density	TS Mod/sev Fire	2.60	-41.1	63	0.041	0.07
<i>Buchanania obovata</i>	tall juv density	TS Mod/sev Fire	1.28	6.7	69	0.083	0.05
	medium juv density	Severe Fires	0.84	-335.6	154	0.097	0.02
<i>Callitris intratropica</i>	basal area	Severe Fires	5.61	-6.3	29	0.014	0.23
	stem density	Severe Fires	3.62	-171.6	29	0.032	0.18
	tall juv density	TS Mod/sev Fire	1.41	-40.9	8	0.216	0.35
	medium juv density	TS Mod/sev Fire	1.09	54.3	14	0.160	0.20
<i>Cochlospermum fraseri</i>	small juv density	Fires	0.47	-455.4	37	0.142	0.07
<i>Corymbia polycarpa</i>	small juv density	Severe Fires	11.11	-3103	42	0.001	0.27
<i>Corymbia porrecta</i>	basal area	Fires	0.05	0.32	43	0.154	0.05
	stem density	TS Mod/sev Fire	1.74	-3.4	43	0.060	0.08
	medium juv density	Severe Fires	6.27	-1022	37	0.009	0.20
<i>Erythrophleum chlorostachys</i>	basal area	TS Mod/sev Fire	0.21	0.02	152	0.143	0.01
	stem density	Fires	1.88	-12.7	152	0.049	0.03
<i>Eucalyptus miniata</i>	small juv density	TS Mod/sev Fire	1.01	76.2	72	0.094	0.04
<i>Eucalyptus tectifera</i>	basal area	Fires	1.42	0.35	38	0.082	0.09
	stem density	BA + Fires	3.47	18.3	38	0.033	0.20
	tall juv density	TS Mod/sev Fire	0.10	21.2	10	0.094	0.19
	medium juv density	Fires	4.7	-125.1	23	0.024	0.25
	small juv density	TS Mod/sev Fire	4.7	96.9	21	0.028	0.27
<i>Eucalyptus tetradonta</i>	small juv density	TS Mod/sev Fire	1.2	-66.3	100	0.083	0.03
<i>Grevillea pteridifolia</i>	basal area	Fires	4.3	-0.6	36	0.025	0.16
	stem density	Fires	3.0	-81.6	36	0.042	0.13
<i>Livistona humilis</i>	basal area	TS Mod/sev Fire	1.5	0.02	63	0.072	0.05
	medium juv density	BA + Fires	0.19	132.8	86	0.152	0.07
	small juv density	Fires	1.14	-609.3	83	0.086	0.04
<i>Owenia vernicosa</i>	basal area	Severe Fires	2.6	-1.0	27	0.037	0.16
	stem density	Fires	2.8	22.8	27	0.049	0.17
	tall juv density	TS Mod/sev Fire	0.90	10.8	16	0.156	0.07
	small juv density	Fires	3.3	370.6	35	0.035	0.14
<i>Pandanus spiralis</i>	basal area	Fires	2.3	0.5	35	0.047	0.12
	stem density	Fires	2.3	36.6	35	0.036	0.12
<i>Persoonia falcata</i>	basal area	Severe Fires	1.7	-0.3	25	0.073	0.14
	stem density	Severe Fires	2.3	-65.0	25	0.061	0.16
	tall juv density	Severe Fires	3.5	-226.6	33	0.033	0.15
	small juv density	Fires	1.9	-236.6	73	0.058	0.05
<i>Planchonia careya</i>	small juv density	Fires	0.96	-446.6	87	0.094	0.03
<i>Pouteria arnhemica</i>	basal area	BA + TS Mod/sev Fire	2.3	-0.02	21	0.087	0.36
	stem density	BA + TS Mod/sev Fire	2.7	-1.8	21	0.057	0.27
<i>Terminalia ferdinandiana</i>	stem density	Fires	0.6	-12.3	57	0.119	0.05
	medium juv density	Severe Fires	2.5	-297.2	80	0.042	0.05
	small juv density	Severe Fires	3.0	-1619	52	0.036	0.09
<i>Xanthostemon paradoxus</i>	small juv density	Severe Fires	1.0	16241	43	0.104	0.07

Notes: A dagger (†) indicates annual grass species. Δ AIC refers to the improvement in the Akaike information criterion compared to the model without the fire term. "Juv" stands for juvenile. See Table 1 for explanations of fire model terms and Table 2 for models.

growth unimpeded by fire, it also implies greater opportunity for fuel build-up and hence increased risk of resultant severe fire. The negative influence of time since moderate or severe fire on large eucalypt stem density presumably reflects an example of the latter case.

For juvenile tree and shrub densities, results from Munmarlary and Kapalga afford somewhat contrasting insights. At Munmarlary, while there was substantial release of understory (<2 m tall) individuals into the midstory (2–8 m) on unburned open-forest and woodland treatments, densities of understory individuals exhibited little change on all open-forest treatments and significant increase on woodland plots independent of treatment, over the 24-year study period (Russell-Smith et al. 2003a). There was corresponding release of only one eucalypt species (on unburned woodland plots). The release of non-eucalypts into the midstory class occurred within four years on open-forest plots and sometime after five years on woodland plots. At Kapalga, while initial densities of juveniles (<1.5 m tall) and saplings (1.5 m tall, <5 cm dbh) were very different from those at Munmarlary (e.g., being much lower and higher for respective classes at open-forest sites; see Prior et al. 2006: Fig. 10), relatively little change was observed over four years of treatments. Reductions in juveniles in both unburned and EDS treatments corresponded with increases in sapling densities (Prior et al. 2006).

In their analysis of assembled Kapalga data, Prior et al. (2006) found that: (1) EDS fires substantially reduced mean height growth of juveniles (0.01 m/yr vs. 0.06 m/yr with no fire), whereas growth was enhanced (0.1 m/yr) with LDS fires; and (2) relative to no fire where dbh increment of saplings was 0.22 cm/yr, both EDS and LDS fires resulted in reduced stem increment (0.11 cm/yr and 0.17 cm/yr, respectively). They attributed the differential seasonal effects of burning on juveniles as reflecting damage to physiologically active individuals in EDS fires, whereas juveniles are effectively dormant later in the season. Conversely, L. D. Prior, R. J. Williams and D. M. J. S. Bowman (*unpublished data*) have found that, relative to the unburned treatment, recruitment into small adults (>3 m tall) was reduced similarly under EDS (by 76%) and LDS fires (by 84%). While recruitment of eucalypt small adults was observed to occur under EDS, LDS, and especially unburned treatments, recruitment rates were shown to decline substantially with increasing stand basal area. Similar effects of basal area on stem recruitment were not so apparent in other taxonomic groupings. Based on the current data set, Prior et al. (2009) found that both EDS and especially LDS fires reduced adult stem (>5 cm dbh) recruitment in lowland plots, whereas, in sandstone plots, EDS fires resulted in slight increases and LDS fires in slight decreases. Under modeled scenarios of no burning, maximum EDS fire frequency, maximum LDS fire frequency, and the average fire regime, these authors observed that net positive recruitment vs. mortality of

eucalypt adult stems occurred only in lowland savannas in the absence of fire.

In this study, time since moderate or severe fire was included as a fire term in five of six “best” models describing juvenile tree density responses: positively in the instances of both tall juvenile tree and tall juvenile eucalypt classes and negatively in the instances of medium juvenile trees and small and medium juvenile eucalypts. Time since moderate or severe fire was included also as a fire term in four “best” or “alternative” models for shrub density and shrub species richness classes, including as a significant term in the best model for tall shrub density, explaining 24% of null deviance. In the absence of other major disturbance, we suggest that, as an artifact of the variable “time since moderate or severe fire,” ground layer competition is likely to have contributed to observed declines in density in smaller woody classes given potential for increased ground layer competition associated with (1) reduced (albeit slight) mean basal area (Bond and van Wilgen 1996, Scholes and Archer 1997), (2) above-average rainfall (Scanlon et al. 2005), (3) limited herbivory (Werner et al. 2006, Petty et al. 2007), and (4) increased fire severity associated with increased fuel load accumulation with time since fire (Murphy and Russell-Smith 2010).

Notably, while we modeled the effect of fire severity variables rather than fire seasonality variables (i.e., frequency of early and late fires) given that fire severity was more strongly correlated with most vegetation structural responses, a post hoc analysis (J. Russell-Smith, O. F. Price, and B. P. Murphy, *unpublished data*) indicates that fire seasonality variables were slightly more strongly associated with changes in juvenile tree densities, whereas fire severity variables were slightly more strongly associated with the responses of juvenile eucalypts. In contrast to Prior et al. (2006), there was no evidence for EDS fires to have disproportionate negative impacts on juvenile eucalypts.

In sum, while declines of juvenile tree densities accompanied by small levels of recruitment into the tree stem class observed in this extensive study conform broadly with similar patterns observed at Kapalga but less so under longer-term Munmarlary experimental treatments, fire effects on juvenile classes observed in the three parks data differ substantially, if not essentially, from those reported from both. At Munmarlary, juvenile densities remained stable in open-forest and increased generally in woodland treatments. Whereas recruitment into tree stem classes was observed in all studies under conditions of reduced fire frequency, at Munmarlary recruitment of eucalypt stems did not occur to any significant degree. Initial stand basal area, a factor observed to have significant impact on height growth of juveniles (Prior et al. 2006) and rates of stem recruitment (Prior et al. 2009), is unlikely to be implicated directly in the lack of response of eucalypt understory at Munmarlary given that it was initially of

the same order as mean basal area in both the present study and at Kapalga. Nonetheless, the competitive influence of the overstory is still likely to have been substantial at Munmarlary since, in contrast to those latter studies, stand basal area increased by 26% in open-forest and 55% in woodland treatments over the study period.

Our discussion here, together with recent African experience, illustrates the challenges inherent in disentangling oftentimes subtly disparate observations and findings associated with complex fire response data sets. Based on analysis of woody structural change resulting from 40 years of experimental fire treatments in semiarid Kruger National Park, South Africa, Higgins et al. (2007) found that fire frequency, seasonality of burning, and fire exclusion had no significant effects on tree stem density, but that fire treatments did have observable (if slight) effects on densities of small trees (<2 m height). While these authors curiously did not account for the likely confounding impacts of grazing, browsing, and destructive behavior (e.g., impacts of elephants) on their observations (e.g., see van Wilgen 2009), they concluded that variable results of different African fire manipulation experiments “make it difficult to generalize about the influence of fire...” (Higgins et al. 2007:1124). We would pose a more fundamental challenge: How do effects of experimental fire treatments (with and without reference to other disturbance factors) in different landscape settings relate to the complexity and generality of ambient fire regimes? Addressing this issue is intrinsic to robust accounting of structural and associated carbon dynamics in globally significant savanna systems (Grace et al. 2006, Murphy et al. 2009, 2010).

Responses of individual taxa

For grasses, the only major comparable assessment in northern Australia concerning changes in sampled frequency with respect to fire regimes is the Munmarlary study (Russell-Smith et al. 2003a). There, in the absence of burning, annuals declined generally, whereas some perennials increased and most decreased. Frequent burning promoted a small number of annual species, especially *Sarga timorensis*. Under frequent burning, *S. timorensis* is widely recognized as an increaser species (e.g., Woinarski et al. 2004, Elliott et al. 2009). In this study, *S. timorensis* frequency increased slightly, but declined in mean cover by 11% over the study period. In modeling, *S. timorensis* frequency was found to decline with time since moderate or severe fire, an observation supported elsewhere in other studies (Russell-Smith et al. 2003a, Woinarski et al. 2004, Scott et al. 2009).

Other than *S. timorensis*, changes in frequency were weakly explained by fire terms in models for seven other common species. The frequency of *Alloteropsis semialata*, a perennial, was observed to increase with fire frequency (but $P = 0.06$; Table 6), an observation supported in other studies (Crowley et al. 2009, Scott et

al. 2009). Of the annuals, three declined with fire or severe-fire frequency, including one species, *Digitaria gibbosa*, which increased on annual LDS treatments at Munmarlary (Russell-Smith et al. 2003a). Notably, however, changes in frequency for a further eight species, including one (*Urochloa holosericea*) that increased in frequency by >10%, were not explained by fire terms. At Munmarlary, very high levels of grass species turnover (both annuals, perennials) were evident for many species, despite sampling with fixed quadrats (Russell-Smith et al. 2003a).

Fire terms were included in supported models for at least one structure class of all 21 common tree species and, while mostly weak, are readily interpreted. For example, of six models describing changes in individual species' densities of tall juveniles, two describe negative effects of severe fires, one describes the same response but expressed as the negative effect of time since moderate or severe fire, while three describe the positive effects of the same variable.

Although it is well recognized that certain “eco-taxonomic” or “functional” groupings are more susceptible to intense fire regimes than others (e.g., non-eucalypt deciduous taxa, Williams et al. 1999, Prior et al. 2006; obligate seeders vs. resprouters, Bond and van Wilgen 1996), under the relatively benign ambient fire regimes of this study there appeared limited tendency for fire effects to disproportionately affect any one grouping. Thus, in the instance of models explaining relatively large amounts of variance ($R^2 > 0.2$; Table 6), four supported models with fire terms related to two fast-growing, relatively short-lived, and readily fire-susceptible *Acacia* spp., four to three hardy evergreen eucalypts, five to three deciduous (or at least semi-deciduous), shorter-statured non-eucalypts, and three to the fire-sensitive coniferous obligate seeder, *Callitris intratropica*. Similarly, and despite mostly observed declines in densities of small and medium-sized juvenile trees that occurred in 17 and 13 species (including all eucalypts), respectively, models with fire terms (predominantly negative effects of fire frequency, severe-fire frequency, time since moderate or severe fire) were supported across all eco-taxonomic groups.

Resprouting is a common feature of savanna trees, and the adaptive value of sprouting and clonality in fire-prone environments is well recognized (Bond and van Wilgen 1996, Peterson and Jones 1997). In this study also, 19 of 21 common savanna tree species are resprouters and most, including three eucalypts (*Corymbia polycarpa*, *C. porrecta*, *Eucalyptus tetrodonta*), are clonal also. Assessments undertaken as part of this study (J. Russell-Smith, O. F. Price, and B. P. Murphy, unpublished data) and scant observations reported elsewhere indicate that seedling recruitment of savanna eucalypts is sporadic and occurs typically at low densities (e.g., approximately one individual per hectare: Russell-Smith and Setterfield 2006). By contrast, annual germination in natural stands of *Callitris* may be substantial,

but highly variable (Stocker 1966, Russell-Smith 2006). *Callitris intratropica* is an important indicator of savanna health, especially with respect to severe fire regimes (Bowman and Panton 1993, Price and Bowman 1994), and it is salutary to note that not only did juvenile densities in all three height classes decline over the decadal study period, but that medium- and tall-sized juveniles were unrecorded at more than half the plots containing adult stems (Table 5). The other obligate seeder, the fast-growing and relatively short-lived *Grevillea pteridifolia*, suffered substantial declines in adult stems but was observed also to recruit substantially into the tall juvenile class (Table 5). In general, however, responses of small and medium-sized juveniles were only weakly explained by supported models with fire terms, echoing similar observations made earlier for woody juveniles in general.

Fire management and the savanna matrix

Fire regimes are recognized as significant modifying drivers of savanna dynamics in a large number of northern Australian experimental and derived modeling studies (Lonsdale and Braithwaite 1991, Williams et al. 1999, Russell-Smith et al. 2003a, Cook et al. 2005, Werner 2005, Prior et al. 2006, 2009, Werner et al. 2006, Liedloff and Cook 2007, Murphy et al. 2009, 2010). Collectively these studies illustrate that, over time and at landscape scales, mesic savannas exhibit significant inter-patch heterogeneity in response to preexisting habitat conditions (e.g., lowland, sandstone, site productivity) and stand structure and species composition, localized rainfall and associated water balance phenomena, and the nature and magnitude of disturbance regimes. The savanna matrix encompasses both extensive characteristic savanna formations, as well as typically more fire-vulnerable and smaller embedded habitat types associated with landscape features such as rocky terrain or freshwater spring and riparian features (Woinarski et al. 2005, Yates et al. 2008).

Over the past few decades concerted efforts have been made by managers of the three Top End reserves considered here to attempt to impose more benign, if variable, fire regimes than those experienced following regional collapse of Aboriginal fire management regimes from the end of the 19th century (Braithwaite 1991, Preece 2002, Ritchie 2009). Specifically, respective park programs have aimed to address a recent history of extensive LDS wildfires and their impacts especially on fire-sensitive vegetation types (rain forest patches, *Callitris* groves, sandstone heaths) through the implementation of more strategic, EDS-focused management. This is in accord with regional observations that EDS fires are substantially less severe and more patchy than LDS fires (Price et al. 2003, Williams et al. 2003a, Russell-Smith and Edwards 2006).

That program has been substantially more effective in Kakadu NP than in the other two parks (Russell-Smith et al. 2009), attributable largely to disparate levels of

resourcing and thereby management effectiveness and significant arson impacts in Litchfield NP. Over the same decadal observation period as that considered here there has been: (1) a 4% net reduction in the extent of burning in Kakadu NP compared with the period 1980–1994, particularly (by 8%) in the LDS period (Russell-Smith et al. 1997b), and associated increase in fire patchiness or heterogeneity (Price et al. 2005); (2) a 10% net increase in the extent of burning since the late 1990s, particularly in the EDS period, in both Litchfield and Nitmiluk NPs (Edwards et al. 2001). Notably, this improvement in fire management in Kakadu occurred in the face of increasing fuel loads following very substantial removal of buffalo in the previous decade. The especially high annual frequency of burning in Litchfield NP over the study period (66% vs. 51% Nitmiluk, 42% Kakadu; Russell-Smith et al. 2009) was found here to incur significant negative changes in many vegetation structure variables relative to the other parks.

It is useful to consider the ecological implications of such changes, especially when mounting evidence implicates fire frequency per se and resultant vegetation structural changes as being complicit in the imminent and apparently accelerating demise of significant components of northern Australian fauna, small mammals, and other relatively immobile species especially (Woinarski et al. 2001, 2005, 2007, Andersen et al. 2005). For illustrative purposes, here we have considered possible changes with reference to three realistic management-imposed scenarios based on statistical models derived from a decade of observations using initial mean values for respective structural components. We are mindful (1) that supported fire terms only weakly explained observed changes in structural variables and (2) that such responses probably better reflect diverse if muted responses to ambient fire regimes than invariant experimental treatments.

The first scenario represents a business-as-usual fire management regime, taking into account a likely increase in regional fire severity in line with projected increases in temperature, but especially increases in number of severe fire weather days, under projected climate changes over future decades (CSIRO and Bureau of Meteorology 2007). Relative to changes observed over the decadal study period, most structural measures decline, with slight increases in some juvenile classes. With a modest reduction in fire frequency and severity under the second scenario, most structural classes increase, including species richness of fruiting trees, with declines predicted for smaller juvenile classes and large eucalypt stem densities. Under the third scenario, fire frequency is markedly reduced but severe-fire frequency is increased in accord with observations that fire severity associated with fuel accumulation in regional savannas increases substantially with time since fire and for at least eight years in the instance of LDS fires (Williams et al. 1999, Murphy and Russell-Smith 2010). This scenario aligns also with indications

that unburned intervals of at least several years are required for recruitment of tree stems, taller shrubs, and associated development of habitat (including logs, older hollow trees) and species structural diversity for a variety of fauna ranging from ants to midstory-dependent birds and small terrestrial and arboreal mammals (Woinarski 1990, Andersen 1991, Andersen et al. 2003, 2005, Russell-Smith et al. 2003b, Woinarski et al. 2005). A majority of structural components are predicted to decrease under this regime, but notably small trees and fruit tree species richness are predicted to increase substantially.

In sum, these scenarios illustrate simply that changes associated with fire frequency and intensity (and related indices) have both positive and negative implications for different structural components in short- and longer-term time frames. Where resources permit, reducing fire frequency to meet a range of biodiversity conservation and emissions abatement goals can be achieved through the implementation of more strategically focused fire management designs and accessing contemporary information and aerial ignition technologies; but increasing fuel loads also incur substantial risk of more severe fires. Given the relative health of regional savanna landscapes prior to European colonization, including extensive stands of fire-sensitive *Callitris* and an abundant small mammal fauna (Russell-Smith et al. 2003b, Woinarski et al. 2007), it is somewhat paradoxical that seasonally labor-intensive and extensive modes of customary fire management as undertaken by Aboriginal managers (Haynes 1985, Russell-Smith et al. 1997a, Yibarbuk et al. 2001, Garde et al. 2009) still provide the benchmark for conservation-effective management of the matrix.

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