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Environmental and allometric drivers of tree growth rates in a north Australian savanna

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Abstract

Frequent fire is a feature of the mesic Australian savannas, yet little is known about its effect on tree growth rates. Growth data are critical for the development of demographic models to understand the consequences of different land management regimes. We used generalized linear mixed effects models and information-theoretic multi-model inference to analyse annual diameter growth of adult trees (≥ 5 cm diameter at breast height, DBH) and saplings (≥ 1.5 m height and < 5 cm DBH) and height growth of juveniles (< 1.5 m height) in response to fire, tree size, stand basal area, annual rainfall, and for adult trees, the presence of the introduced Asian swamp buffalo (a potentially growth-limiting herbivore). The analysis was based on two medium-term datasets from natural eucalypt savanna in Kakadu National Park in the Australian monsoonal tropics. One dataset was based on a 7-year experiment examining the effect of buffalo removal during which three fires occurred, and the second was derived from a 4-year study in which three experimental fire treatments (annual early dry season fire, annual late dry season fire and no fire) were imposed. An unplanned, extremely severe fire burnt some of the previously unburnt trees in the final year of this latter experiment, so we considered it as an additional fire treatment. Despite high variance, there was strong evidence for differential effects of the fire treatments on tree growth, and these effects differed among the three size groups. Late and extreme fires resulted in a high proportion of individuals with negative DBH increments (due to burning or shedding of bark, and also to stems being killed and replaced by small stems), and decreased average DBH growth of saplings (-0.17 and -1.38 cm year⁻¹, respectively—*cf.* 0.22 cm year⁻¹ for no fire) and adult trees (0.01 and 0.03 cm year⁻¹, respectively—*cf.* 0.18 cm year⁻¹ for no fire). Early fires decreased DBH growth of saplings (0.11—*cf.* 0.22 cm year⁻¹ for no fire) but increased growth of adult trees (0.29—*cf.* 0.18 cm year⁻¹). Height growth of juvenile trees was reduced by early fires (0.01—*cf.* 0.06 m year⁻¹ for no fire) but was increased by late fires (0.10 m year⁻¹), probably because juveniles are physiologically active early in the dry season, but are effectively dormant in the late dry season. When stand basal area was high there was evidence of growth suppression in adults, saplings and juveniles. Growth of adult trees was lower in years with high rainfall and where buffalo were removed, possibly because of increased competition from ground layer vegetation. Our study casts doubt on the sustainability of the frequent, early dry season fires that have become a management goal in much of northern Australia.

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1. Introduction

The mechanisms that allow the long-term persistence of tropical savannas have fascinated ecologists and remain a

central, unresolved question in tropical biology, although it is well accepted that fire and herbivory are key processes that maintain tropical savannas (Walker, 1987; Scholes and Archer, 1997; Sankaran et al., 2004). Tropical savannas present an intriguing example of a metastable system because there is a complex and dynamic coexistence between two fundamentally different and competing life-forms—grass and trees.

In the savanna regions of northern Australia, there is much concern about the most appropriate fire regimes for nature conservation areas such as the World Heritage-listed Kakadu National Park. Since proclamation of the Park in 1979, fire

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management has focussed on early dry season burning to reduce fuel loads and attempt to prevent extensive late dry season fires (Russell-Smith et al., 1997; Kakadu Board of Management, 1998). However, declines in mammal abundance over the last two decades have been documented in Kakadu, with possible causes being the changes in fire regimes that followed the cessation of Aboriginal fire management, changes in populations of feral Asian swamp buffalo (*Bubalus bubalis*) or both (Woinarski et al., 2001; Pardon et al., 2003; Andersen et al., 2005). There is also uncertainty about the effects of timing, frequency and intensity of fires on the biota (Braithwaite, 1991; Bowman and Prior, 2004). It is known that fires in this region, particularly the relatively high-intensity fires that occur late in the dry season, can increase stem and tree mortality (Williams et al., 1999; Werner, 2005), alter leaf and reproductive phenology (Williams et al., 2003), reduce seed production (Setterfield, 1997), decrease levels of soil nitrate-N (Russell-Smith et al., 2003), and increase susceptibility of soils to erosion and nutrient loss (Townsend and Douglas, 2000). Indeed, a 23-year fire experiment showed that in woody vegetation dominated by mature eucalypts, frequent, low-intensity fires reduced the density of mid-storey stems relative to that in unburnt plots, but concluded that vegetation structure was stable in the burnt plots (Russell-Smith et al., 2003). However, that study did not measure effects of fire on tree growth, recruitment or mortality.

Large herbivores such as cattle (*Bos taurus* and *B. indicus*), buffalo, horses (*Equus caballus*) and donkeys (*E. asinus*) were introduced to Australia by European settlers throughout the last two centuries, and in many areas these animals formed large, free-ranging and uncontrolled populations (Freeland, 1990). In the Kakadu region, buffalo increased substantially between the cessation of commercial hunting in the mid-1950s until the 1980s, when a stringent control program was implemented. However, small herds of buffalo are kept on native savannas of the region, including within Kakadu National Park (Kakadu Board of Management, 1998), and feral buffalo numbers are likely to increase again following relaxation of control measures (Saalfeld, 1999). Werner (2005) and Werner et al. (2006) found that buffalo initiate a cascade of effects on savanna vegetation by changing ground-level biomass, with consequent changes to fire frequency and intensity and thus tree growth and demography.

We investigated the effects of fire, buffalo, inter-tree competition, rainfall and tree size on growth of trees in tropical eucalypt savannas in Kakadu National Park. Growth is an important variable in understanding the response of trees to disturbance, and models show that the rate of stem growth and likelihood of resprouting after fire strongly influence the biomass of trees relative to grasses in savannas (Higgins et al., 2000). However, there are few data available on growth of savanna stems (Higgins et al., 2000), which is an essential input to models of tree population dynamics. A fire-mediated recruitment bottleneck exists in mesic savannas (Walter, 1971; Bond and Van Wilgen, 1996; Andersen et al., 1998; Werner, 2005; Werner et al., 2006), because recruitment of trees is limited by the ability of juveniles to escape the zone affected

by grass fires and become adults (Higgins et al., 2000; Sankaran et al., 2004). In general, reliable wet seasons mean that in most years, establishment of juvenile plants should not be restricted by water availability. Thus, in mesic savannas, juveniles with fast growth rates are most likely to pass through the recruitment bottleneck (Higgins et al., 2000). Tree seedlings may persist for many years as suppressed juveniles (Fensham and Bowman, 1992; Bond and Van Wilgen, 1996) when stems resprout repeatedly after being burnt back by frequent fires.

This growth pattern complicates modelling the system because replacement of a large stem by a smaller one leads to large apparent negative 'growth' (regression) rate for that individual tree (genet). To date there has been little development of statistical techniques that can accommodate negative growth increments, nor of ideas on how they may influence model predictions. In most studies of tree growth, annual negative growth increments have occurred in only a small proportion of measurements and their magnitude is typically small (e.g., Clark and Clark, 1999; King et al., 2005), although there are instances when they have been more common and larger (e.g. Daubenmire, 1972; Lieberman, 1982; Birkett and Stevens-Wood, 2005; Werner, 2005). In general, negative increments have been included in estimations of medians and variance. Here we investigate the effect of truncating the negative tail of the growth increment distributions (i.e., assuming different numerical thresholds to distinguish real negative stem growth from stem replacement), and whether this alters conclusions about the effects of fire on tree growth.

Our present dataset is derived from two medium-term studies of tree growth, survival and recruitment in Kakadu National Park. Patterns of tree growth, mortality and recruitment from one study have been published (Werner, 2005), but only mortality rates from the second study have been reported thus far (Williams et al., 1999). Combining the two datasets allowed for a more representative and powerful analysis using a variety of statistical modelling techniques embedded within an information-theoretic framework of tree growth. Thus, our study provides a more comprehensive account of the factors hypothesised to influence tree growth than has been achieved previously for north Australian savanna systems given the longer time span, greater range of sites and variation in stand basal area, and wider diversity of fire and buffalo regimes experienced.

2. Methods

2.1. Study area

Our analyses were based on two extensive datasets from studies done within Kakadu National Park at the former Kapalga Research Station (located at 132°22'E, 12°34'S), which was managed by the Commonwealth Scientific and Industrial Research Organisation (CSIRO). Kakadu National Park is located about 180 km east of Darwin in the monsoonal tropics of northern Australia (Fig. 1). Rainfall is strongly seasonal. The town of Jabiru, in the north of the Park, receives

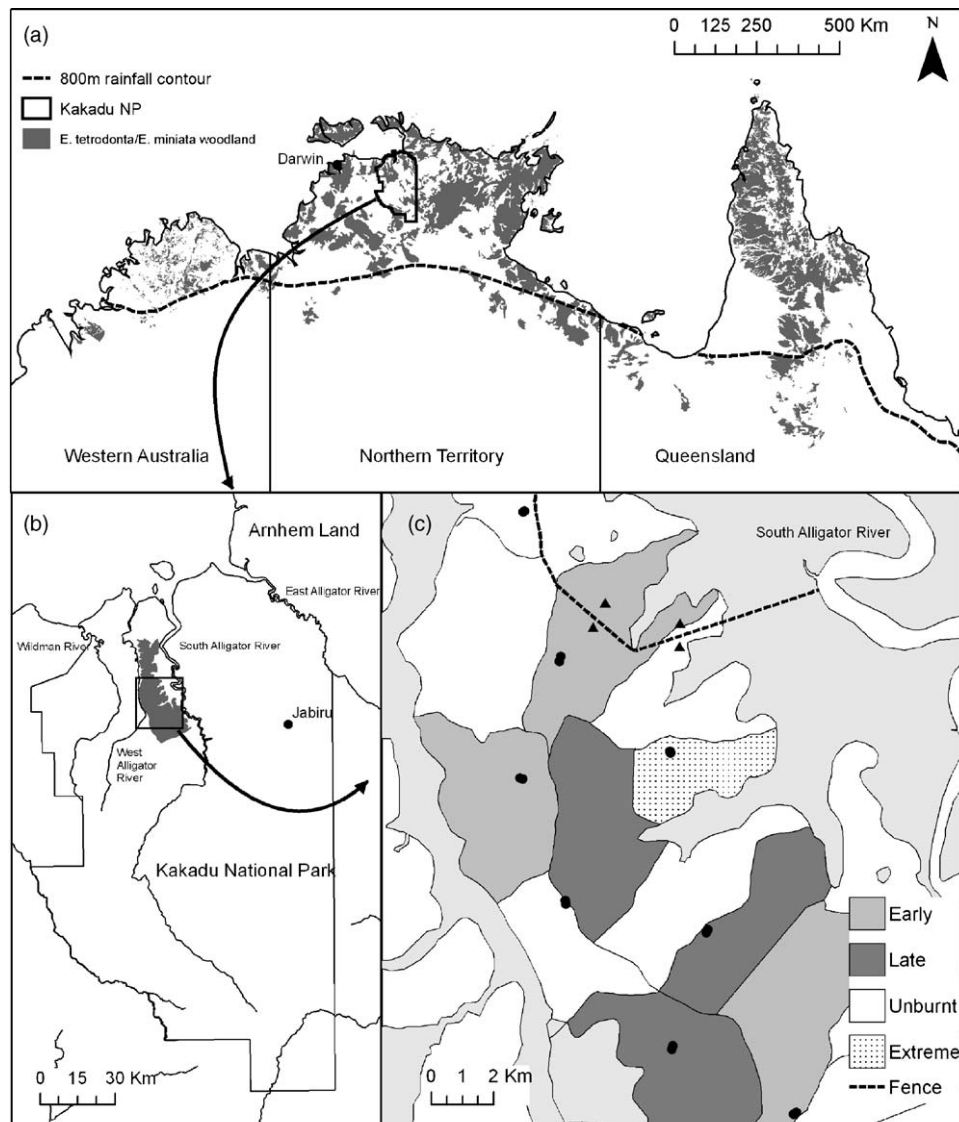


Fig. 1. (a) Distribution of *Eucalyptus tetrodonta*/*E. miniata* woodland in northern Australia (from Fox et al. (2001)) in relation to the 800 mm rainfall isohyet, with the location of Kakadu National Park shown, (b) Kakadu National Park, with locations of the town of Jabiru, and Kapalga shown as the dark area, and (c) the location of the study sites in Kapalga in relation to the buffalo fence and the fire treatments. Buffalo were removed from the south side of the fence (dashed line) in 1982, and from the north side of the fence in 1988. Fire treatments during the 1990–1994 period are shown as mid-grey (early), dark grey (late) and white (unburnt). An unplanned, extreme fire in 1994 (stippled area) burnt one of the previously unburnt compartments. The Werner plots are shown as triangles and the Williams plots as circles.

96% of its annual average total of 1485 mm during the wet season months of November–April (Bureau of Meteorology, <http://www.bom.gov.au/>). Temperatures are high year round, with average monthly maximum temperatures ranging from 31.5 °C in June to 37.5 °C in October, and average monthly minimum temperatures between 18.4 and 24.8 °C. The study areas are located in vegetation dominated by *Eucalyptus tetrodonta* and *Eucalyptus miniata*, two evergreen species that are widespread across northern Australia in areas with well-drained soils where annual rainfall exceeds about 800 mm (Fox et al., 2001; Fig. 1). The mid-storey consists of largely deciduous broad-leaved woody species, and the under-storey is dominated by a mixture of annual grasses such as *Sarga* spp. Descriptions of Kapalga may be found in Andersen et al. (2003), and experimental methods of tree marking and

monitoring in Williams et al. (1999, 2003) and Werner (2005). Nomenclature follows that of the Northern Territory Herbarium (2005).

The two experiments this study is based on are summarised in Table 1. The Werner (2005) study was conducted between 1982 and 1989 as part of a CSIRO landscape-scale experiment examining the effect of buffalo on flora and fauna (Ridpath and Waithman, 1988; Skeat et al., 1996). In the early 1980s, feral buffalo in the open forest of Kapalga were near their peak density of 15 animals km⁻² (Ridpath et al., 1983). In 1982, Kapalga was divided into two sections by a buffalo-proof fence and 97% of the buffalo were removed from the south side of the fence, with annual control measures keeping the population at <0.5% of the maximum. Buffalo on the north side of the fence remained high until August–October 1988, after which all

Table 1
Summary of the Werner and Williams datasets

	Werner	Williams
Measurement period	1982–1989	1991–1995
Treatments	Buffalo present <i>cf.</i> buffalo removed; fires entered some plots in September 1985, September 1987 and May 1988	Three relevant fire treatments (no fire, annual early, annual late), and the wildfire (extreme) that entered two previously unburnt plots in September 1994; buffalo removed from all plots by 1988
Total area	30 m × 30 m plots × 10 plots/location × 2 locations = 1.8 ha total	50 m × 20 m plots × 2 plots/compartments × 9 compartments = 1.8 ha total
Measurements		
(i) Height increment of juveniles (<1.5 m high)	Not reported	4718 observations
(ii) DBH increment of saplings (≥1.5 m high and <5 cm DBH)	None present	2518 observations
(iii) DBH increment of adults (≥5 cm DBH)	2978 observations	2013 observations
Key references	Werner (2005), Werner et al. (2006)	Williams et al. (1999, 2003)

The number of growth observations used in the analyses include all annual height increments, and annual DBH increments >−2.7 cm. The Werner experiment spanned 7 years, thus there were up to seven observations on an individual tree.

remaining buffalo on Kapalga were removed. In September 1982, Werner established permanent plots in pairs on either side of the buffalo-proof fence along a topographic gradient. For our analyses we used data from the areas corresponding to the ‘ridge-top’ and ‘slope’ areas described in Werner (2005). For both these locations, there were 10 plots, 5 on either side of the fence (total study area 1.8 ha). Within these plots, all trees >1.4 m in height were marked permanently with metal tags, and diameter at breast height (DBH) was measured in October each year for the following 8 years. Deaths and new recruits were also recorded. The study sites were protected from fire for the first 3 years (1982–1984), but fires entered some of the plots in other years, namely in September 1985 and 1987 (late dry season; high intensity), and in May 1988 (early dry season; low intensity); details are given by Werner (2005).

The Williams study was part of another landscape-scale experiment in Kapalga examining the effect of four experimental fire treatments on flora, fauna and soils of north Australian mesic savannas (Andersen et al., 1998, 2003). The experiment was setup in a part of Kapalga that had had no fire for the previous 3 years, and no buffalo for the previous 9 years. The three fire regimes considered here were annual early dry season (June) fires, annual late dry season (September) fires, and no fire (control; Williams et al., 1999, 2003). Experimental fires were lit annually between 1990 and 1994 in three replicate compartments, each 15–20 km². In addition to the prescribed fires, one of the control compartments, which had been unburnt for 7 years, was burnt by an unplanned, high-intensity fire in September 1994 (extreme fire). Our analyses used data from two of the permanent plots that Williams et al. (1999) established in each compartment; this represented a total area of 1.8 ha (Table 1). Within these plots, all trees taller than 3 m or with a DBH >3 cm were tagged. In addition, within one plot per compartment, all woody plant regeneration within a 4 m × 50 m strip was marked by tags on a small metal stake. Height of woody regeneration and DBH of tagged trees were measured between 1991 and 1995 at the start of the dry season each

year before fires occurred. Where available, rainfall data for Kapalga were used in analyses (Robert Eager, pers. commun.). Otherwise, data were obtained for Jabiru, about 50 km east of Kapalga (Bureau of Meteorology, 2005); while there is large spatial variability for individual rainfall events, there is much less on over an entire year. July–June rainfall totals, which incorporated a complete wet season, were used. Average annual rainfall was 1365 mm during the Werner study and 1371 mm during the Williams study. Stand basal area was used as a proxy for tree competition, although it also reflects habitat quality.

2.2. Tree growth measurements

We used DBH increment as a measure of growth for trees taller than 1.5 m because DBH is easily measured and can be largely self-scaling: a given DBH increment represents more biomass in large than in small trees, and because large trees generally grow more biomass in absolute terms, average DBH increment is often similar for a large range of tree sizes (Prior et al., 2004).

Observed average height and DBH increments as a function of tree size showed that the effect of fire differed for juveniles (height <1.5 m), saplings (≥1.5 m high and <5.0 cm DBH) and adult trees (≥5.0 cm DBH) (Fig. 2), so models were fitted separately for these three size classes. The terms ‘juveniles’, ‘saplings’ and ‘adults’ are used for convenience rather than to indicate developmental or reproductive status of these groups, while ‘tree’ refers to an individual of any size. The Werner dataset did not include height measurements of juveniles, and there were no saplings present. This was the only dataset for which buffalo were still present in some plots, thus it was possible to examine the effect of buffalo only for adult trees.

Growth increments were calculated for all trees and intervals for which there were measurements at the start and finish of the interval. Many DBH increments on surviving stems were negative, due to burning or shedding of bark and, to a smaller

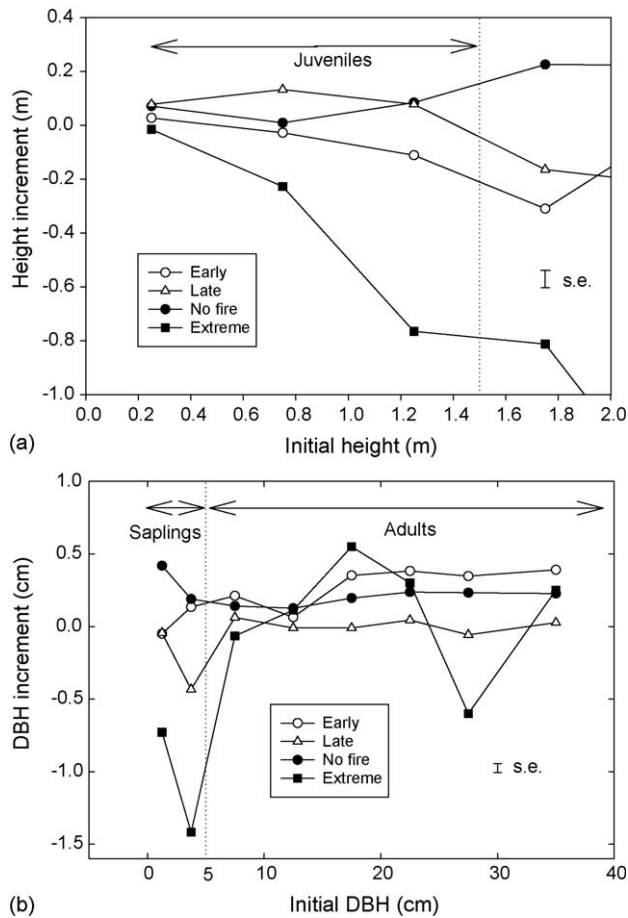


Fig. 2. (a) Mean annual height increment vs. initial height and (b) annual DBH increment vs. initial DBH of all species combined for no fire (closed circles), early fire (open circles), late fire (open triangles) and extreme fire (closed squares). Data were grouped into arbitrary size classes to show fine scale trends, with DBH values < -2.7 cm excluded. Height increments for trees > 1.5 m tall were not used in further analyses. Standard error averaged across data points is indicated in the bottom right of each graph.

degree, shrinkage of stems and experimental error. In addition, for late and extreme fires the number of stem deaths was substantial: often these were replaced by new stems, leading to large negative diameter increments (Fig. 3) and hence, bimodal distributions of the data (Fig. 4). We operationally defined that increments < -2.7 cm year⁻¹ were the result of death of the original stem and recruitment of a new shoot, and these data were excluded from our main set of growth analyses. For less negative DBH increments, it was not possible to distinguish clearly between death of the stem, damage through loss of bark or stem shrinkage. Stem shrinkage in savanna trees during the dry season has been reported by Prior et al. (2004). There were almost no DBH increments < -2.7 cm year⁻¹ for trees subject to early or no fire, but 35% of the increments for the extreme fire and 2% for the late fire were below this threshold. In addition to our main set of analyses, we investigated the sensitivity of average growth estimates to the negative values. For this, we started by including all increments, then progressively excluded the negative values from calculations of means for each fire regime, finally retaining only the non-negative values. We also

modelled DBH increments for all species combined when all negative diameter increments were excluded.

2.3. Statistical analyses

Our analytical approach was to employ multi-model inference based on information theory and model averaging because designation of a single 'best' model is often unsatisfactory when there are a large number of closely related models (Burnham and Anderson, 2002). Model comparison using information theory is also preferable to stepwise multiple regression techniques using significance tests for the analysis of noisy ecological data based on both theoretical grounds and ease of interpretation (Burnham and Anderson, 2002; Johnson, 2002; Johnson and Omland, 2004). Model averaging can provide a more stable and less-biased estimate of effect size than any single best model. Akaike's information criterion for small samples (AIC_c) was used to rank and weight the models. The AIC_c identifies the model(s) most strongly supported by the data based on the bias-corrected, maximised log-likelihood of the fitted model and a penalty for the number of parameters used (Burnham and Anderson, 2002). We used this multi-model approach to assess the importance and estimate the magnitude of the effects of fire, buffalo, rainfall, initial plant size and plot basal area on DBH and height increment. These factors have all been shown to affect tree growth rates in the seasonal tropics in Australia (Werner, 2005) or elsewhere (Worbes, 1999; Péliissier and Pascal, 2000; Hoffman, 2002; Chidumayo, 2005; Namaalwa et al., 2005), thus justifying their inclusion as fixed effects in the candidate model set. For each analysis, 32 models representing all combinations of these five fixed effects comprised the candidate model set. Fire during each interval for each plot was categorised as (i) early (May or June), (ii) late (September), (iii) extreme—the wildfire that occurred following 7 years of fire exclusion, and (iv) absent. The data were spatially and temporally unbalanced with respect to buffalo because they were present only during the Werner experiment (in half the plots). We were thus able to investigate the effect of presence of buffalo only for adult trees, for which buffalo were characterised as (i) still present, (ii) removed for ≤ 3 years, (iii) removed for 4–7 years, and (iv) removed for > 7 years. Initial plant size was expressed as either DBH at the start of the interval (adults and saplings) or tree height (juveniles). Stand basal area for each plot was calculated as the sum of the cross-sectional area at breast height of all the trees in the plot divided by the ground area. Plot basal area varied between 6.0 and 10.1 m² ha⁻¹ in the Werner dataset and between 5.0 and 17.2 m² ha⁻¹ in the Williams dataset. Analyses were undertaken for all species combined, and individually for the most abundant species within each size class, i.e. those with > 100 observations (Tables 2 and 3).

It was necessary to use mixed-effects models to account for the repeated measures of individual plants and the spatial correlations within the data (Crawley, 2002; Buckley et al., 2003). Individual trees nested within plots were entered as random effects into generalized linear mixed-effects model

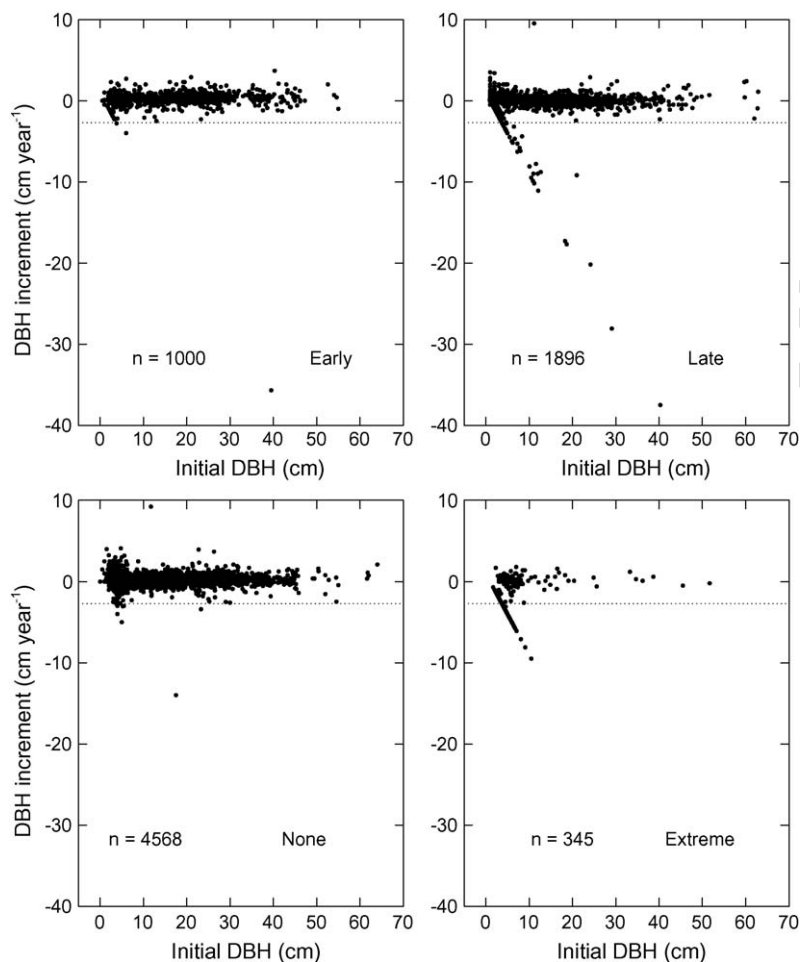


Fig. 3. The relationship between annual DBH increment and initial DBH of all species combined for the four fire categories. All trees that were alive, and for which there was a DBH at the start and end of the interval, are represented; n indicates the number of observations for each fire category. The large negative increments are the result of a large stem dying, and being replaced by a smaller one; these points approach the negative 1:1 relationship. Values less than $-2.7 \text{ cm year}^{-1}$ (indicated by the dotted line) were excluded from analyses.

structures (Crawley, 2002). There was no evidence of correlation of observations of plots within compartments, so plots were treated as independent. In general, data were homoscedastic and residuals were distributed approximately normally. To determine the relative importance of the fixed effects in each analysis, AIC_c weights (Burnham and Anderson, 2002) were calculated for all 32 models in the candidate set using maximum likelihood (ML) rather than restricted maximum likelihood (REML) to allow for comparison of models with different fixed-effects structures (Buckley et al., 2003; Crawley, 2002). For each fixed effect, the weight of evidence (w_{+i}) was calculated as the sum of the AIC_c weights for all the models in which the effect was present (Burnham and Anderson, 2002). However, the w_{+i} values are relative, not absolute because they will be >0 even if the predictor has no contextual explanatory importance (Burnham and Anderson, 2002). To judge which predictors were relevant to the data at hand, a baseline for comparing relative w_{+i} across predictors was required. Following Burnham and Anderson (2002), we randomised the data for each predictor separately within the dataset, re-calculated w_{+i} , and repeated this procedure 100 times for each predictor. The median of this new randomised

w_{+i} distribution for each predictor was taken as the baseline (null) value (w_{+0}). For each term the absolute weight of evidence (Δw_{+i}) was obtained by subtracting w_{+0} from w_{+i} . Predictors with Δw_{+i} of zero or less have essentially no explanatory power. We also calculated the percent deviance explained (analogous to r^2 calculated using least squares) by each model in each model set as $([\text{null deviance} - \text{residual deviance}]/\text{null deviance}) \times 100$, where null deviance is the deviance of the null model, which contains no fixed predictor variables. Weighted average coefficients were then calculated from the model set to assess the magnitude and direction of the effects of the fixed factors on growth of all trees combined and the most abundant species. All models and associated analyses were derived using the R statistical package v. 2.1.0 (R Development Core Team, 2005).

3. Results

3.1. Comparison of datasets

The major tree species and total basal area and were similar for the two datasets (Table 2). In both, the dominant

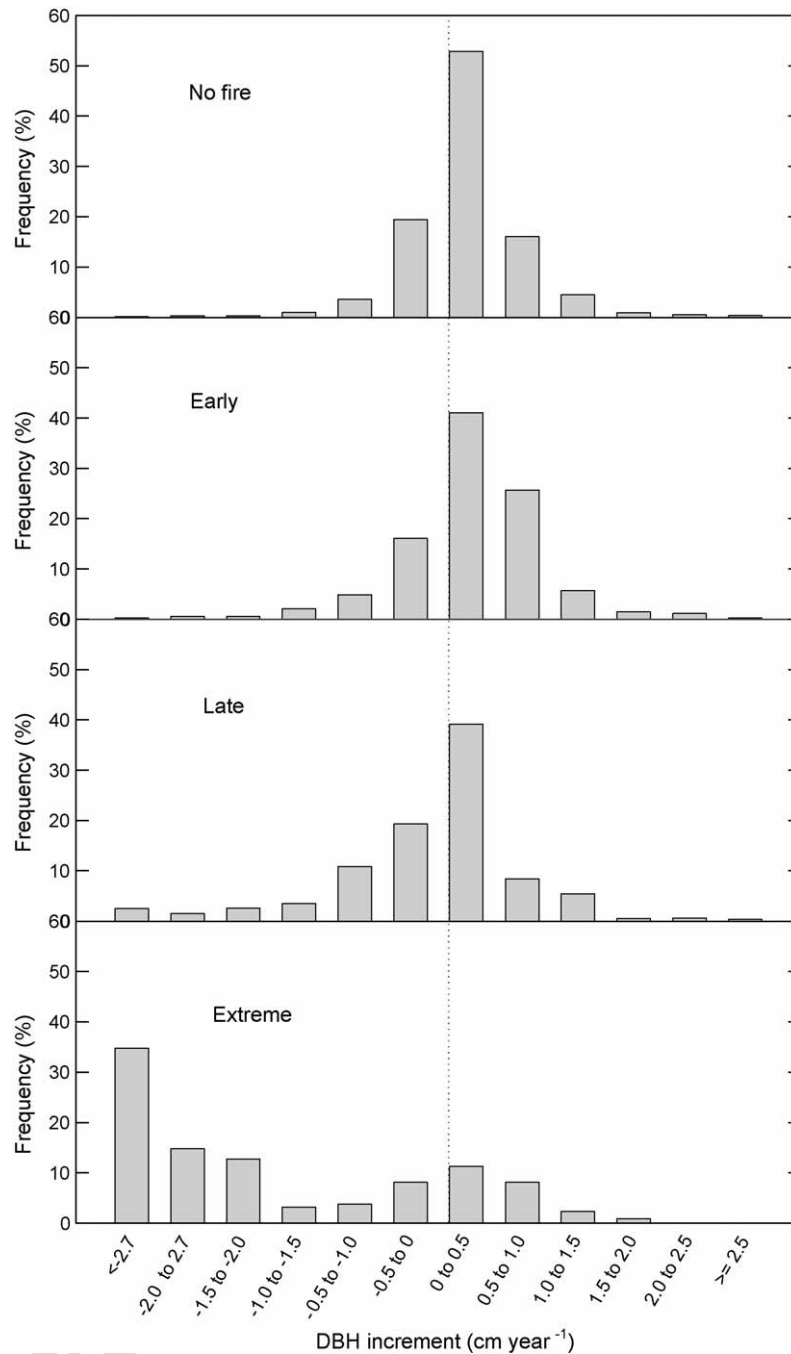


Fig. 4. Frequency distribution of DBH increments for the four fire categories. Note that the distribution was bimodal for the extreme fire.

species in terms of abundance and total basal area were *E. miniata*, *E. tetradonta*, *Corymbia porrecta* and *Erythrophleum chlorostachys*, with *Terminalia ferdinandiana* and *Xanthostemon paradoxus* also abundant in the Williams dataset. The total stem density was much larger for the Williams plots only because the latter contained saplings (700 stems ha⁻¹ in the 0.1–5 cm DBH class), whereas there were no saplings present in the Werner plots (Table 2; Fig. 5). Trees in the 5–10 cm DBH class were also more abundant in the Williams plots, but there was little difference for the other size classes.

3.2. Sensitivity of average DBH increments to including negative DBH increments

DBH increments of trees ≥ 1.5 m high were negative for 31% of the observations where trees were alive at the start and finish of the interval, and an even higher proportion for the late (45%) and extreme (77%) fires. The frequency distribution for the relationship between DBH increment and initial DBH was bimodal for the extreme fire (Fig. 4), requiring truncation of the extreme negative values. We found that the overall mean growth rate was highly sensitive to the threshold used to

Table 2

Species contributions to basal area, and stem density of saplings (≥ 1.5 m high) and adults, for both the Werner and the Williams datasets at the start of their measurements

Species	Relative basal area (%)		Sapling density stems (ha^{-1})		Adult density stems (ha^{-1})	
	Werner	Williams	Werner	Williams	Werner	Williams
<i>Eucalyptus miniata</i> Cunn. ex Schauer	38.4	44.1	0	137	52	124
<i>Eucalyptus tetradonta</i> F. Muell.	32.5	27.9	0	144	102	56
<i>Corymbia porrecta</i> (TS Blake) KD Hill & LAS Johnson	14.5	11.7	0	48	54	38
<i>Erythrophleum chlorostachys</i> (F. Muell.) Baillon	5.3	9.3	0	112	10	24
<i>Eucalyptus tectifca</i> F. Muell.	3.1	<0.1	0	6	20	0
<i>Corymbia bleeseri</i> (Blakely) KD Hill & LAS Johnson	2.3	0.9	0	3	9	4
<i>Terminalia ferdinandiana</i> Exell	0.9	2.0	0	85	8	14
<i>Xanthostemon paradoxus</i> F. Muell.	0.1	1.8	0	33	1	18
<i>Terminalia carpentariae</i> C. T. White	0.8	<0.1	0	1	2	1
<i>Buchanania obovata</i> Engl.	0.5	0.1	0	13	2	1
<i>Pandanus spiralis</i> R. Br.	0.2	0.4	0	16	1	3
<i>Planchonia careya</i> (F. Muell.) Knuth	0.5	0.1	0	9	2	1
<i>Brachychiton diversifolius</i> R. Br.	0	0.5	0	9	0	2
<i>Livistona humilis</i> R. Br.	0.4	0.1	0	1	7	2
<i>Corymbia latifolia</i> (F. Muell.) KD Hill & LAS Johnson	0.4	0	0	0	1	0
<i>Corymbia polysciada</i> (F. Muell.) KD Hill & LAS Johnson	0	0.3	0	12	0	3
<i>Acacia latescens</i> Benth.	0	0.2	0	20	0	2
Total—all species	100	100	0	700	272	303

Species are listed in order of decreasing basal area. Species contributing $>0.1\%$ of the basal area are shown; this was 8.23 and $9.63 \text{ m}^2 \text{ ha}^{-1}$ for the Werner and Williams datasets, respectively. Saplings were absent in the Werner data set, but juveniles (<1.5 m) high were present. For both datasets, plots comprised a total area of 1.8 ha .

exclude the negative diameter increments (Fig. 6): if no data were excluded the growth rate was $0.01 \text{ cm year}^{-1}$, but it was $0.40 \text{ cm year}^{-1}$ if all negative increments were excluded. Certain subsets of the data were affected even more strongly. The corresponding averages for the extreme fire ranged between -1.92 and $0.50 \text{ cm year}^{-1}$, and that of the late fires varied between -0.24 and $0.37 \text{ cm year}^{-1}$ according to different threshold values (Fig. 6). When all growth increments were included in the analyses, the effect of fire was very important for both adults and saplings ($\Delta w+$ was 0.88 for both, similar to values in the main set of analyses in which values $<-2.7 \text{ cm}$ were excluded). When all negative values were excluded, however, the effect of fire was much less important for adults ($\Delta w+ = 0.40$), and not important for saplings ($\Delta w+ = -0.03$).

3.3. Importance and magnitude of fixed effects on growth

3.3.1. Adults

All factors examined, namely fire, buffalo, initial DBH, rain and plot basal area had some influence on DBH increment of all species combined, with the global model (the one including all the predictor variables) receiving 99.5% of the AIC_c weight. This was reflected in high $\Delta w+$ values (Fig. 7). Fire had the strongest effect, with the late and extreme fires reducing growth by a predicted 0.22 and $0.08 \text{ cm year}^{-1}$, respectively, whilst early fire increased growth by $0.06 \text{ cm year}^{-1}$ compared to when fire was absent (Fig. 8 and Table 4). The effect of fire on growth was important for seven of the nine individual species examined (Fig. 7). There were no *C. bleeseri* trees exposed to early fire, but of the other six species, growth rates were larger

for early fire than for no fire, while late fire reduced growth. Table 3 shows observed means; their rankings within each species concurred with model predictions.

High rainfall had an important and negative effect on growth of seven individual species (Fig. 7). The effect of high plot basal area was negative and important for three species—*C. porrecta*, *C. bleeseri*, *E. miniata* (Fig. 7; Supplementary information). Initial DBH was important for five species—the correlation with growth rates was positive for *C. porrecta*, *E. tectifca* and *E. tetradonta* but negative for *E. chlorostachys* and *T. ferdinandiana*. In the presence of buffalo, modelled growth rates were $0.14 \pm 0.04 \text{ cm year}^{-1}$ higher than in plots where buffalo had been removed for 4–7 years, but were similar in plots where buffalo had been removed for periods longer or shorter than this (Table 4). These buffalo effects were not, however, consistent among species (Supplementary information).

Despite high variability in the data and percent change in deviance for the fixed effects of the global model of only 3% ($1-27\%$ for individual species), there was generally strong support for the best statistical models as indicated by low AIC_c weights for the null and many other reduced models, and thus high $\Delta w+$ values (Fig. 7). The exceptions were *E. chlorostachys* and *X. paradoxus*, for which the null model received the most support.

3.3.2. Saplings

The effects of fire and plot basal area were stronger on the growth of saplings than that of the other two size classes (Figs. 7 and 8). For all species combined, the model that received the most support was the one incorporating basal area, fire and initial DBH (AIC_c weight = 0.51). Growth was reduced by late

Table 3
Observed mean growth rates of the three size classes subject to the four fire categories, listed by species

Fire category species	Early	Late	No fire	Extreme
Juveniles—height increment (m year⁻¹)				
<i>B. obovata</i>	-0.01 (0.01, 352)	0.00 (0.01, 97)	0.03 (0.02, 21)	n.a.
<i>C. porrecta</i>	0.00 (0.01, 443)	0.12 (0.03, 240)	0.03 (0.02, 104)	0.01 (0.22, 4)
<i>E. miniata</i>	0.20 (0.13, 31)	0.30 (0.05, 150)	0.30 (0.26, 15)	n.a.
<i>E. tetradonta</i>	-0.01 (0.02, 177)	0.17 (0.02, 340)	0.03 (0.02, 211)	-0.30 (0.15, 2)
<i>E. chlorostachys</i>	0.05 (0.02, 264)	0.10 (0.03, 164)	0.13 (0.03, 184)	-0.18 (0.03, 37)
<i>Livistona inermis</i>	-0.05 (0.10, 12)	0.09 (0.05, 20)	0.04 (0.02, 89)	n.a.
<i>P. careya</i>	0.00 (0.01, 192)	-0.01 (0.01, 242)	0.03 (0.02, 155)	-0.28 (0.12, 8)
<i>T. ferdinandiana</i>	0.04 (0.02, 105)	0.05 (0.02, 148)	0.04 (0.02, 155)	0.75 (n.a., 1)
<i>X. paradoxus</i>	-0.02 (0.01, 285)	0.05 (0.08, 54)	0.46 (0.22, 5)	n.a.
All species	0.01 (0.01, 2071)	0.10 (0.01, 1583)	0.06 (0.01, 1006)	-0.15 (0.04, 58)
Saplings—DBH increment (cm year⁻¹)				
<i>A. latescens</i>	-0.17 (0.19, 6)	-0.30 (0.24, 12)	0.18 (0.06, 133)	-1.70 (n.a., 1)
<i>C. porrecta</i>	0.21 (0.10, 21)	-0.21 (0.16, 61)	0.25 (0.06, 106)	0.63 (0.22, 3)
<i>E. miniata</i>	0.14 (0.09, 70)	0.07 (0.06, 203)	0.31 (0.04, 237)	-1.15 (0.31, 14)
<i>E. tetradonta</i>	0.02 (0.09, 63)	-0.42 (0.07, 128)	0.12 (0.05, 142)	-2.20 (0.20, 2)
<i>E. chlorostachys</i>	0.11 (0.17, 23)	-0.31 (0.15, 41)	0.15 (0.04, 168)	-1.76 (0.17, 22)
<i>T. ferdinandiana</i>	0.04 (0.20, 14)	-0.15 (0.11, 27)	0.20 (0.03, 380)	-1.56 (0.14, 59)
<i>X. paradoxus</i>	0.23 (0.15, 12)	n.a.	0.24 (0.04, 143)	n.a.
All species	0.11 (0.04, 225)	-0.17 (0.04, 502)	0.22 (0.01, 1648)	-1.38 (0.10, 143)
Adults—DBH increment (cm year⁻¹)				
<i>C. bleeseri</i>	n.a.	0.15 (0.06, 27)	0.06 (0.03, 98)	n.a.
<i>C. porrecta</i>	0.29 (0.05, 106)	-0.02 (0.04, 207)	0.20 (0.02, 536)	1.20 (n.a., 1)
<i>E. miniata</i>	0.37 (0.04, 294)	0.10 (0.03, 359)	0.24 (0.02, 741)	0.05 (0.12, 44)
<i>E. tectifera</i>	0.35 (0.15, 15)	0.05 (0.07, 33)	0.14 (0.03, 185)	n.a.
<i>E. tetradonta</i>	0.38 (0.05, 147)	-0.12 (0.04, 258)	0.18 (0.01, 1152)	0.40 (0.10, 2)
<i>E. chlorostachys</i>	0.16 (0.09, 68)	0.04 (0.10, 30)	0.04 (0.05, 165)	0.05 (0.55, 2)
<i>T. ferdinandiana</i>	0.06 (0.08, 42)	0.14 (0.08, 29)	0.10 (0.04, 109)	-0.71 (0.32, 9)
<i>X. paradoxus</i>	0.02 (0.07, 40)	-0.14 (0.17, 5)	0.12 (0.05, 98)	n.a.
All species	0.29 (0.02, 757)	0.01 (0.02, 964)	0.18 (0.01, 3290)	0.03 (0.09, 80)

Standard errors and number of observations are shown in brackets. Data are presented for abundant species, i.e. all species with over 100 observations in that size class. Note that there are up to 4 observations (1 year⁻¹) for an individual juvenile or sapling, and up to 7 observations for an individual adult. Where a DBH increment was < -2.7 cm year⁻¹ it was excluded from the dataset. 'All species' includes observations for abundant species and the less abundant species not listed here. 'n.a.' indicates no observations available. The species shown in bold are those for which statistical modelling indicated an important effect of fire category ($\Delta w + > 0.1$; see Fig. 7).

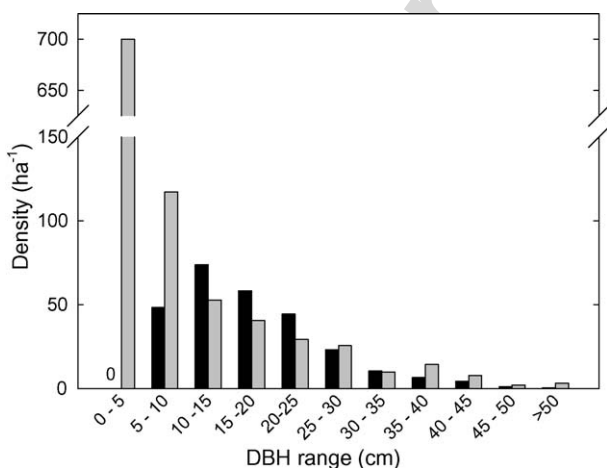


Fig. 5. Frequency distributions, as stem density per ha, of initial DBH of trees at the start of Werner's measurements in 1982 (black bars) and Williams's measurements in 1991 (grey bars). Note the absence of trees in the 0–5 cm DBH range in the Werner plots.

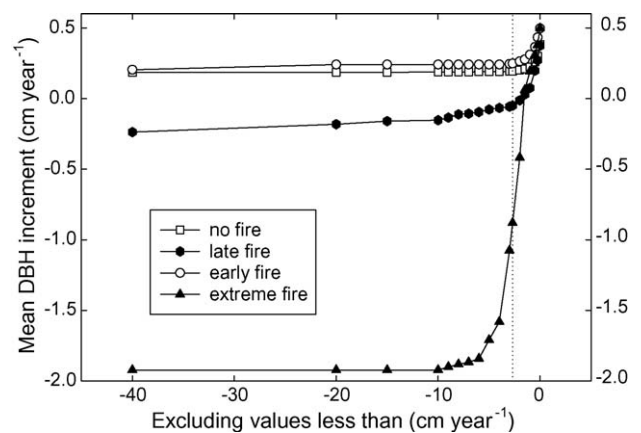


Fig. 6. Effect on mean DBH increment of excluding DBH increments less than the value shown on the x-axis, for the four fire categories. For the late and extreme fires, the mean was very sensitive to the chosen cut-off value in the range of -5 to 0 cm year⁻¹. When all negative values were excluded, means were similar for all fire categories.

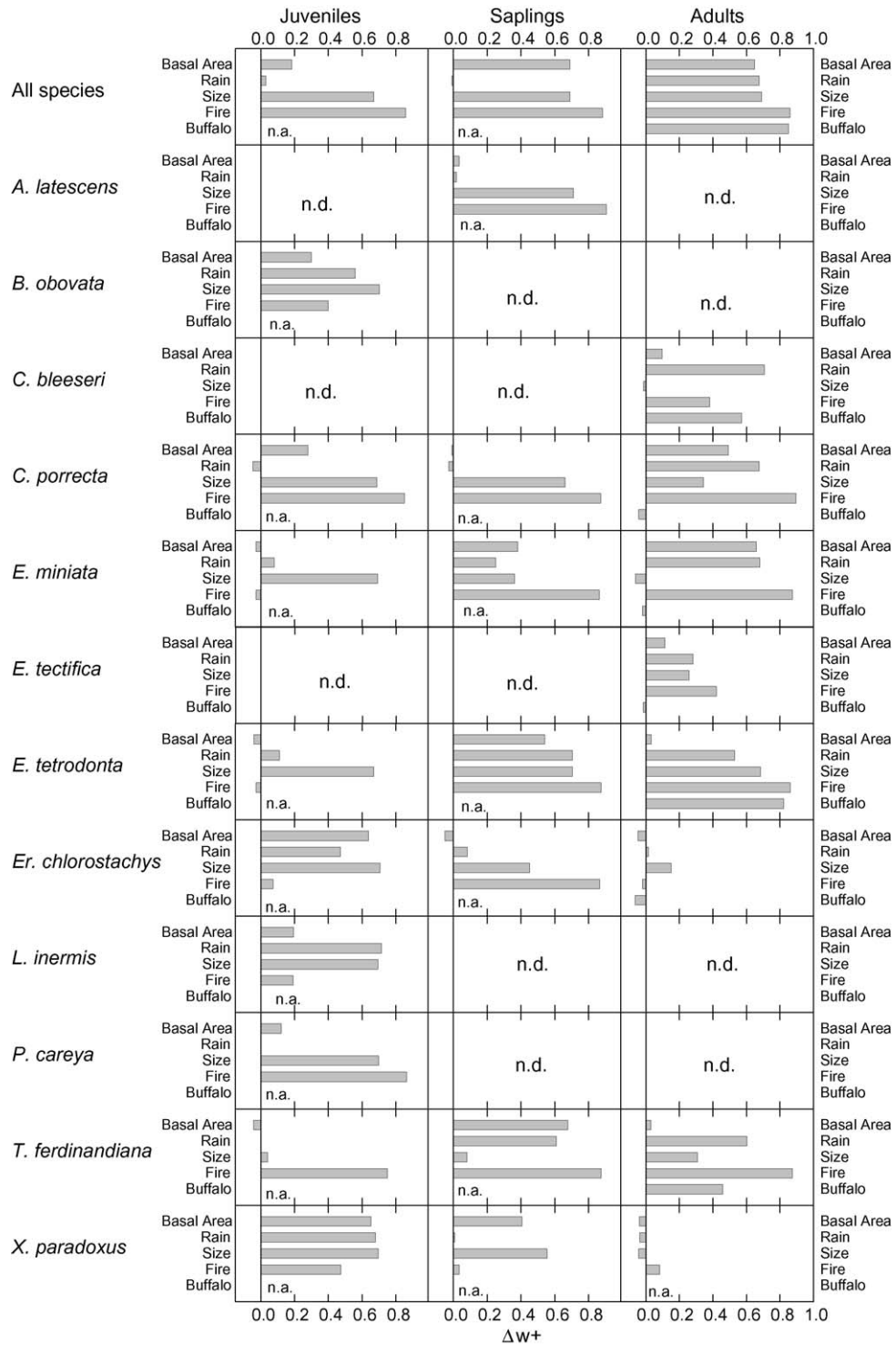


Fig. 7. The relative importance of the factors plot basal area (BA), rainfall, fire category, buffalo and initial size on height and DBH increment for all species combined, and the most abundant individual species, as indicated by $\Delta w+$, in each of the three size classes. The abundant individual species in a particular size class were those for which there were >100 observations. The $\Delta w+$ value reflects the weight of evidence for a factor influencing the response variable, with a high value indicating the factor is present in the most highly supported models; its derivation is described in Section 2. DBH increments < -2.7 cm were excluded from these analyses. Full species names (other than for *Livistona inermis* R. Br., for which only juveniles were abundant) are listed in Table 3. *C. bleeseri* trees were exposed to only the no fire and late fire treatments. 'n.d.' indicates not determined, because fewer than 100 observations for that species in that size class, and 'n.a.', not applicable, because the effect of buffalo was examined only for DBH increment of adults.

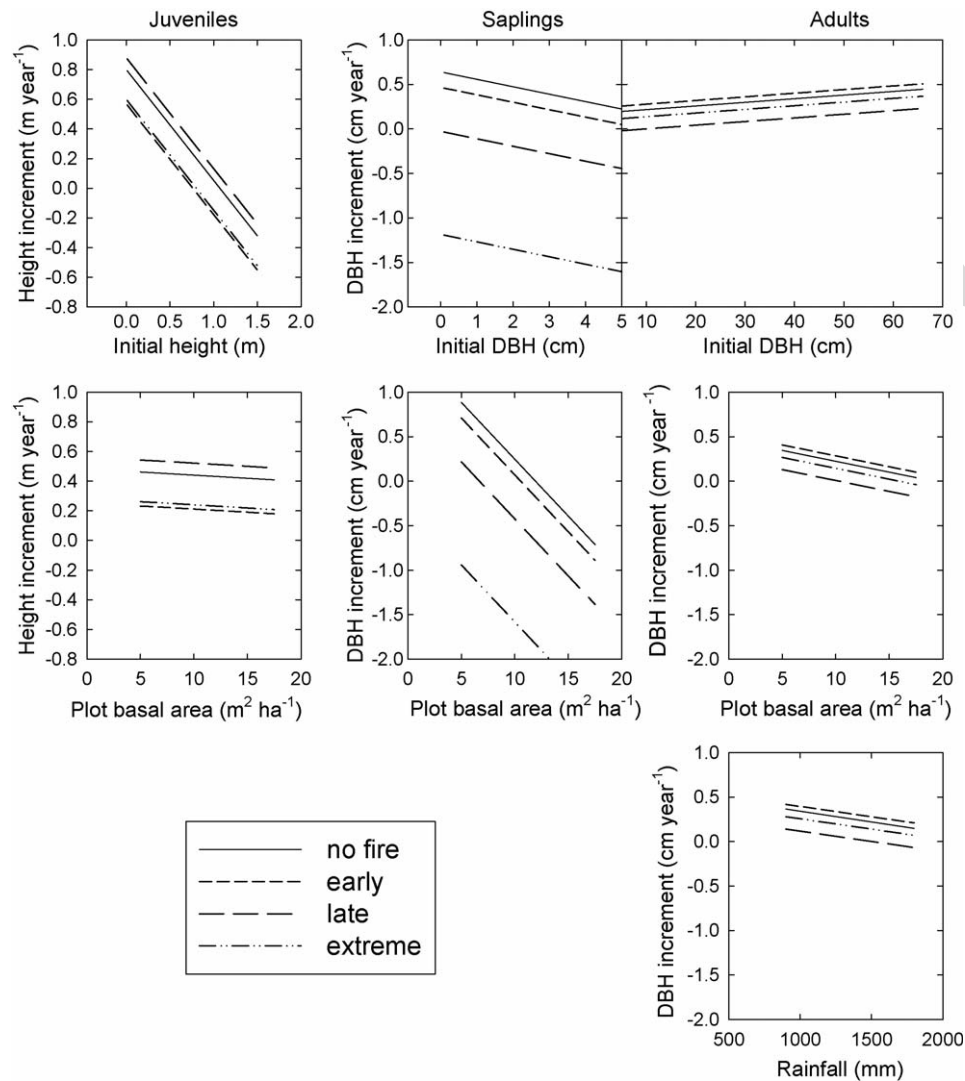


Fig. 8. Modelled responses of growth increment to initial height (juveniles) or DBH (saplings and adults), plot basal area, and annual rainfall (adults only), for the four fire categories for all species combined. Values are weighted model averages and assume buffalo long removed, and unless stated otherwise, mean values of plot basal area ($9 \text{ m}^2 \text{ ha}^{-1}$), rainfall (1370 mm), and initial size (0.48 m high for juveniles; 3.2 cm DBH for saplings and 17.6 cm DBH for adults) were used.

and especially extreme fires to such an extent that for these categories, modelled DBH increments were negative for virtually all plot basal areas and sizes of saplings (Fig. 8). Relative to late fires, early fires had a smaller negative effect on modelled (Fig. 8) and observed (Table 3) sapling growth for all species. However, *A. latescens* saplings were particularly susceptible to early fire, which caused negative average growth rates in this species (Table 3). Increased plot basal area was associated with lower growth rates in all species, although this was important for only three species (Fig. 7). Modelled growth was smaller for large than for small saplings, a trend that was consistent for all species (Supplementary information). Rainfall had virtually no effect on sapling growth of all species combined, but high rainfall increased growth of *E. tetradonta* and reduced growth of *T. ferdinandiana* saplings (Fig. 7; Table 4). Growth rates were highest for *E. miniata* saplings in the absence of fire, and this was the only species exhibiting positive growth when saplings were subjected to late fire (Table 3). *A. latescens* saplings appeared particularly suscep-

tible to early fire, and *E. tetradonta* saplings to late and extreme fires (Table 3). Percent change in deviance for the global model was 11% for all species combined (Table 4), and ranged from 4 to 28% among species. The strength of evidence for influence of the fixed effects on sapling growth was reflected in the extremely low AIC_c weights of the null models (e.g. 2.5×10^{-143} for all species combined).

3.3.3. Juveniles

Fire and initial height had an important effect on modelled height increment of juveniles, with the large $\Delta w+$ values indicating these factors explained some of the variation in growth (Fig. 7). The early and extreme fires both had large and adverse effects on juvenile growth compared with late or no fire (Tables 3 and 4 and Fig. 8). Fire also featured in the strongly supported models for many individual species (Fig. 7). The influence of plot basal area was relatively weak and generally positive (Table 4), and there was no effect of rainfall (Fig. 7). Modelled height growth was markedly faster for short than for tall juveniles for all

Table 4
Weighted model averaged coefficients for growth of juveniles, saplings and adults of all species combined^a

Size class	Intercept	$k_1 \times \text{plot basal area}$	$k_2 \times \text{rain} (\times 10^5)$	$k_3 \times \text{initial size}$	k_4 (late fire)	k_5 (no fire)	k_6 (extreme fire)	k_7 (buffalo removed ≤ 3 years)	k_8 (buffalo removed 3–7 years)	k_9 (buffalo removed > 7 years)	% Change in deviance
Juveniles	0.552 (0.026)	-0.004 (0.001)	0.417 (0.059)	-0.746 (0.003)	0.309 (0.033)	0.229 (0.036)	0.029 (0.036)				4.4
Saplings	1.605 (0.107)	-0.128 (0.007)	1.006 (0.520)	-0.084 (0.008)	-0.494 (0.108)	0.175 (0.104)	-1.652 (0.108)				11.2
Adults	0.732 (0.083)	-0.024 (0.007)	-23.20 (3.06)	0.004 (0.001)	-0.277 (0.037)	-0.061 (0.032)	-0.139 (0.072)	0.005 (0.039)	-0.144 (0.045)	0.042 (0.050)	3.1

Weighted model averaged standard errors associated with the coefficients are shown in brackets. Percent change in deviance for the fixed effects in the global model relative to the null model is also shown. The coefficients were derived from separate analyses. For juvenile, units are in m year^{-1} height increment, while for saplings and adults they are in cm year^{-1} DBH increment. The effects of buffalo were estimated only for adults.

^a Growth increment = intercept + $k_1 \times \text{plot basal area} (\text{m}^2 \text{ha}^{-1}) + k_2 \times \text{rain} (\text{mm}) + k_3 \times \text{initial size} (\text{height, m or DBH, cm}) + (0 \text{ or } k_4 \text{ or } k_5 \text{ or } k_6)$ for early fire, late fire, no fire and extreme fire, respectively + (0 or k_7 or k_8 or k_9) for buffalo present, removed ≤ 3 years, removed 4–7 years or removed > 7 years, respectively (thus the intercept shown is for early fire and, for adults, buffalo present).

species separately and combined (Fig. 7; Table 4; Supplementary information). This is most likely due to the fact that extreme fire reduced growth rates of large juveniles much more than that of small juveniles (Fig. 2). The percent change in deviance for the fixed effects of the global model was 4.4% for all species combined (Table 4), and 4–29% for individual species. The ΔAIC_c of the null models exceeded 10 for 8 of the 9 individual species investigated, and was 107 for all species combined. This demonstrates generally strong support for the best model, which, for all species combined, was the one incorporating basal area, fire and initial height (AIC_c weight = 0.33).

4. Discussion

Compared to other areas of the seasonally dry tropics receiving similar total rainfall, tree growth rates in Australian savannas are relatively low. For example, mean DBH increment in five studies in South and Central America and Africa was $0.35 \text{ cm year}^{-1}$ (range 0.14–0.50) (Daubenmire, 1972; Hoffman, 2002; Baker et al., 2003; Marín et al., 2005; Namaalwa et al., 2005), compared with $0.19 \text{ cm year}^{-1}$ for unburnt trees in this study, $0.16 \text{ cm year}^{-1}$ in unburnt *E. tetradonta* open forest near Darwin (Prior et al., 2004), and $0.17 \text{ cm year}^{-1}$ for trees subjected to a varied fire regime over 13 years in Kakadu National Park (Cook et al., 2005). The factors responsible are probably the same as those favouring the dominance of evergreen trees in Australian savannas—extremely low soil fertility, extreme rainfall seasonality, and perhaps higher temperatures and evaporation rates (Bowman and Prior, 2005).

Previous studies in the seasonal tropics have reported negative (Namaalwa et al., 2005), positive (Pélissier and Pascal, 2000; Werner, 2005) or neutral (Clark and Clark, 1999; Prior et al., 2004) correlations between tree size and growth rate. We found the effect of tree size on growth rates of adults and saplings was relatively small. Such inconsistent and weak relationships support the appropriateness of DBH increment as a self-scaling measure of growth for comparing species or treatments, which often obviates the need to control for tree size. By contrast, measures of basal area increment and relative growth rates depend strongly on tree size (Clark and Clark, 1999; Prior et al., 2004).

Tree growth rates were highly variable, with the fixed effects of our models accounting for only 3–11% of that variance, and the random effects (plot and individual tree) a similarly small amount. Thus, even within species there is large individual variability, presumably arising from variation in micro-site resources and competition and temporal effects other than total annual rainfall (the only temporal factor in the analysis). In addition, our study only investigated the highly variable above-ground growth of stems whilst neglecting the growth of lignotubers and roots, and storage of carbohydrates in these organs. Below-ground carbon storage is likely to be critical to survival and recovery of trees after fire and thus account for some of the variation observed above ground. The large envelope of tree growth rates explains an apparent paradox in our statistical analyses: the substantial effect of fire on growth rates, yet the small portion of the variability in growth rates explained by this

variable. An unresolved question is the importance of these small changes to average growth rates on tree population dynamics: the large variance in the data masks the growth potential of the fastest-growing individuals and unduly weights the numerous small, slow-growing trees that in reality are probably irrelevant to the stand dynamics. The growth rates of tropical rainforest trees have also been shown to be idiosyncratically variable for most species over most size classes (Clark and Clark, 1999). Indeed, Clark and Clark (1999) considered that DBH increments in tropical rain forests “could be thought of as falling within bounds defined by constraint lines, rather than as simple, central tendency line functions”. To get around this problem, they calculated the average growth rates of only the fastest-growing individuals of each species, which are likely to play a crucial role in tree population dynamics.

When negative diameter increments were excluded, the differences among fire treatments were small, consistent with findings of Werner (2005) for *E. miniata*. This is somewhat surprising considering that even trees with positive growth rates may have been temporarily defoliated by late and extreme fires (Williams et al., 2003), and that the positive growth may be under-estimated because of the loss of bark and damage to wood. McBride and Lewis (1984) found that 50% of early fires and 78% of late fires resulted in detectable scarring in tree growth rings of *E. tetrodonta* and *E. miniata*. It may be that growth rates are enhanced by early dry season fires through reduced competition or release of nutrients, but this effect is masked by the negative impacts of fire damage. The effects of fire treatments differed amongst different size-class categories (Fig. 9), suggesting that there are interactions between tree-life stage, fire intensity and season of fire. The early dry season fires slightly enhanced growth of adult trees, possibly in response to nutrients released from the burnt ground layer vegetation or less competition from the reduced ground-level herbaceous vegetation (Hoffman, 2002; Werner, 2005). Late dry season fires, however, decreased growth of both saplings and adults substantially (Fig. 9), and the extreme fire event led to negative diameter increments in 77% of individual trees. The early dry season and the extreme fires reduced the growth of juveniles,

but late dry season fires did not. The adverse effect of early dry season fires on juveniles is explicable because at this time of year photosynthetic rates are high but above-ground growth rates are negligible (Prior et al., 1997, 2004), implying that carbohydrates are stored underground to produce new growth as the wet season approaches. By killing leaves at this productive time of year, early fires must adversely affect the carbohydrate balance and subsequent growth of small trees. By contrast, in the late dry season few leaves remain on juvenile trees and burning at this time appeared to have little effect. The negative effect of early fires on juvenile growth would make it more difficult for juvenile trees to pass through the recruitment bottleneck to become saplings. This, combined with the negative effect of all fires on seed production (Setterfield, 1997) and seedling establishment (Setterfield, 2002), means that the current, frequent fire regimes are likely to have adverse effects on recruitment of trees in savannas in northern Australia.

The experimental design and lack of available data for the pre-experimental periods did not allow us to contrast the effects of annual fires statistically with less-frequent fires at similar times of the year. However, the single extreme late dry season fire that occurred in long unburnt plots caused a much larger decrease in average DBH increments than did the individual annual late dry season fires (Fig. 6). However, when all the large DBH decrements are included, the effect of this extreme fire event was approximately five times larger than that of the individual late fires treatments relative to no fire treatments, so that over the 5 years of the experiment the overall effects of the recurrent late dry season fires and a single extreme fire on DBH growth were similar. The relative effects varied for individual species, however, because differences in fire responses among species were most marked for the extreme fire event. The adult eucalypts all showed positive DBH increments following the extreme fire (Table 3), so it is possible that their bark had thickened during the long fire-free interval and protected these trees. *C. porrecta* appeared most resistant to the extreme fire, and this species has particularly thick bark (McBride and Lewis, 1984).

The negative correlation between growth of adult trees and annual rainfall total may be a result of high wet season solar radiation in below-average wet seasons; at such times, adults, with their larger root systems (Prior and Eamus, 1999), can continue to freely access soil water, and their canopies are also more exposed to the additional direct solar radiation, so that photosynthetic rates are close to maximal. Hutley et al. (2000) estimated that vegetation water requirements were approximately 1000 mm year⁻¹ for mesic savannas in northern Australia. Even wet seasons with well below average rainfall provide an excess of moisture to maintain water requirements, and this, coupled with higher radiation integrals, may result in increased growth relative to above-average wet seasons (L.B. Hutley, pers. commun.). Alternatively, the negative relationship of tree growth with rainfall may be explained indirectly, by effects on ground layer vegetation. It is likely that during dry years, the ground layer biomass is reduced so that both competition for nutrients (Werner et al., 2006) and fuel loads are reduced; adult trees should be able to take advantage of the

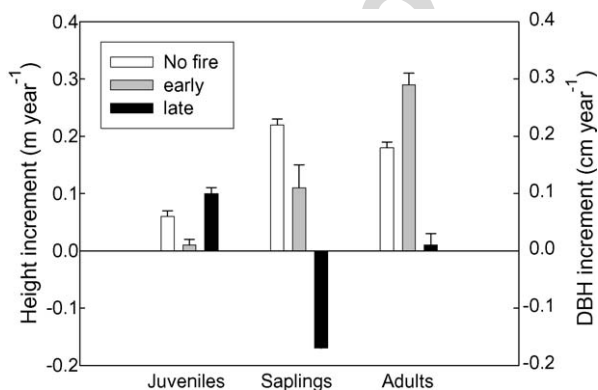


Fig. 9. Summary of the effects of the three main fire treatments (no fire, annual early and annual late fire) on annual growth of juveniles (height increment) and saplings and adults (DBH increment) for all species combined. DBH increments < -2.7 cm were excluded from the means, and error bars indicate S.E.M. Juveniles defined as <1.5 m high; Saplings <5 cm DBH; Adults ≥5 cm DBH.

putative reduced ground cover competition because they can access soil moisture at depth and thus maintain assimilation through the dry season (Eamus et al., 1999; Hutley et al., 2000). On the other hand, juveniles and saplings may be less able to utilise the additional nutrients because they have a smaller root

system and are demonstrably water-stressed, unlike the adult trees (Prior and Eamus, 1999).

The reduction in adult tree growth rate with the removal of buffalo is most likely also related to increased competition from ground-layer vegetation, as has been demonstrated by clipping

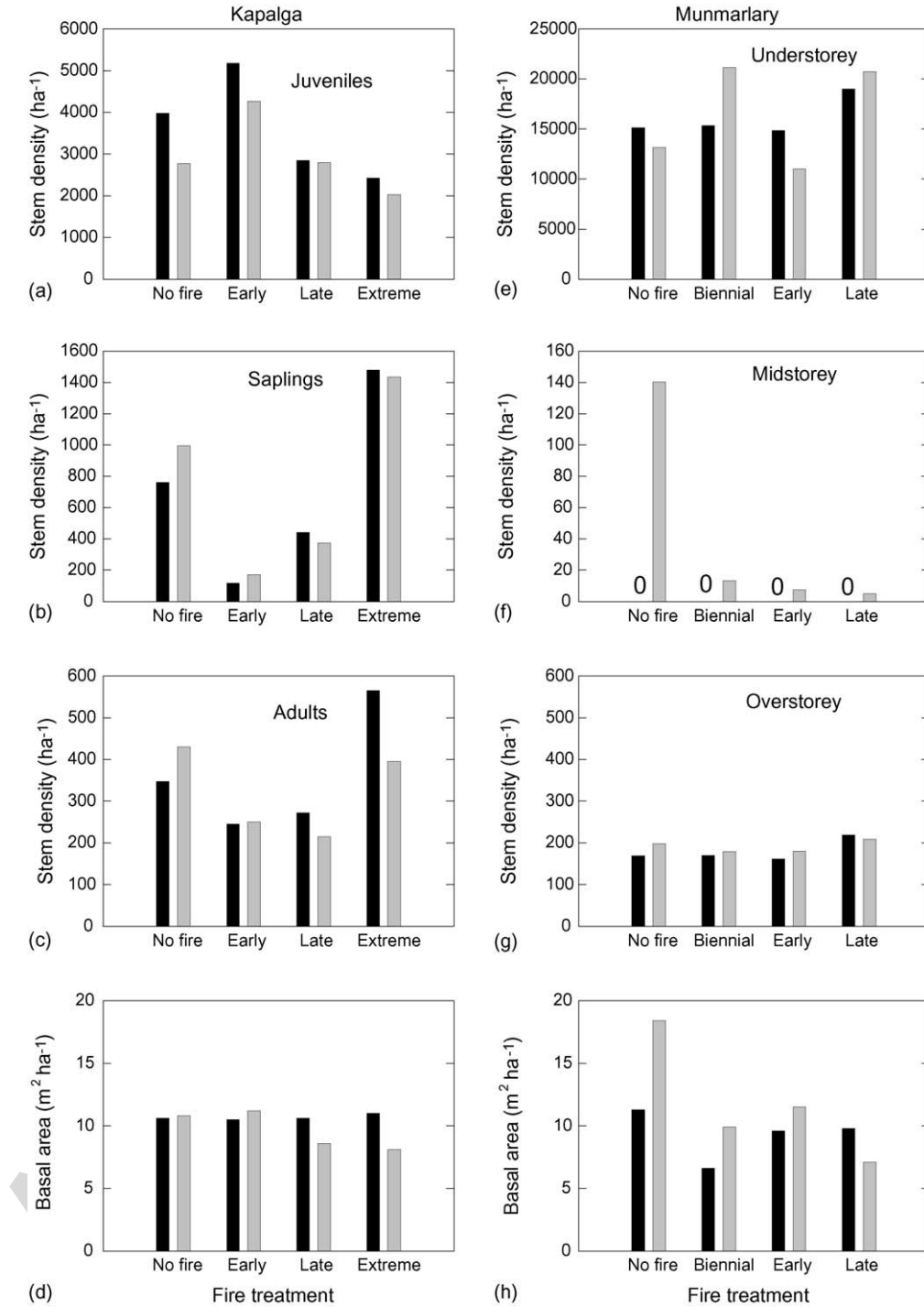


Fig. 10. Effects of fire treatment on change in density of trees in three size classes, and stand basal area, at Kapalga between 1991 and 1995 (Williams dataset), and in eucalypt open forest at Munmarlary between 1973 and 1994 (recalculated from Russell-Smith et al. (2003)). Black bars represent the start of the experimental period, and grey bars the end. There was only one extreme fire during the Kapalga experiment, and the changes shown for this treatment occurred over 1 year. At Munmarlary, fire treatments were complete protection from fire, biennial early dry season fire, annual early dry season fire and annual late dry season fire; most changes occurred in the first 3 years. Understorey stems were defined as those <2 m high, mid-storey stems as 2–8 m high, and overstorey stems as >8 m high. Note the different scales on the y-axes between the two experiments for the two small size classes.

experiments around juvenile trees (Werner et al., 2006). Further, the removal of buffalo is associated with greater fire intensity and subsequent mortality from fire because of heavy herbaceous fuel loads (Werner, 2005; Werner et al., 2006). Nonetheless, buffalo probably had a direct destructive effect on tree populations by trampling; for example there were no saplings in the <5 cm DBH size class in Werner plots in 1982, despite an abundance of juveniles <1.5 m high (Werner et al., 2006). Such 'U'-shaped size-class distributions were characteristic for most of northern Kakadu National Park (Werner and Press, unpublished data) and were probably related to the high buffalo densities at the time. Alternatively, they could have resulted from the early dry season fires that occurred almost annually in the lead-up to the experiment (Werner, 2005). Russell-Smith et al. (2003) also reported an absence of mid-storey stems (2–8 m tall) in 1973 in open forest at nearby Munmarlary, but during the fire experiment that was subsequently undertaken, trees were recruited into this size class (Fig. 10). The recruitment was greatest in the unburnt treatment, but was also present in the three fire treatments; most occurred within the 3 years to 1976. Interestingly, buffalo numbers were still high at this site until the mid-1980s (Russell-Smith et al., 2003), so it is unclear what factors allowed movement of understorey woody species through the recruitment bottleneck into the mid-storey class, even in plots subject to fire. However, it would appear that at Kapalga, the removal of buffalo some 9 years before the Williams study began, and the lack of any fires in the preceding 3 years, probably created a 'recruitment window' for juveniles to move into the sapling size range in those plots.

Another driver of demography, mortality, was reported for these same experiments by Williams et al. (1999) and Werner (2005). They found that late fire increased mortality of both small (<20 cm DBH) and large trees (>35 cm DBH), but there was little mortality of medium sized trees (20–35 cm DBH range) irrespective of fire regime. Low intensity, early dry season fires slightly increased mortality of trees with DBH <25 cm, but had no effect on the survival of larger trees (Williams et al., 1999; Werner, 2005). The presence of buffalo was associated with higher rates of recruitment, and lower mortality of both adult (Werner, 2005) and juvenile trees (Werner et al., 2006) compared to sites from which buffalo had been removed. This effect was probably mediated through the effect of buffalo reducing biomass of ground layer vegetation. Combining our growth results with the mortality rates for the same trees (Williams et al., 1999; Werner, 2005) allows the following conclusions: (i) late dry season fires had an adverse effect on both growth and survival of adult trees; (ii) early dry season fires had a negligible effect on survival of adults and stimulated growth of the surviving stems; (iii) early dry season fires had little effect on sapling survival but caused slightly decreased growth relative to unburnt sites; (iv) late dry season fires increased the mortality and decreased growth rates of saplings; (v) late dry season fires stimulated growth of juveniles whilst early season fires reduced average growth to almost zero.

The adverse effects of high-intensity, late dry season fires on savanna tree density and stand basal area are well-understood

(e.g. Andersen et al., 1998; Williams et al., 1999; Russell-Smith et al., 2003; Werner, 2005). What is not generally appreciated is that a regime of annual early fires, while favouring growth and survival of adult trees, may reduce the growth and survival of juvenile trees, with consequent effects on recruitment of saplings and adult trees and thus the sustainability of tree populations in the longer-term. Cook et al. (2005) have shown that repeated low-intensity fires would drive a stand towards a dominance of trees with stem diameters greater than 10–20 cm and towards greater dominance of eucalypts, trends that are consistent with our results. At Munmarlary, only fire protection was found to favour the recruitment of small stems: at the start of the experiment there were no mid-storey trees in any treatment, and after 23 years only a few stems had been recruited into the mid-storey of plots subject to any of the fire treatments (Russell-Smith et al., 2003; Fig. 10). In contrast, in the Williams' Kapalga dataset, sapling density at the start of the experiment was high, and increased slightly in both the no fire and early fire treatments (Fig. 10). The paucity of mid-storey tree recruitment at Munmarlary compared with Williams' Kapalga experiment is not easy to explain. It is unlikely that the different time scale of the two experiments is responsible given that mid-storey tree density was almost constant over the last 20 years of the Munmarlary experiment. Furthermore, one would expect differences between the unburnt and early fire treatments to be less at Munmarlary given that fire intensities were consistently lower than at Kapalga (Russell-Smith et al., 2003). One possibility is that saplings have greater carbon stores than suppressed juveniles and hence have a greater capacity to recover following fire.

Fire in the mesic savannas of Kakadu National Park, as in other parts of northern Australia, is extremely frequent. During the period 1980–1995, 50–60% of lowland savanna was burned each year, and 70% burned at least once every 2 years (Gill et al., 2000). Interestingly, there was a near 1:1 trade-off between burning in the early and in the late dry season, and an apparent shift to more, early season burning in the latter part of that period. It has been estimated that in these savannas, fire-free intervals of at least 4 years are required for woody sprouts to escape the fire trap, but <10% of the lowland savanna area of Kakadu remained unburnt for this long (Andersen et al., 2005). Thus while frequent, early dry season fires have become a management goal in much of northern Australia, the long-term sustainability of such a regime is uncertain and needs further investigation using demographic modelling.

5. Conclusion

This paper has provided a comprehensive analysis of tree growth under various disturbance regimes. On their own, tree growth data are incapable of resolving (i) the long-term demographic consequences of disturbance or, more importantly and (ii) of indicating the most appropriate ways to manage landscapes. Clearly what is required is the quantitative integration of stem growth, mortality and recruitment to model the drivers of demographic processes in Australian mesic savannas and thus predicting tree population trajectories under various management regimes.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.foreco.2006.06.034](https://doi.org/10.1016/j.foreco.2006.06.034).

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