FIRE AND TREES IN THE SAVANNAS OF THE WORLD HERITAGE KAKADU NATIONAL PARK, NORTHERN AUSTRALIA

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ABSTRACT

Annual, dry season fires are largely unavoidable in the tropical savannas of northern Australia. However, the nature and biological impacts of such fires are poorly understood. Land managers, especially those managing conservation areas, need to optimize the use of fire, to ensure that their long-term goals are met, while minimizing excessive risks. As part of a landscape-scale experiment designed to address such issues, we examined the behavior of a variety of prescribed dry season fires, and the effects of these fires, on the tree stratum in a tropical savanna in Kakadu National Park, northern Australia. The fire regimes were annual early dry season (June) fires, annual late dry season (September) fires, and control, or no fires. Prescriptive fires were lit annually, between 1990 and 1994, in replicate compartments, each 15–20 square kilometers. One of the control compartments was burned by a high-intensity wildfire in September 1994. Although accidental, the wildfire provided a rare opportunity to compare the behavior and impacts of prescribed burning and wildfire. Average fuel loads on the annually burned plots ranged from 2–4 tonnes per hectare; on the control plots, fuels reached approximately 8 tonnes per hectare within 2–3 years of the cessation of burning. Average Byram-intensities were 2100 and 7700 kilowatts per meter, respectively, for the early dry season fires and late dry season fires. Late dry fires were consistently of higher intensity than early dry fires because of increases in fuel, reductions in fuel moisture, and more severe fire weather with the progression of the dry season. Whole tree mortality (i.e., death of stem and no basal resprouting) was highest in the late-dry and wildfire regimes (approximately 17%). Stem mortality (i.e., death of stem, but basal resprouting) was substantially higher than whole-plant mortality, and was proportional to stem size and fire intensity. Significantly, stem death following the single, high-intensity fire in the control compartment (75%) was similar to that of five years of annual late dry season burning. Stem survival was also species-dependent, being higher in the dominant species of *Eucalyptus* than in the subdominant, broad-leaved deciduous trees. In the absence of fire for 5–10 years, the structure and composition of the tree stratum of these savannas becomes more complex than in sites burned more frequently, especially by high-intensity fire. Such a long-term absence of fire may be a conservation objective for some areas of savanna. However, the accumulation of fuel during a 5–10 year period of fire absence, or even a 2–3 year absence, may predispose the savannas to high-intensity, late dry season fires. If the structural and compositional features of a fire-excluded savanna are desirable management goals, then careful attention should be given to periodic, prescribed fuel-reduction burns very early in the dry season when fire intensity can be minimized.

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INTRODUCTION

Extensive, frequent fires are a feature of the landscape of northern Australia (Graetz et al. 1992). Here, rainfall is highly seasonal, with >90% falling in the six-month October-March summer period. The wet season occurs predictably each year (Taylor and Tulloch 1985), ensuring a consistent, annual production of fine fuels. The dry season (May-September) is also consistent, ensuring that fuels cure each year. The dominant vegetation type of the region is tropical savanna woodland (discontinuous trees over continuous grass; Gillison 1994), and the savannas of the northern half of the Northern Territory (NT) are typically burned annually or biennially (Braithwaite and Estbergs 1985, Press 1988, Russell-Smith 1995).

The vast majority of these fires occur during the dry season, and are lit by humans. This begs the question—what is the "natural" fire regime? The pre-aboriginal regimes (approximately 100,000 years BP) were probably concentrated in the very late dry season or early wet season, when there was both dry fuel, and an ignition source (i.e., lightning). Aboriginal people, which have been in the region for at least 50,000 years, burned throughout the dry season, commencing as early as the late wet season (March/April), with a peak of activity in the early-mid dry season, ceasing in the early-mid wet season with the onset of the heavy rains (Braithwaite 1991). In more recent times (especially over the past 50 years), there appears to have been an increase in the incidence of intense, late dry season fires (Russell-Smith 1995). Such late dry season fires may be deliberately lit, may be flare-ups of fires which began earlier in the dry season, or may be due to lightning strikes. Whatever their origin, they are of concern to all land management agencies, because of their potential effects on flora and fauna, and on life and property.

Although savannas are relatively resistant to the effects of annual fires (Stocker and Mott 1981), the frequent occurrence of high-intensity fires in the savannas of the humid, sub-coastal Northern Territory may be leading to a gradual attrition of non-savanna ecosystems such as monsoon vine forest (Russell-

Smith 1995), a loss of tree cover (Bowman et al. 1988a), and excessive loss of nitrogen (Cook 1994). There is also some concern about the release of photochemically active trace gases from the fires and the possible net release of CO_2 if the trees are killed (Cook et al. 1995).

Fire exclusion, or the prescribed use of less frequent fires could address many of these concerns. However, if fire is excluded, the increase in fuel loads over time in savannas which remain unburned for several years (Gill et al. 1990) may increase the risk of destructive fires—whether from wildfires or prescribed burns—causing substantial attrition of trees. Clearly a balance needs to be struck between the possible or perceived deleterious effects of a frequent fire regime and the risks of very intense fires if a low-frequency regime is pursued.

This paper addresses the issue of prescribed burning and wildfire in a savanna within the World Heritage Kakadu National Park in the Northern Territory (NT). We describe the behavior of a number of prescribed, experimental fires, of varying intensity, including one non-prescribed wildfire which severely burned an experimental plot, that had been fire-free for approximately 7 years. We assess the impact of these prescribed fires, and the unplanned wildfire, on the tree component of the savanna, and discuss the implications for attempts to exclude fire or reduce the frequency of prescribed fires in savannas.

STUDY AREA

The study was conducted at Kapalga Research Station (132°22′E 12°34′S), 180 kilometers east of Darwin. Annual rainfall is approximately 1400 millimeters. Open eucalypt savannas predominate on the well-drained lateritic soils of the drainage divides. Floodplain areas are occupied by treeless grasslands, and there are several pockets of monsoon vine forest. Kapalga Research Station is subdivided into approximately 20 management compartments, which represent the catchments of minor, ephemeral streams which drain into the surrounding major river systems—the West Alligator and the South Alligator Rivers. Each compartment is 15–20 square kilometers in area. The vegetation of the creek margins is woodland, dominated by *Eucalyptus alba* and *E. papuana*; the understory is mostly perennial grasses. The vegetation of the better-drained soils is open forest of *E. miniata* and *E. tetrodonta,* with the understory dominated by a mixture of annual grasses such as *Sorghum intrans* and perennial grasses such as *Heteropogon triticeus* (Wilson et al. 1990).

METHODS

Fire Treatments

For the purposes of this component of the fire experiment, 9 of the 20 management compartments were used. Each compartment was subject to one of three fire regimes; for each regime, there were initially three replicate compartments. These regimes represent a range of management options for the savannas of the Top End of the NT. The regimes were:

1. "Early dry season"; burned annually, once during the early part of the dry season (early June).
2. "Late dry season"; burned annually, once during the late dry season (late September).
3. "Unburned" or control; fire was excluded from each of these compartments.

In September 1994 one of the unburned compartments was burned extensively by an accidental wildfire of high intensity (see below).

All prescribed fires were lit around midday, from vehicle-based ground crews, and controlled by a series of double fuel breaks between compartments, combined with back burning along the leeward sides of the compartments. The burning regimes were applied annually between 1990 and 1994.

Fuels and Fires

Byram fire-line intensity (heat content of fuel × fuel load × rate of forward spread; Byram 1959) was determined within a single, relatively uniform area of approximately one hectare for all but one of the prescribed experimental early and late dry season fires lit between 1990 and 1994. Fire intensity was determined for the forward burns (heading fires) only. The mineral-free heat of combustion of the fuel was assumed to be 20,000 kilo joules per kilogram, which represents the ash-free components of the fuel (Gill and Knight 1991). Fuel weight (kilograms per square meter) was determined directly by 5 0.5 × 0.5 meter quadrats within each sample site. Fuel weight was measured just prior to each fire each year. Rate of forward spread (meters per second) was determined using a series of electronic fire residence time meters arranged in triangles, with sides 10–50 meters, over a representative half hectare area, as described by Simard et al. (1984) and Moore et al. (1995).

The wildfire which burned one of the control, unburned compartments was an extensive fire which commenced on floodplains more than 20 kilometers away. The compartment which was burned, like the other compartments in the experiment, had been subjected to fires annually or biennially until 1986. In 1987, the compartment, along with the other unburned compartments, was prescribe-burned early in the dry season. It remained unburned until mid-September 1994, when the wildfire entered the compartment, and burned it completely. Fire intensity could not be determined for this fire, but was estimated from empirical relationships between char height (a surrogate for flame height) and fire intensity (Williams et al., unpublished data).

Tree Survival

As part of an ongoing study on the effects of fire on forest structure, composition and demography, every tree with diameter at breast height (dbh) greater than 2 centimeters on each of three or four one-tenth hectare plots within each compartment had been tagged in 1990, prior to any fires. Each plot contained approximately 50–100 trees, and some 2100 trees were sampled in total. Tree size was resurveyed in May 1995, after the completion of the fire treatments. For each tree, whole-plant survival and stem survival were determined. Whole-plants were deemed to have survived if there was evidence of branch, epicormic or basal resprouting from a tagged stem; stems were deemed to have survived only if there was evidence of resprouting in the canopy or from the trunk of the stem; individuals were scored as dead if there was no resprouting at all. Trees were identified to species level, and were grouped into one of the following five functional types: evergreen eucalyptus, deciduous eucalypts, evergreen (non-eucalypt) trees, deciduous (non-eucalypt) trees, and palms.

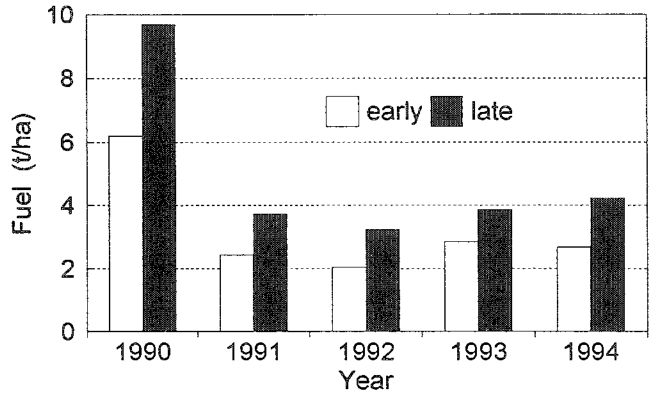

Fig. 1. Mean fuel loads (tonnes per hectare) for the period 1990–94 on early dry season compartments (early) and late dry season compartments (late) at Kapalga Research Station, Kakadu National Park, northern Australia. For each mean, n=3, except for the late compartments, 1990, when n=2.

Statistical Analyses

The variation in fuel load, fuel moisture and fire intensity with respect to fire regime (early or late dry season) and year (1990–1994) was tested using a split-plot design. Block (compartment) was the random factor, and year was the split factor. For these analyses, N = 3 for each year, except for 1990, when there was one missing value (in that year one of the late dry season compartments was accidentally burned during the early dry season; hence N = 2). In this design, the effect of fire (1 degree of freedom) was tested against the residual compartment-within-fire term (4 degrees of freedom). Year (4 degrees of freedom) was tested against the residual term (16 degrees of freedom).

The effect of the fires on trees was assessed in terms of changes in live basal area, and tree survival (either whole-plant or stem), over the period 1990–1995. Percentage reduction in basal area in relation to fire regime (early, late, unburned and unplanned fire) was not assessed formally, because the unplanned wildfire regime had only one replicate. However, the mean percentage reduction in live basal area was calculated from the individual plots-within-compartments. We used the standard error of this mean based on individual tenth hectare plots (i.e., within compartments) as our measure of variation for informal comparative purposes.

Tree survival, at the individual tree level, was analyzed in relation to fire regime, stem size, and functional type by Generalized Linear Models (GLMs). For each analysis, the data from the individual 0.1 hectare plots were pooled for each compartment. Survival was treated as binary data (the tree or stem either survived or died; Collett 1991), with a logit link function used for each model. In each GLM, fire regime and stem size (as defined by prefire diameter at breast height) were fitted first (with stem size a covariate). Plant functional type or plant species was fitted subsequently (as a factor), followed by the interaction terms. Analysis was restricted to those species or functional groups with 10 or more individuals.

The output of such GLMs is the deviance (analogous to a sum of squares), and the test statistic is chi-square. The significance of the deviance is determined by comparing with chi-square, at the appropriate degree of freedom for each term—e.g., one for tree size, three for fire regime, and four for functional type. If the deviance is greater than the critical chi-square, the term is significant (Agresti 1996).

Significant terms and interactions were included in the final models; non-significant terms were collapsed into the residual term. The final models were then used to predict the probabilities of survival across fire regime for each of the plant functional types. For the trees subject to the high-intensity unplanned fire, variation in stem survival according to stem size was modelled by fitting both the linear (i.e., first order) and quadratic (i.e., second order) components of stem size, each with one degree of freedom. Where reported, significant treatment effects are at $P < 0.05$. Similar approaches to the analysis of mortality/survival of trees following disturbance in northern Australia have been used by Williams and Douglas (1995) and Fordyce et al. (1997). All analyses were performed using GENSTAT 5.

RESULTS

Fuels and Fires

There was substantial variation in the fuel load during the course of the experiment, both between fire regimes and between years (Figure 1). Average fuel loads varied from approximately 2 tonnes per hectare to a little under 10 tonnes per hectare. Fuel loads were significantly higher ($P < 0.05$) in the initial year of burning (1990) than in later years (1991–94), wherein there was no significant difference between years. Average fuel loads on the early burn compartments (3.24 tonnes per hectare) were significantly lower ($P < 0.05$) than those of the late-dry season compartments (4.99 tonnes per hectare). Fuels were primarily grass, although the proportion of leaf litter in the fuel was significantly higher in the late burn regime (47%) than the early burn regime (19%; Williams et al. 1995).

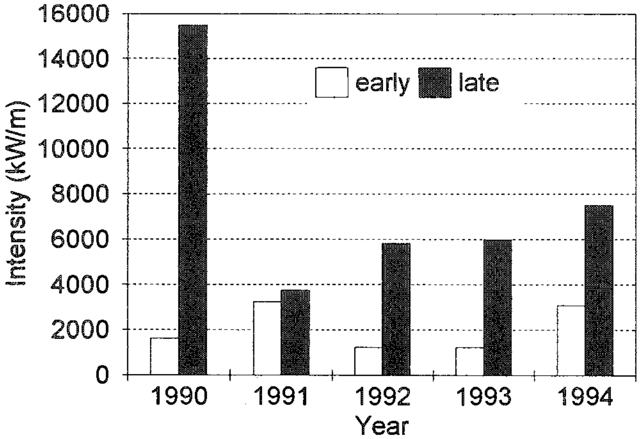

Fig. 2. Mean fire intensity (kilowatts per meter) for the period 1990–94 on early dry season compartments (early) and late dry season compartments (late) at Kapalga Research Station, Kakadu National Park, northern Australia. For each mean, N=3, except for the late compartments, 1990, when N=2.

Fuel moisture content was significantly lower on the late burn compartments (11%) than on the early burn compartments (19%; Williams et al. 1995). On the unburned compartments, fuel loads were between 6 and 8 tonnes per hectare (Cook et al. 1995). At the time of the wildfire, the fuel load on the compartment burned by the wildfire was approximately 8 tonnes per hectare.

Fire Intensity

The seasonal and inter-annual patterns of average fire intensity for the early and late dry season fires for the years 1990–1994 are given in Figure 2. Intensities ranged from 500 kilowatts per meter to 18,000 kilowatts per meter, the latter recorded on one of the late fire compartments in September 1990. The fires of 1990 were more intense than all other years ($P < 0.05$), although there was no significant difference between years over the period 1991–1994. The mean intensity of early, dry season fires over the whole study period (2100 kilowatts per meter) was significantly lower, by a factor of nearly four, than that of the late dry season fires (7700 kilowatts per meter; $F_{1,4} = 236$; standard error of difference between means = 290 kilowatts per meter; $P < 0.05$). There was, however, annual variation in this pattern. In 1991 there was no significant difference in the average intensity of the early and late fires; in all other years late dry season fires were significantly more intense than were the early dry season fires.

Following the wildfire in the unburned compartment, ground scorch was complete, and tree canopies were scorched to the very tops of the tallest trees (22 meters). Leaf char height (a surrogate for flame height; Moore et al. 1995) was 3–5 meters across the plot, peaking at 10 meters in some areas. Fire intensity in the region of our monitoring plots was estimated to be approximately 20,000 kilowatts per meter, on the basis of leaf char height.

Table 1. Change in live tree basal area (square meters per hectare) between 1990 and 1995 in four fire regimes, and average percentage reduction in basal area (% change; ± SE) at Kapalga Research Station, Kakadu National Park. Fire regimes: Unburned, no fire, 1990–1995. Early; annual early dry season fires, 1990–1994. Late; annual late dry season fire, 1990–1994. Wildlife; single high intensity wildfire, September 1994 after 6 years of no fire; intensity approximately 20,000 kilowatts per meter. Number of compartments and sample 0.1 ha plots indicated. Standard errors in % Change columns calculated from N Plots.

Regime	1990	1995	% Change	Compartment number, number of plots
Unburned	9.87	9.86	−0.01 ± 7.4	2, 6
Early	8.78	8.75	−0.4 ± 0.6	3, 9
Late	11.09	9.97	−27.9 ± 4.5	3, 9
Wildfire	11.41	6.62	−41.9 ± 7.4	1, 4

Fire Impact on Trees

Variation between Fire Regimes

The impact of fire on total live-stem basal area varied substantially with fire regime (Table 1). Over the 1990–1995 period, basal area was reduced least in the unburned and early regimes, and most in the late dry season regime and the wildfire. Basal area was reduced by 42% following the 1994 wildfire, and the majority of this reduction was due to substantial stem mortality (>75%) in the largest trees (Figure 3).

Tree survival depended on fire regime, tree size, and tree functional type. The modelled survival of trees greater than 2 centimeters dbh from 1990–1995 for the three experimental regimes—unburned, early dry season and late dry season, and the high-intensity wildfire are given in Table 2; the significance of the main effects is summarized in Table 3. Whole-plant survival over the five year period was 80% or more, and was highest in the unburned plots, at approximately 98%; stem survival was 96%. In the early dry season regime, survival of whole plants and stems was, respectively, 90% and 85%. In comparison, stem

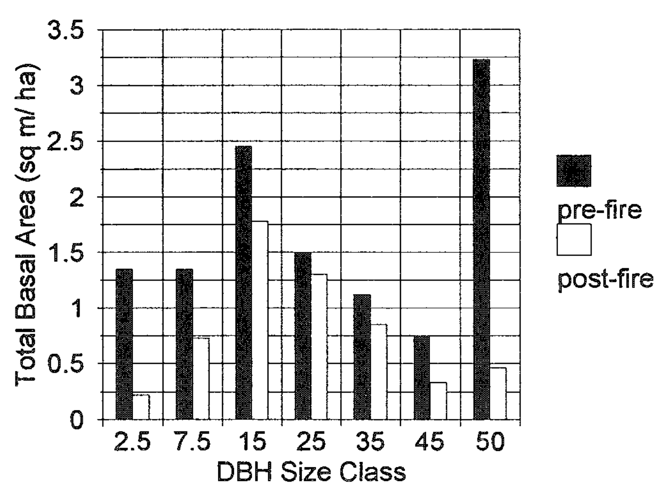

Fig. 3. Changes in tree basal area by tree size class, pre-and post-wildfire, Kapalga Research Station, northern Australia.

Table 2. Overall stem- and whole plant survival, 1990–1994, by fire regime, Kapalga Research Station, Kakadu National Park, northern Australia. Fire regimes: Unburned (No fire 1990–1995; 2 replicates); Early dry season (Annual early dry season fire, 1990–1994; Average intensity 2100 kilowatts per meter); Late dry season (Annual late dry season fire, 1990–1994; average intensity 7700 kilowatts per meter); Wildfire (September 1994; Intensity approximately 20,000 kilowatts per meter).

Fire regime	Stem survival	Plant survival	Number of individuals
Unburned	96.2	98.0	495
Early Dry Season	85.4	90.1	274
Late Dry Season	37.5	85.4	590
Wildfire	26.0	86.0	815

survival in both the late dry season fire regime and following the wildfire were substantially lower than in the unburned and early dry season regimes. Only 37% of stems survived five years of late dry season burning; stem survival was significantly lower (26%) following the wildfire. Survival in the dominant, evergreen and deciduous eucalypts was significantly higher than other deciduous trees, acacias and palms (Table 4). Survival of the stems of non-eucalypt deciduous trees was particularly low (16–20%) in the late and wildfire regimes.

Impact of Wildfire

Of the 31 tree species sampled pre- and post-fire, *Eucalyptus miniata, E. tetrodonta, Erythrophleum chlorostachys,* and *Terminalia ferdinandiana* were the most common, accounting for 68% of individual stems and 84% of the total basal area before the fire. Evergreen eucalypts, deciduous eucalypts, and other deciduous trees accounted for 94% of all individual stems.

There was substantial inter-specific variation in post-fire whole-plant and stem survival. *Wrightia saligna, Pogonolobus reticulatus,* and *Acacia* spp. did not survive the fire, but were represented by very few individuals (Table 5). *Alphitonia excelsa, Croton arnhemicus* and *Livistona spp.,* were also severely affected with the latter two species having less than 40% whole-plant survival. In contrast to the generally high level of plant survival, stem survival was low in most species; only 26% of stems survived the wildfire.

Modelled stem survival was significantly affected by both the linear and quadratic components of stem dbh. Survival increased sharply with tree size over the range of 2–20 centimeters dbh, but fell sharply in trees with dbh > 40 centimeters. There was significant inter-functional type and inter-specific variation in survival probabilities (Figure 4). Stem survival was greatest in the eucalypts, with no significant difference in survival probability between evergreen and deciduous eucalypts. Survival probability for deciduous non-eucalypt trees and palms was significantly lower, across all size classes (Figure 4a). Species-based analyses of stem survival showed that there was significant intra-functional group variation in survival probabilities. Of the evergreen eucalypts, survival in *E. miniata* was significantly higher than in *E. tetrodonta.* Within the deciduous eucalypts, stems of *E. polysciada* (formerly *E.clavigera*) were more likely to survive than those of *E. porrecta* (Figure 4b). *Terminalia ferdinandiana* and *Erythrophleum chlorostachys* were the two least fire-resistant species of the dominant trees (Figure 4c).

Table 3. Summary of degrees of freedom (df), deviance (Dev) and significance (P) of tree diameter (dbh), fire regime and tree functional type terms of a generalized linear model fitted to stem and whole plant survival under various fire regimes. Fire regimes: unburned control, annual early dry season fire, annual late dry season fire and wildfire. Tree functional type: evergreen eucalypts, deciduous eucalypts, deciduous non-eucalypts, acacias, palms. NS, non significant (P > 0.05).

		Stem survival		Whole-plant survival	
Term	df	Dev	P	Dev	P
Tree dbh	1	330	<0.001	1	NS
Fire Regime	3	787	<0.001	84	<0.001
Functional Type	4	78	<0.001	33	<0.001
dbh-Type	4	6	NS	12	<0.05
Fire-Type	12	19	NS	36	<0.001
Residual	2145	1782		1280	

DISCUSSION

Seasonal and Annual Patterns of Fuels and Fires

The inter-annual and inter-seasonal variation in fuel loads at Kapalga was primarily a consequence of local fire history, tree phenology, and fire weather. Fuel loads were highest in 1990 (approximately 10 tonnes per hectare) because most compartments had remained unburned for 2 years prior to the initial fires. Fuel loads of this order have been reported for eucalypt savanna in parts of humid northern Australia which have remained unburned for at least 4 years (e.g., 10–15 tonnes per hectare, Gill et al. 1990; 5–10 tonnes per hectare; Mott and Andrew 1985). At Kapalga, subsequent to 1990, however, on the annually burned compartments, fuel loads were most commonly between 2 and 5 tonnes per hectare, clearly indicating that annual burning maintained relatively low fuel loads. Moreover, our data indicate that, in the absence of fire, fuel loads can double from approximately 5 tonnes per hectare to 10 tonnes per hectare in 2–3 years.

In the prescribed fires, the higher fuel loads in the late dry season compared with the early dry season

Table 4. Modelled survival of stems (± SE) by fire regime and plant functional type (pooling tree size). Data are fitted values, based on Generalized Linear Models fitted to survival data.

	Tree functional type				
Fire regime	Evergreen eucalypts	Deciduous eucalypts	Deciduous trees	Acacias	Palms
Unburned	98 ± 1	93 ± 3	96 ± 1	99 ± 1	98 ± 13
Early	87 ± 3	79 ± 7	77 ± 5	99 ± 1	85 ± 9
Late	42 ± 3	39 ± 5	16 ± 4	29 ± 17	99 ± 1
Wildfire	47 ± 3	45 ± 7	20 ± 2	0	29 ± 13

Table 5. Summary abundance and survival data for 31 species of tree and tall shrub subject to high-intensity wildfire, Kapalga Research Station, northern Australia. Columns are: Species; Functional group (evergreen eucalypt, evgreuc; other evergreen tree, evgrtree; deciduous eucalypt, deceuc; deciduous tree, dectree; palm; acacia); Number of individuals (No. Indiv.); Whole plant survival (plant Surv.); Stem survival (Stem surv.); % Plant survival (% Plant Surv.); % Stem survival (% Stem Surv.). Nomenclature follows Dunlop et al. (1990) and Brooker and Kleinig (1994).

Species	Functional group	No. Indiv.	Plant Surv.	Stem Surv.	% Plant Surv.	% Stem Surv.
Terminalia ferdinandiana	dectree	213	194	24	91	11
Eucalyptus miniata	evgreuc	211	175	100	83	47
Erythrophleum chlorostachys	dectree	98	86	10	88	10
Eucalyptus polysciada	deceuc	43	37	15	86	35
Terminalia latipes	dectree	40	37	15	93	38
Eucalyptus tetrodonta	evgreuc	35	34	13	97	37
Alphitonia excelsa	evgrtree	20	15	0	75	0
Ficus spp	dectree	17	17	6	100	35
Planchonia careya	dectree	16	16	2	100	13
Eucalyptus porrecta	deceuc	15	15	6	100	13
Croton arnhemicus	dectree	14	7	2	50	14
Buchanania obovata	dectree	13	11	1	85	8
Syzigium spp	dectree	12	12	1	100	8
Livistona spp	palm	11	4	3	36	27
Brachychiton spp	dectree	8	7	4	88	50
Denhamia obscura	evgrtree	6	4	1	67	17
Gardenia megaphylla	dectree	5	4	1	80	20
Terminalia carpentariae	dectree	5	5	2	100	40
Flueggea virosa	dectree	5	4	0	80	0
Planconella pohlmaniana	dectree	4	2	1	50	25
Cochlospermum fraseri	dectree	4	3	0	75	0
Acacia spp	acacia	4	0	0	0	0
Briedelia tomentosa	dectree	4	4	0	100	0
Persoonia falcata	evgrtree	3	3	0	100	0
Clerodendrum floribundum	dectree	2	2	2	100	100
Breynia cernua	dectree	2	2	0	100	0
Wrightia saligna	evgrtree	1	0	0	0	0
Vitex glabrata	dectree	1	1	0	100	0
Stenocarpus cunninghamii	evgrtree	1	1	0	100	0
Pogonolobus reticulatus	dectree	1	0	0	0	0
Terminalia grandiflora	dectree	1	1	0	100	

were primarily a consequence of the leaf phenology of the trees within the tropical savanna. Leaf fall in semi-deciduous and evergreen species peaks in the latter part of the dry season (Wilson et al. 1996, Williams et al. 1997). Hence, by late in the dry season fuels were more abundant, with a greater proportion of leaf litter, than early in the dry season. By the late dry season, fuels are also substantially drier, as a consequence of senescence of annual grasses, decreases in soil moisture, and decreases in relative humidity as the dry season progresses (Gill et al. 1990, Cheney et al. 1993, Gill et al. 1996).

This variation in fuel load, composition and moisture is reflected in the significant inter-seasonal variation in fire intensity. In addition, the observed pattern is consistent with the seasonal patterns of both Forest- and Grassland Fire Danger Indices as determined by Gill et al. (1996). This is due to seasonal changes in a number of meteorological factors. Afternoon relative humidity decreases progressively throughout the dry season, thus increasing the potential rates of spread (Gill et al. 1990, Gill and Knight 1991, Cheney et al. 1993). Moreover, winds, especially afternoon and evening winds, are stronger in September than June (Gill et al. 1996).

The intensity of the Kapalga fires is low compared with the potential intensities of wildfires in eucalypt forests in southeastern Australia (Gill and Knight 1991, Williams et al. 1995). The wildfire which burned the unburned compartment (approximately 20,000 kilowatts per meter) was the most intense of the fires monitored in 5 years at Kapalga; only one of the 30 experimental fires was of a similar intensity (18,000 kilowatts per meter on one of the late burn compartments in September 1990). Such fires are very intense by northern Australian standards.

Fires, Fire Regimes, and Trees

Despite considerable differences in fire intensity between regimes, there was relatively little difference between regimes in whole-plant survival (85–90%). This indicates a high degree of fire resistance at the level of individual plant. The capacity for vegetative regeneration postfire is well-developed in virtually all woody species in Australian savannas (Lacey 1974).

At the level of individual stems however, fire regime had dramatic effects at Kapalga. There was little difference between the early-dry season fire regime and the unburned regime. Stem survival in both was approximately 90%, and the changes in live basal area over 5 years were also relatively small (approximately 10%). This was in stark contrast to the impacts of the annual late dry season regime, and the single, unplan-

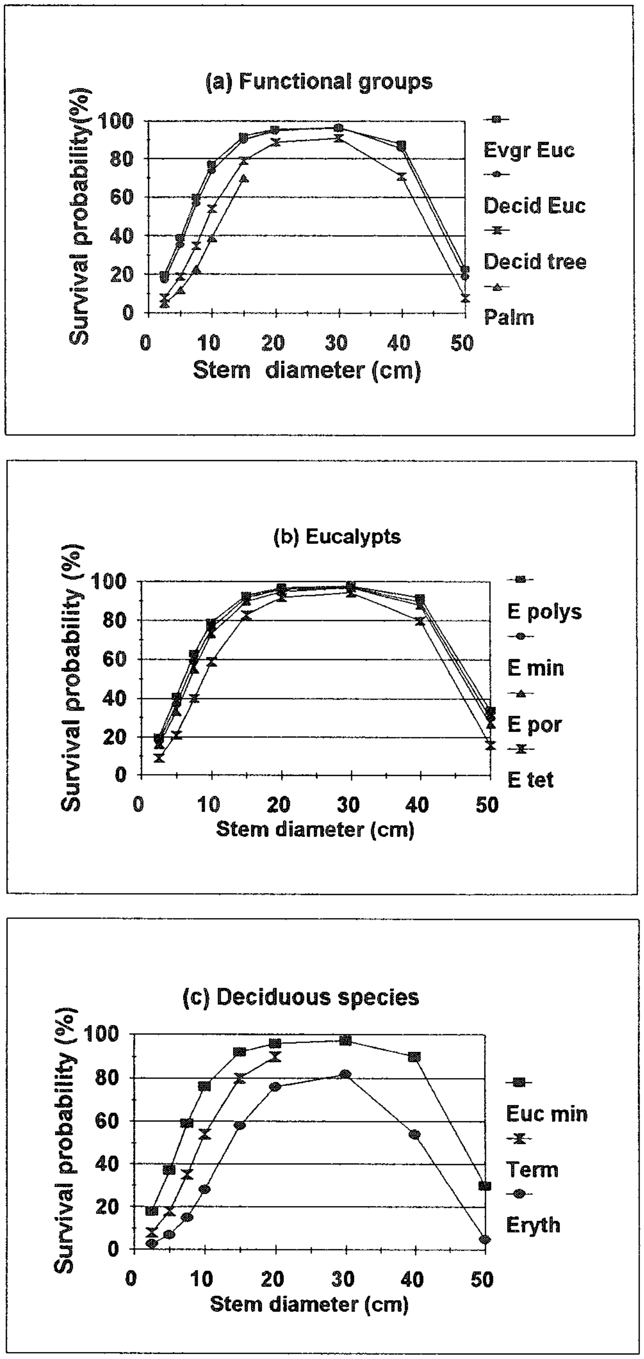

Fig. 4. Predicted stem survival (from GLMs) by tree functional type and species following wildfire, Kapalga Research Station, northern Australia. (a) Functional Types: Eucalypts (evergreen, Evgr Euc and deciduous, Decid Euc); deciduous non-eucalypt trees, Decid tree, and palms; (b) *Eucalyptus* Species: *Eucalyptus polysciada* (E polys; deciduous); *E. miniata* (E min, evergreen); *E. porrecta* (E por, deciduous); *E. tetrodonta* (E tet, evergreen); (c) Common deciduous tree species: *Terminalia ferdinandiana* (Term) ; *Erythrophleum chlorostachys* (Eryth), with the evergreen species *Eucalyptus miniata* (Euc min) included for comparison.

ned high-intensity wildfire, where stem survival was only approximately 30%, and, in the case of the wildfire, basal area reduced by approximately 40%.

The impact of the wildfire on forest structure and composition was substantial—live basal area was reduced by 40%, and, while whole-plant survival was relatively high (86%) only 26% of stems survived the fire; the stems of most of the larger trees were killed. These data show clearly that single, intense wildfires can substantially alter the structure and, due to differential species susceptibility, the composition of the tree stratum.

The variation in sensitivities between species and functional types following the wildfire was similar to that described at Kapalga by Lonsdale and Braithwaite (1991) for a wildfire of unknown intensity, and by Williams (1995) for the relatively intense fires of 1990 at Kapalga. These studies also showed that the deciduous non-eucalypt species, such as *Terminalia* and *Erythrophleum,* were more fire sensitive than were the dominant eucalypts such as *E. miniata* and *E. tetrodonta.*

Stem survival was clearly related to stem size, but not in a linear manner. Over the low-mid range of stem sizes (2–30 centimeters dbh), survival increased with stem size. The low survival of the smaller stems is likely to be compensated for by high rates of lignotuberous resprouting in these smaller-sized individuals, and the cohort of individuals 2–3 centimeters in dbh should persist in the medium term (decades) given a relatively benign fire regime. Survival was low in the largest stems (40–50 centimeters dbh), as has been reported by Bowman (1991) in the largest individuals of the rainforest tree *Allosyncarpia ternata* in Kakadu National Park. The high mortality of the largest stems in the present study may be related to the high incidence of "piping" of the trunks and larger branches by termites. Such "piped" trunks may be hollowed out by termites, which weakens the tree, or makes it more susceptible to internal ignition (Lonsdale and Braithwaite 1991, Williams and Douglas 1995). The low survival in the intermediate-sized stems (25% to 50% of those with a with a dbh between 5 and 10 centimeters) is also cause for concern in the long term. It remains to be seen over what period of time the growth of the remaining mid-sized trees can replace the very large trees.

Wildfire: The Consequences of Fire Exclusion in Savannas?

These results show clearly that a single fire in a hitherto fire-excluded savanna can result in as great a structural and compositional change as 5 years of late dry-season fires—a period during which average fire intensity in late burn plots was 7700 kilowatts per meter. The high intensity of the single fire of this study was due to (a) a buildup of fuel over the 7-year non-fire period and (b) the entry of a wildfire to the compartment during the late dry season, when fire weather conditions are conducive to maximum seasonal rates of spread (Gill et al. 1996).

The short-medium term outcome of this single high-intensity wildfire was high mortality of tree stems (in both the medium- and large-sized trees), extensive reduction in canopy cover, substantial reduction in living basal area, and a large reduction in the abundance of deciduous species. Other short-medium term impacts of single-intense fires appear to be a reduction in flowering and fruiting in the dominant eucalypts (Setterfield and Williams 1996), and in other main functional types of tree, especially the deciduous species, both eucalypts and non-eucalypts (Williams 1997). Such impacts simplify both the structure and composition of the tree stratum of the savanna. In contrast, the long-term (decadal) absence of fire from such savannas appears to result in more complex compositional and structural attributes of the tree stratum (Bowman et al. 1988b, Gill et al. 1990, Braithwaite 1995, Williams 1995). However, under such conditions, fuel loads also appear to increase from 2–5 tonnes per hectare, to 5–10 tonnes per hectare (Gill et al. 1990, Cook et al. 1995). Indeed, the majority of the buildup appears to occur in the first 2–3 years.

Herein lies, therefore, a management paradox, or dilemma. If the long-term (decadal) preservation of fire-protected savannas is a management goal in the humid savanna zone of northern Australia, then consideration must be given to the consequences of infrequent, but high-intensity fires which are eventually likely to occur in such fire-protected sites. The judicious use of fuel reduction burns has to be a part of such management. Such fires may be relatively infrequent, if necessary, but, if tree stratum complexity and stem survival are to be maximized, prescribed fires should occur very early in the dry season (April/May), when fire intensity can be minimized. The use of early dry season prescribed fire within Kakadu National Park by park managers, as a means of fuel reduction, is therefore appropriate. The impacts of such a fire regime on the tree stratum appear to be relatively benign, compared with repeated late dry season fires, and the impact of even a single high-intensity wildfire.

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