Frequent fires reduce tree growth in northern Australian savannas: implications for tree demography and carbon sequestration

BRETT P. MURPHY*†, JEREMY RUSSELL-SMITH*‡ and LYNDA D. PRIOR§†

*Bushfires NT, Northern Territory Government, Winnellie, NT, Australia, †School of Plant Science, University of Tasmania, Hobart, TAS, Australia, ‡Tropical Savannas Management Cooperative Research Centre, Charles Darwin University, Darwin, NT, Australia, §School for Environmental Research, Charles Darwin University, Darwin, NT, Australia

Abstract

Tropical savannas are typically highly productive yet fire-prone ecosystems, and it has been suggested that reducing fire frequency in savannas could substantially increase the size of the global carbon sink. However, the long-term demographic consequences of modifying fire regimes in savannas are difficult to predict, with the effects of fire on many parameters, such as tree growth rates, poorly understood. Over 10 years, we examined the effects of fire frequency on the growth rates (annual increment of diameter at breast height) of 3075 tagged trees, at 137 locations throughout the mesic savannas of Kakadu, Nitmiluk and Litchfield National Parks, in northern Australia. Frequent fires substantially reduced tree growth rates, with the magnitude of the effect markedly increasing with fire severity. The highest observed frequencies of mild, moderate and severe fires (1.0, 0.8 and 0.4 fires yr^{-1}, respectively) reduced tree growth by 24%, 40% and 66% respectively, relative to unburnt areas. These reductions in tree growth imply reductions in the net primary productivity of trees by between $0.19\,t\,C\,ha^{-1}\,yr^{-1}$, in the case of mild fires, and $0.51\,t\,C\,ha^{-1}\,yr^{-1}$, in the case of severe fires. Such reductions are relatively large, given that net biome productivity (carbon sequestration potential) of these savannas is estimated to be just $1–2\,t\,C\,ha^{-1}\,yr^{-1}$. Our results suggest that current models of savanna tree demography, that do not account for a relationship between severe fire frequency and tree growth rate, are likely to underestimate the long-term negative effects of frequent severe fires on tree populations. Additionally, the negative impact of frequent severe fires on carbon sequestration rates may have been underestimated; reducing fire frequencies in savannas may increase carbon sequestration to a greater extent than previously thought.

Keywords: carbon sequestration, fire management, net primary productivity, northern Australia, tree demography, tree growth, tropical savanna

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Introduction

The dynamics of tropical savannas have received enormous attention in recent years, with much focus on mechanisms that allow trees and grasses to coexist, and factors determining the relative abundance of these two functional groups (Scholes & Archer, 1997; Sankaran et al., 2004, 2005, 2007; Bucini & Hanan, 2007). Interest in the biomass dynamics of tropical savannas has also been increased by the prominent role this biome plays

in the global carbon cycle, contributing around 30% of global terrestrial net primary production (NPP), roughly equivalent to that of tropical forests (Grace et al., 2006). However, because of the very high fire frequencies in savannas, with around 20% burnt annually (Dwyer et al., 2000), much of the carbon captured is quickly released back to the atmosphere, such that savannas store little carbon relative to other highly productive biomes, such as tropical forests (Grace et al., 2006). The large fluxes of carbon through savannas has led to suggestions that active management of this biome, through reductions in fire frequency or grazing intensity, for example, could lead to large increases in

Correspondence: Brett P. Murphy, PMB 44, Winnellie, NT 0822, Australia, e-mail: brettpatrickmurphy@hotmail.com

carbon sequestration (Williams et al., 2004; Grace et al., 2006; Beringer et al., 2007). Indeed, experimental reductions in fire frequency have been demonstrated to lead to substantial increases in savanna woody biomass, and hence stored carbon, throughout the tropics (San José et al., 1998; Russell-Smith et al., 2003; Higgins et al., 2007).

While it is clear that frequent fires tend to reduce woody biomass in savannas, other factors strongly limit the abundance of woody biomass per unit area, particularly water availability in semiarid savannas (Sankaran et al., 2005, 2007; Bucini & Hanan, 2007), and a conclusive theory to predict the current state of savannas remains elusive, despite much recent attention (Scholes & Archer, 1997; Sankaran et al., 2004). Most models of tree–grass coexistence are either competition-based models, where coexistence is mediated by spatial or temporal niche separation, or demographic bottleneck models, where coexistence is mediated by either interannual climatic variability or periodic disturbance (Sankaran et al., 2004). However, it is emerging that the competition-based and demographic-bottleneck models of tree–grass coexistence are not mutually exclusive. For example, Sankaran et al. (2005, 2007) and Bucini & Hanan (2007) have recently found that in arid and semiarid African savannas, woody cover is primarily controlled by water availability, supporting a competition-based model, while in more mesic African savannas, complete canopy closure is possible, and tree–grass coexistence is only facilitated by disturbances such as grazing and fire, supporting a demographic-bottleneck model. In a recent review, Sankaran et al. (2004) advocate an approach that integrates both paradigms, whereby processes such as tree–grass competition, rainfall variability and disturbance are considered purely in terms of their effects on tree demography, namely the rates of recruitment from one life-history stage to another, e.g. seed, seedling, sapling, adult. To the best of our knowledge, the only process-based predictive model to utilize a similar approach is the FLAMES model developed by Liedloff & Cook (2007) for northern Australian savannas.

To develop models that can accurately predict the response of savanna vegetation to altered fire regimes, we require an understanding of how simple demographic parameters, such as tree recruitment, mortality and growth rates, respond to fire. While the negative effects of fire on recruitment and mortality are well established (Lonsdale & Braithwaite, 1991; Glitzenstein et al., 1995; Grace & Platt, 1995; Williams et al., 1999; Hoffmann & Solbrig, 2003; Werner, 2005; Werner et al., 2006), if not well quantified, until recently its effect on growth rates was virtually unknown. Hoffmann (2002) briefly reported a negative effect of fire on tree growth, finding that stem diameter growth rates of two species

of Brazilian cerrado trees were reduced by around 30–50% 1 year after fire, with growth rates recovering by the following year. He concluded that the reduction in growth was due to the loss of photosynthetic ability following canopy scorch. In more detailed analyses, utilizing data from the Kapalga Research Station in Kakadu National Park, northern Australia, Werner (2005) and Prior et al. (2006) showed that severe fires reduced stem diameter growth rates by around 95% in the year following fire. Current models of savanna dynamics do not account for this effect (e.g. Higgins et al., 2000; Holdo, 2007; Liedloff & Cook, 2007), and may therefore overestimate the recruitment of individuals into larger, fire resistant size classes, and hence underestimate the negative impact of frequent fires on tree biomass, and hence, carbon sequestration.

Building on the recent work of Werner (2005) and Prior et al. (2006), we report the results of a large, 10-year study of adult tree growth throughout a large expanse of savanna in northern Australia. We examine the relationship between tree growth rates and fire frequency within a diverse, ambient fire regime, and consider the likely impact of such a relationship on the carbon sequestration potential of savannas.

Materials and methods

Study area

The study was undertaken in three large national parks, Kakadu (19 092 km²), Nitmiluk (2924 km²) and Litchfield (1464 km²), in northern Australia (Fig. 1). The vegetation is dominated by eucalypt (Eucalyptus and Corymbia spp.) open forests and woodlands, with a grassy understorey, referred to throughout this paper as mesic savanna (Finalyson & von Oertzen, 1996).

The climate is typical of monsoonal northern Australia, with high, extremely seasonal rainfall, ranging from about 900 mm annually in the southeast to about 1400 mm in the northwest (Fig. 1), with 90% typically occurring during the summer wet season (c. December–April). This climate is particularly conducive to high fire frequencies, with the wet season promoting grass growth, and the dry season (c. May–November) promoting grass curing. Typically 46%, 40% and 56% of Kakadu, Nitmiluk and Litchfield National Parks, respectively, are burnt annually (Russell-Smith et al., 1997; Edwards et al., 2001).

Tree growth rates

As a measure of tree growth rate, we used the annual increment in stem diameter at breast height (1.3 m; DBH). Between December 1994 and February 1997,
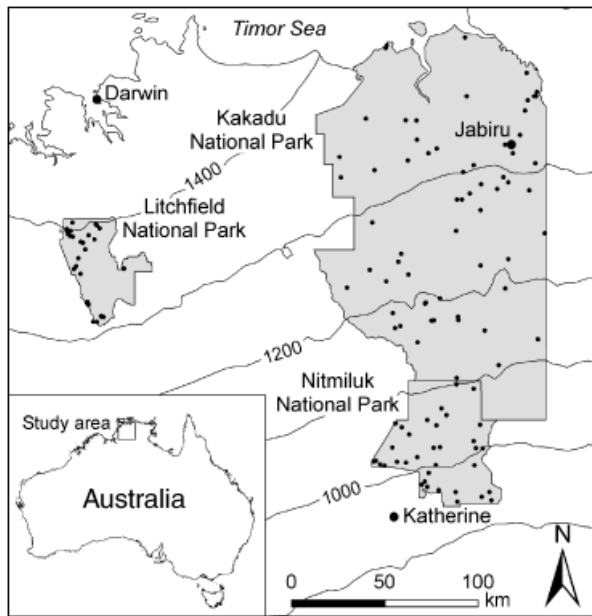
Fig. 1 Location of 137 vegetation monitoring plots in mesic savanna throughout Kakadu, Nitmiluk and Litchfield National Parks, northern Australia. Contour lines represent mean annual rainfall (mm).

220 vegetation monitoring plots were established throughout the three parks, as part of an ongoing monitoring programme. We restricted our analysis to 137 of the plots that were located in mesic savanna (Fig. 1).

Each monitoring plot measured $20\,m \times 40\,m$, within which all live adult trees ($DBH > 5\,cm$) were permanently marked with metal tags and DBH recorded. Where trees possessed multiple stems, the DBH of the largest stem was recorded. At two intervals, each approximately 5 years, DBH measurements were repeated. New trees with DBH $> 5\,cm$ were tagged and measured, and deaths of tagged trees recorded. Annual DBH increments were then calculated for each individual tree present throughout each interval. Increments were not calculated for trees that died during a given interval, nor for arborescent monocotyledons. DBH measurements took place during the wet season, in order to minimize the confounding effects of seasonal stem shrinkage, which can be substantial (Prior *et al.*, 2004).

Fire frequency

Russell-Smith & Edwards (2006) provide a detailed description of the assembly of the fire histories for the Kakadu and Nitmiluk monitoring plots, and the fire histories for the Litchfield plots were assembled in an identical way, as part of the same ongoing fire and vegetation monitoring programme. Each monitoring plot was visited and photographed once or twice each year throughout the 10-year study. Using the photos, plots were scored as recently burnt or unburnt, and if burnt, the fire was categorized as mild, moderate or severe, using the severity index developed by Russell-Smith & Edwards (2006), based on the scorch height of leaves. Leaf scorch height has been shown to be closely related to measured Byram fire-line intensity in these savannas ($R^2 = 0.85$; Williams *et al.*, 1998), underpinning the validity of the fire severity classification. Mild fires had scorch heights $\leq 2\,m$, suggesting Byram fire-line intensities of $< 1\,MW\,m^{-1}$. Moderate fires scorched the canopy to less than mid-height, suggesting intensities of 1–$2\,MW\,m^{-1}$. Severe fires scorched the canopy to its full height, suggesting intensities of $> 2\,MW\,m^{-1}$. Fires were also classified in terms of seasonality, with early fires occurring in the wet season (c. December–April) or early dry season (c. May–July) and late fires occurring in the late dry season (c. August–November). Using these fire histories, we calculated the annual frequency of mild, moderate and severe fires, and early and late fires, for each plot in each of the two intervals.

Other variables affecting DBH increment

In addition to fire frequency, we chose four variables that were most likely to affect DBH increment: (1) the amount of rainfall during the 5-year interval (e.g. Chidumayo, 2005; Prior *et al.*, 2006); (2) DBH of the tree at the start of the interval (e.g. Werner, 2005; Prior *et al.*, 2006); (3) total basal area of trees within the plot at the start of the interval (e.g. Hoffmann, 2002; Prior *et al.*, 2006); and (4) functional group of the tree (e.g. Prior *et al.*, 2004).

Functional groups were those used by Williams *et al.* (1999): *Acacia* species; deciduous eucalypts; other deciduous trees; evergreen eucalypts; and other evergreen trees. The rainfall each plot received during the 5-year interval was estimated from interpolated monthly rainfall grids (Australian Bureau of Meteorology, Canberra).

Transformation of DBH increments

Prior *et al*. (2006) provide a detailed discussion of the impact of large negative DBH increments on modelled DBH increment, suggesting that negative increments can readily be caused by numerous factors, including stem shrinkage, bark loss, measurement error, and death and subsequent replacement of stems. They assumed that increments more negative than $-2.7\,cm$ over a 1-year period were due to either measurement error or stem death and replacement, and excluded these increments from their analysis. The results of Werner (1986) suggest that such large negative DBH increments are unlikely to be due to stem shrinkage,

especially if seasonal stem shrinkage is controlled by sampling at a consistent time of year. She examined a large number of *Eucalyptus tetrodonta* trees in Kakadu National Park, and did not record DBH increments more negative than −0.1 cm over 2 years.

We followed an approach similar to that of Prior *et al.* (2006), although we used a minimum DBH increment more in line with the findings of Werner (1986). We assumed that stems could not shrink by more than 0.5 cm DBH, regardless of the time period. With a 5-year monitoring interval, this equates to a minimum DBH increment of −0.1 cm yr^{-1}. All increments more negative than −0.1 cm yr^{-1} were excluded from the analysis. By using a minimum DBH increment less negative than that used by Prior *et al.* (2006) we can be more certain that all negative increments were truly due to stem shrinkage rather than stem replacement, and we are more likely to underestimate the negative effects of fires, rather than overestimate them.

Overall frequency of DBH increments was not normally distributed, but displayed strong positive skew, so a normalizing transformation was applied to DBH increment before analysis. We added 0.1 to each increment measurement (to avoid negative values) and raised this value to the power of 0.2.

The final dataset was large, consisting of 4924 observations from 3075 individual trees (2494 trees in the first 5-year interval, and 2430 in the second).

Statistical analysis

Following the modelling approach used by Prior *et al.* (2006) and Werner & Prior (2007), we evaluated the importance of seven variables on DBH increment: (1) mild fire frequency; (2) moderate fire frequency; (3) severe fire frequency; (4) functional group; (5) annual rainfall; (6) plot basal area; and (7) initial DBH.

We chose to include fire severity variables (i.e. mild, moderate and severe fire frequencies) in the main *a priori* analysis, rather than fire seasonality variables (i.e. early and late fire frequencies). This was done: (1) to limit the number of candidate models under examination; and (2) because we considered fire severity to be more critical to tree growth than fire seasonality. While annual rainfall and fire frequency could be expected to be positively correlated at some spatial scales, there was no relationship between fire frequency and annual rainfall in our dataset ($P > 0.05$, $R^2 = 0.01$), consistent with a recent analysis of fire frequency in northern Australia that found little differences in fire frequency between 900 and 1400 mm annual rainfall (Spessa *et al.*, 2005).

Models representing all combinations of the seven variables, without interactions, were constructed as linear mixed effects models in the statistical package R

(version 2.5.0; R Foundation for Statistical Computing, Vienna, Austria). The inclusion of interaction terms rapidly increases the number and complexity of models under examination. Without prior reason to suspect that an interaction exists, we considered it appropriate to focus on the main effects of the seven variables. Mixed effects models allowed us to account for: (a) repeated measurements of growth rate of the same tree; and (b) correlation of growth rates of trees occurring in the same plot, by specifying a random effect (individual trees nested within plot).

Models were evaluated using a robust form of Akaike's Information Criterion, AIC$_c$, a model selection index favouring both model fit and model simplicity (Burnham & Anderson, 2002). Lower values of AIC$_c$ indicate greater support for a model, relative to other models in the same candidate set. From AIC$_c$, Akaike weights (w_i) were calculated for each model, and these are equivalent to the probability of a given model being the best in the candidate set. The importance of each variable was evaluated by calculating $w+$, the sum of w_i for all models in which that variable occurred. For each variable, $w+$ is equivalent to the probability of the best model containing that variable, and is a useful expression of the weight of evidence for the importance of the variable. The magnitude and direction of the fixed effects were assessed using coefficients from the entire model set, weighted according to w_i.

Initial graphical assessment of the data suggested a curved relationship between DBH increment and fire frequency (Fig. 3), so fire frequencies were squared prior to analysis, in order to linearize the relationship. In the case of mild fires and, to a lesser extent, moderate fires, there was also evidence of a 'humped' relationship, with a peak in DBH increment at around 0.2–0.4 fires yr^{-1}. Such a humped relationship is readily accommodated in the models by incorporating a second fire frequency term, allowing a horizontal shift in the maximum DBH increment (i.e. DBH increment ∼ fire frequency^2 + fire frequency). To evaluate whether the inclusion of additional model terms was justified, we compared the original global model (i.e. including all seven explanatory variables) with three similar models, incorporating additional terms for mild and moderate fire frequency (i.e. allowing humped relationships for mild and/or moderate fire frequency), using AIC$_c$:

$$\text{DBH increment} \sim \text{global model} + \text{mild fire frequency},$$

$$\text{DBH increment} \sim \text{global model} + \text{moderate fire frequency};$$

$$\text{DBH increment} \sim \text{global model} + \text{mild fire frequency} + \text{moderate fire frequency}.$$

The effect of fire frequency on NPP of savanna trees

Cook *et al.* (2005) developed an allometric method for estimating NPP of savanna trees at Kapalga in Kakadu National Park, requiring knowledge of initial tree DBH and annual DBH increment. For six common tree species, they provide equations that relate NPP to stem cross-sectional area (CSA) and its increase over a given period.

We used this method to investigate the likely effects of fire frequency on NPP of savanna trees, based on the observed relationship between fire frequency and DBH increment. For each of the 137 monitoring plots, we calculated CSA of live adult trees at the end of the 10-year study. Tree NPP for each plot was then calculated assuming DBH increments associated with a range of fire frequencies.

While Cook *et al.* (2005) provided allometric equations for six tree species that were common at Kapalga (*Corymbia bleeseri*; *Corymbia porrecta*; *Erythrophleum chlorostachys*; *Eucalyptus miniata*; *E. tetrodonta*; and *Terminalia ferdinandiana*), these six species were also very common throughout our study area, typically representing 49% of adult tree CSA in each monitoring plot at the end of the 10-year study. For other eucalypt species (*Corymbia* and *Eucalyptus* spp.), we averaged the allometric equations of the four eucalypt species. For other *Terminalia* species, we used the equations for *T. ferdinandiana*. For all other species for which allometric equations were unavailable, we averaged all six sets of allometric equations.

Results

Fire frequency

Generally, fire frequencies were high, with most monitoring sites experiencing three or more fires in each 5-year monitoring interval (Fig. 2). Most fires were mild and occurred early in the dry season. Severe fires were infrequent, with only 19% of sites experiencing them.

Initial graphical assessment of mean DBH increments clearly suggested a decline in growth with increasing fire frequency (Fig. 3). The magnitude of the effect appeared to be related to fire severity, with severe fires having a dramatic effect compared with the more modest effect associated with mild fires. This pattern was generally consistent among the five functional groups and among the common tree species (see supporting information Table S1).

While there appeared to be a 'humped' relationship between DBH increment and mild fire frequency, with a modest peak in DBH increment at mild fire frequencies of around 0.2–0.4 fires yr^{-1}, this observation was not supported by the statistical analysis. The original global
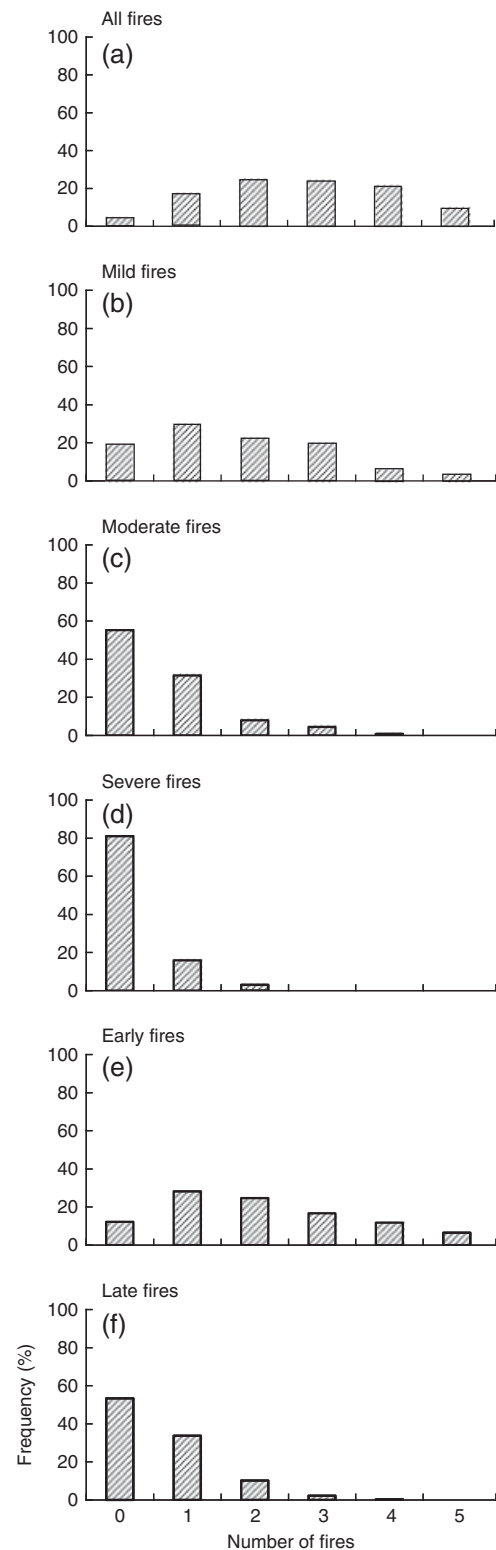

Fig. 2 Frequency distributions of number of fires experienced by each monitoring plot in each 5-year monitoring interval. Separate histograms are shown for: (a) all fires; (b) mild fires; (c) moderate fires; (d) severe fires; (e) early fires; and (f) late fires.
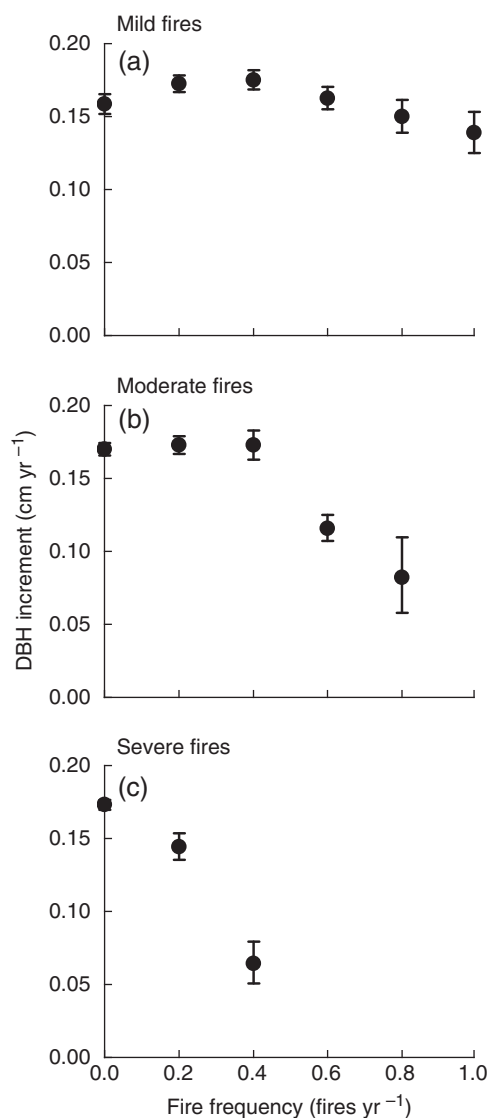
Fig. 3 Mean values of measured DBH increment plotted against the frequency of (a) mild, (b) moderate, and (c) severe fires. Standard errors are shown. DBH, diameter at breast height.

model, not incorporating humped relationships, had a lower AIC$_c$ value than similar models incorporating humped relationships for mild fire frequency and/or moderate fire frequency, suggesting it was superior to those models.

The initial observation of a negative relationship between DBH increment and fire frequency was confirmed by the statistical analysis. There was a high level of support for a relationship between DBH increment and the three fire frequency variables. In the case of moderate and severe fire frequencies, the level of support was very high; the probability ($w+$) of each of these variables being in the best model was >0.99 (Fig. 4). In the case of mild fire frequency, the level of support was slightly less, but still very high, with $w+$ of 0.92.

The modelled effect of fire frequency on DBH increment was large, with the magnitude of the effect increasing with fire severity (Fig. 5a). The most frequent severe fires (0.4 fires yr^{-1}) were associated with a substantial, 66%, reduction in DBH increment relative to unburnt areas. The most frequent moderate fires (0.8 fires yr^{-1}) were associated with a 40% reduction in DBH increment relative to unburnt areas. Even frequent mild fires (1.0 fire yr^{-1}) were associated with a 24% reduction in DBH increment.

The regression equations relating DBH increment to fire frequency, derived using multimodel averaging of the entire candidate set, are provided in Appendix S1.

The relative importance of fire severity and seasonality

In northern Australian savannas, there is strong congruence between fire severity and fire seasonality, with fires occurring in the wet season and early dry season typically of low severity and those occurring in the late dry season typically of high severity (Williams *et al.*, 1998; Russell-Smith & Edwards, 2006). The effects of early and late fire frequencies on DBH increment were of similar direction to the effects of mild and severe fire frequencies, but of intermediate magnitude (Fig. 5).

To evaluate the relative importance of fire severity (i.e. mild, moderate and severe fire frequencies) and fire seasonality (i.e. early and late fire frequencies), we undertook a simple *a posteriori* analysis. Using AIC$_c$, we compared the most highly ranked model of DBH increment from the earlier main analysis:

$$\text{increment} \sim \text{group} + \text{basal area} + \text{mild fires} + \text{moderate fires} + \text{severe fires},$$

to similar models incorporating early and late fire frequency, rather than moderate and severe fire fre-
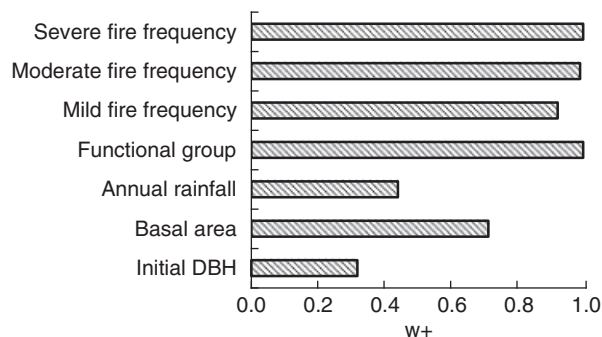

Fig. 4 The importance of the seven variables examined as determinants of DBH increment. $w+$ is the probability of a given variable occurring in the best model, and therefore reflects the weight of evidence of a relationship between that variable and DBH increment. DBH, diameter at breast height.
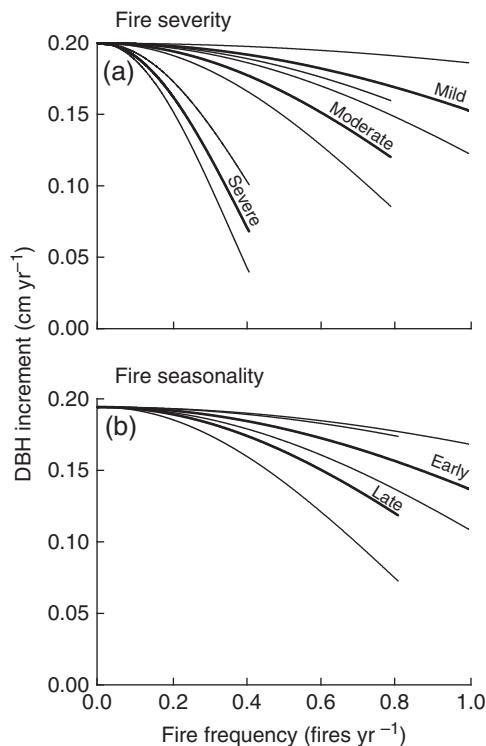
Fig. 5 The modelled effect of fire frequency on DBH increment, with fires separated according to (a) severity and (b) seasonality, based on multimodel averaging of all candidate models. Predictions for each of the five functional groups are averaged, and mean values for basal area ($8.4 \, m^2 \, ha^{-1}$), initial DBH (14.5 cm), and annual rainfall (1478 mm) assumed. 95% confidence intervals for the effect of fire frequency are shown. DBH is diameter at breast height.

quency (Table 1). Using this approach, it was clear that DBH increment was more closely related to fire severity than fire seasonality. The model incorporating mild, moderate and severe fire frequencies was clearly superior to those incorporating early and late fire frequencies, with a probability (w_i) of >0.99 of being the best in the candidate set (Table 1).

Other variables affecting DBH increment

Other than fire frequency, functional group was the only other variable that had a clear relationship with DBH increment. The probability ($w+$) of functional group being in the best model of DBH increment was >0.99 (Fig. 4). Of the functional groups, *Acacia* had the highest modelled DBH increment, followed by evergreen trees and then deciduous trees (Fig. 6). The difference in modelled DBH increment between eucalypts and noneucalypts was very small (Fig. 6).

To evaluate the strength of modelled evidence of differences between functional groups, we undertook

a series of *a posteriori* pairwise comparisons within subsets of functional groups of the entire data set. First, we examined the difference between *Acacia* and non-*Acacia* trees, replacing the original variable 'functional group' with a binary variable expressing a tree's status as *Acacia* or non-*Acacia*, and calculating $w+$ for this variable. The very high value of $w+$ for the *Acacia*/non-*Acacia* variable (>0.99; Table 2) was strong evidence of a difference in DBH increment between *Acacia* and non-*Acacia* trees.

Similarly, we examined the differences between deciduous and evergreen trees, and eucalypts and noneucalypts (Table 2). For this second part of the *a posteriori* analysis, *Acacia* trees were excluded. The very high values of $w+$ for the deciduous vs. evergreen comparisons (>0.99; Table 2) provide strong evidence of a difference in growth increment between deciduous and evergreen trees. The low values of $w+$ for the eucalypt vs. noneucalypt comparisons suggested there was little discernible difference between those groups.

There was limited support for a relationship between DBH increment and plot basal area, with $w+$ of 0.71 (Fig. 4). Values of $w+$ relatively close to 0.5, such as this, reflect substantial model selection uncertainty; that is, the data are insufficient to either confirm or deny a relationship between DBH increment and this variable. There was very little evidence of a relationship between DBH increment and either annual rainfall or initial DBH, with low $w+$ values (<0.5) for these variables (Fig. 4).

We undertook a simple, *a posteriori* analysis to determine whether there was an interaction between initial DBH and fire frequency. We could expect such an interaction because small trees may be more severely affected by fires than large trees. We compared the most highly ranked model from the main analysis, with similar models incorporating interactions between initial DBH and each of mild, moderate and severe fire frequencies. All combinations of the three interaction variables (i.e. initial DBH × mild fire frequency, initial DBH × moderate fire frequency, initial DBH × severe fire frequency) were examined (i.e. $2^3 = 8$ models), such that an importance value ($w+$) could be calculated for each. All three importance values were relatively low: 0.43 for the interaction with mild fires; 0.70 for that with moderate fires; and 0.67 for that with severe fires, suggesting there is little evidence of an interaction between initial DBH and fire frequency.

The effect of fire frequency on NPP of savanna trees

The modelled reductions in DBH increment in response to the highest observed frequencies of mild, moderate and severe fires (0.05, 0.08 and $0.13 \, cm \, yr^{-1}$,

Table 1 Results of an *a posteriori* analysis of the importance of fire severity and fire seasonality as predictors of DBH increment

Model	AIC_c	Δ_i	w_i
Group + basal area + mild fires + moderate fires + severe fires	−6794.8	0.0	>0.99
Group + basal area + early fires + late fires	−6753.3	41.5	0.00
Group + basal area + early fires	−6744.0	50.8	0.00
Group + basal area + late fires	−6741.7	53.2	0.00
Group + basal area	−6738.4	56.4	0.00

Δ_i is the difference between a model's AIC_c value and the minimum value in the candidate set. w_i is the probability of a model being best in the candidate set.

DBH, diameter at breast height; AIC, Akaike's Information Criterion.

respectively; Fig. 5a) suggested a reduction in tree NPP of 0.19, 0.32 and 0.51 t C ha^{-1} yr^{-1}, respectively (Fig. 7).

Discussion

We have clearly demonstrated that frequent moderate and severe fires substantially reduce tree growth rates across a large expanse of mesic savanna in northern Australia. It is likely that this reduction in growth is a direct result of canopy damage caused by fire, with moderate and severe fires resulting in partial and complete canopy scorch, respectively. Such a relationship between growth rate and canopy damage is well supported by the recent literature, with savanna trees shown to experience a period of lost productivity and substantial carbon and nutrient costs associated with rebuilding the canopy following defoliation by fire (Beringer *et al.*, 2003; Cernusak *et al.*, 2006). The magni-
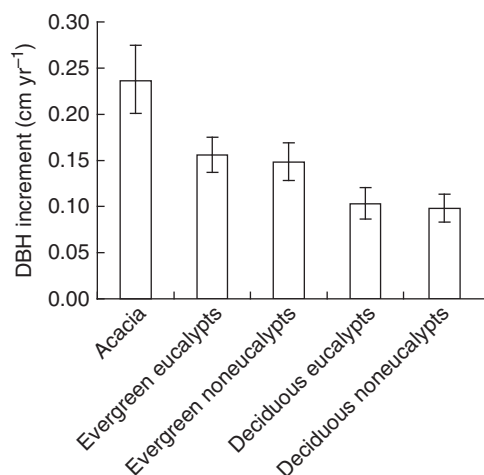
tude of the effect of frequent severe fires on tree growth is similar to that reported by Prior *et al.* (2006). Analysing data from the Kapalga fire experiment in Kakadu National Park, they found that annual late dry season fires reduced DBH increments by 0.22 cm yr^{-1}, relative to trees in unburnt areas. Those imposed fires tended to be very severe, averaging 7.7 MW m^{-1}, and while our dataset contained no plots that were subject to severe fires on an annual basis, extrapolating beyond the range of our data suggests that DBH increments would be reduced to zero under a regime of annual severe fires, a reduction of 0.20 cm yr^{-1}, relative to trees in unburnt areas. Hoffmann (2002) also reported a similar reduction in DBH increment in the year following a fire of unspecified severity in a Brazilian savanna (0.23–0.25 cm yr^{-1}).

Werner (2005) and Prior *et al.* (2006) reported that while late dry season fires substantially reduced adult tree growth at Kapalga, early dry season fires had a slight positive effect. They suggested that this may be due to reduced competition from grasses, release of nutrients from burnt biomass, or both. Indeed, Werner *et al.* (2006) have demonstrated that the removal of surrounding vegetation by clipping increases growth rates of juvenile trees. However, we found little evi-

Fig. 6 The modelled effect of tree functional group on DBH increment, based on multimodel averaging of all candidate models. Mean values for basal area (8.4 m^2 ha^{-1}), initial DBH (14.5 cm), annual rainfall (1478 mm), and mild, moderate and severe fire frequency (0.34, 0.13 and 0.04 fires yr^{-1}) are assumed. Standard errors associated with each functional group are shown. DBH, diameter at breast height.

Table 2 Results of six *a posteriori* analyses of differences in DBH increment between functional groups

Functional group comparison	$w+$
Acacia vs. non-*Acacia*	>0.99
Deciduous vs. evergreen (*Acacia* excluded)	
All species	>0.99
Eucalypts only	>0.99
Noneucalypts only	>0.99
Eucalypt vs. noneucalypt (*Acacia* excluded)	
Deciduous only	0.27
Evergreen only	0.28

$w+$ for 'functional group' is shown for each analysis, and can be interpreted as the probability of there being a difference between the two groups examined.
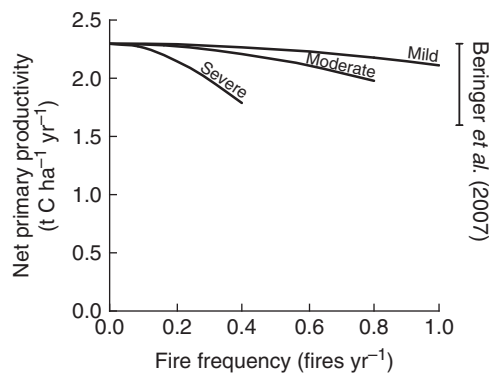
DBH, diameter at breast height.

Fig. 7 Estimated net primary productivity (NPP) of trees subject to varying fire frequencies. The reduction in NPP due to annual moderate-severe fires ($0.7 \, t \, C \, ha^{-1} \, yr^{-1}$), estimated by Beringer *et al.* (2007), is indicated by the vertical bar.

dence that mild or early season fires had a positive effect on tree growth; in fact, our data suggest that both early fires and mild fires had a clear negative effect on tree growth (Fig. 5). Reasons for the discrepancy between our results and those from Kapalga remain unclear, particularly as the early dry season fires at Kapalga had relatively high fire-line intensities, typically $2.1 \, MW \, m^{-1}$, whereas most (79%) of the early fires in our study were mild (equivalent to $<1 \, MW \, m^{-1}$).

Our results clearly suggest that tree growth is more closely related to fire severity than fire seasonality. Models of DBH increment incorporating measures of fire severity (i.e. frequency of mild, moderate and severe fires) were overwhelmingly superior to models incorporating measures of fire seasonality (i.e. frequency of early and late fires). This is consistent with the suspected mechanism for the relationship between severe fire frequency and tree growth; that is, fires of greater severity scorch the canopy to a greater extent. In the earlier studies of Werner (2005) and Prior *et al.* (2006), fire severity and seasonality were confounded, such that these authors were unable to gauge the relative importance of these factors. The intermediate magnitude of the effects of early and late fire frequencies, relative to mild and severe fire frequencies (Fig. 5) may simply reflect the imperfect relationship between severity and seasonality; some severe fires occur in the early dry season and some mild fires occur in the late dry season. However, it is important to note that direct effects of fire seasonality on tree growth cannot be ruled out. While the effects of fire seasonality on savanna tree demography, independent of fire severity, are not well known, Prior *et al.* (2006) did find that early fires had a much greater negative effect on the growth of juvenile trees, though not saplings or adults, than did late fires. They suggest that juveniles are still actively storing carbohydrates during the early dry season, preparing for subsequent growth at the onset of the wet season, and early fires interrupt this process to a greater extent than late fires.

Our finding that *Acacia* trees have substantially higher growth rates than other trees is consistent with previous findings (e.g. Prior *et al.*, 2004) and can be easily explained by their life history. In northern Australian savannas, *Acacia* tree species tend to be relatively fire-sensitive (Williams *et al.*, 1999), and high growth rates would increase the chance of reaching maturity between fires of sufficient intensity to kill the tree. Furthermore, the ability of many *Acacia* species to fix atmospheric nitrogen would ensure their growth is not limited by the availability of this otherwise scarce nutrient (Schmidt *et al.*, 1998).

Our finding that evergreen trees have higher growth rates than deciduous trees is an effect that, to the best of our knowledge, has not been reported previously. A simple explanation is that mature evergreen trees are able to maintain relatively constant rates of transpiration and photosynthesis throughout the year, including the dry season when deciduous trees shed their leaves and transpiration and photosynthesis virtually cease. Eamus *et al.* (2002) suggest that evergreen trees are able to do this by developing a large root system, typically two to three times larger than deciduous trees of similar DBH. Janos *et al.* (2008) also suggest that evergreen trees are able to extract water via deep roots throughout the dry season. It is therefore likely that evergreen trees have a longer growing season than deciduous trees. While the high growth rates of evergreen trees may contribute to their anomalously high abundance in Australian savannas (Bowman & Prior, 2005), the similarity in growth rates between eucalypt and noneucalypt species, despite the high abundance of eucalypts in these savannas, suggests that other factors, such as mortality, may also be critically important for determining the relative abundances of the functional groups.

Tree size may partly explain differences in growth rate between some of the functional groups. While the fastest growing group, *Acacia*, was also the smallest (mean DBH: 10.2 cm), there appeared to be some positive concordance between growth rate and tree size among the other groups. Specifically, the faster growing evergreen trees tended to be larger than the slower growing deciduous trees (mean DBH: 19.2 cm for evergreen eucalypts; 14.1 cm for evergreen noneucalypts; 14.3 cm for deciduous eucalypts; 11.8 cm for deciduous noneucalypts). However, in general we found little evidence of a relationship between DBH increment and initial DBH, and this result is not inconsistent with previous studies from elsewhere in the seasonal tropics, where reported relationships have been highly variable

(e.g. positive: Pélissier & Pascal, 2000; neutral: Clark & Clark, 1999; negative: Namaalwa *et al.*, 2005). Even within the Northern Territory's mesic savannas, the relationship has been reported as positive (Werner, 2005; Prior *et al.*, 2006), neutral (Prior *et al.*, 2004; Werner *et al.*, 2008) and negative (Prior *et al.*, 2007). While Prior *et al.* (2006) did find a positive relationship, they concluded that the general relationship between DBH increment and initial DBH in the seasonal tropics was inconsistent and weak.

Similarly, our finding of no clear relationship between DBH increment and plot basal area is in contrast to the negative relationship reported by Prior *et al.* (2006) at Kapalga. The findings of Prior *et al.* (2006) suggest that competition is greater in plots with high basal area, resulting in lower growth rates. While such relationships may hold true in a spatially restricted, relatively homogeneous setting, such as Kapalga, it is unlikely to hold true across a much wider geographic range, encompassing a much broader range of environmental conditions, such as in our study. Such discrepancies between our results and those of previous studies (e.g. Werner, 2005; Prior *et al.*, 2006) probably highlights the limitations of our study design; it is probably unsuitable for detecting more subtle effects, such as those of tree size and competition.

Implications

The negative relationship between the frequency of moderate and severe fires and tree growth has important implications for the carbon sequestration potential of northern Australian savannas. Under current management regimes, typified by frequent, late dry season fires (Russell-Smith *et al.*, 1997; Edwards *et al.*, 2001), it is assumed that these areas represent a weak carbon sink (Williams *et al.*, 2004; Cook *et al.*, 2005; Beringer *et al.*, 2007), although in the long-term, infrequent large-scale disturbances such as tropical cyclones may result in these areas being carbon neutral, or even a carbon source (Cook & Goyens, 2008). It has been suggested that by decreasing the frequency of fires in savannas, especially severe fires, losses of carbon to the atmosphere can be substantially reduced, thereby increasing the strength of the carbon sink (in Australia: Williams *et al.*, 2004; South America: San José *et al.*, 1998; globally: Grace *et al.*, 2006).

Discussions about using fire management to increase carbon sequestration by savannas have typically only considered the direct effects of fire on sequestration, namely losses of carbon to the atmosphere through combustion (Williams *et al.*, 2004; Cook *et al.*, 2005). More recently however, some attention has been given to indirect effects of fire, such as canopy damage and subsequent reductions in the NPP of surviving trees (Beringer *et al.*, 2007). Our results clearly suggest that frequent fires may have substantial indirect negative effects on carbon sequestration due to their effect on the NPP of trees, even without considering the negative effects of fire on stem and tree survival (Williams *et al.*, 1999; Cook *et al.*, 2005). The reduction in DBH increment that we have found to be associated with a regime of frequent mild, moderate or severe fires (1.0, 0.8 or 0.4 fires yr^{-1}, respectively) is likely to accompany a reduction in NPP (and hence NBP) of 0.2, 0.3 or 0.5 $t\,C\,ha^{-1}\,yr^{-1}$, respectively (Fig. 7). These results are in strong agreement with the recent findings of Beringer *et al.* (2007). Working at a site in mesic savanna near Darwin (Fig. 1), they estimated that fires reduced NPP of trees by 0.7 $t\,C\,ha^{-1}\,yr^{-1}$, although the fire regime at their study site was particularly severe, with either moderate or severe fires occurring annually. However, the magnitude of this reduction in NPP is generally consistent with the reduction in NPP we have observed (Fig. 7).

Reductions in NPP by 0.3–0.5 $t\,C\,ha^{-1}\,yr^{-1}$ accompanying frequent moderate or severe fires are relatively large and of an order of magnitude similar to the direct losses of carbon through combustion. For example, Beringer *et al.* (2007) suggest that around 1.6 $t\,C\,ha^{-1}$ would be lost through combustion during a late dry season fire in mesic savanna near Darwin, and annualizing their figure according to fire frequencies of 0.4–0.8 fires yr^{-1} suggests that combustion losses amount to around 0.6–1.3 $t\,C\,ha^{-1}\,yr^{-1}$ at these fire frequencies. Therefore, the reduction in tree NPP associated with frequent moderate or severe fires may be equivalent to between 25% and 85% of the direct losses of carbon to the atmosphere through combustion. This suggests that appropriate fire management has the potential to increase the carbon sequestration potential of these landscapes to a greater extent than previously thought, especially in currently unmanaged areas that experience very frequent moderate and severe fires. Carbon sequestration is likely to be maximized by a management regime that makes extensive use of strategic early dry season burning, with fires deliberately lit at times of mild fire weather, and in parts of the landscape where burnt areas will be most effective as firebreaks. Such burning is likely to reduce the occurrence of large late dry season fires, that are typically severe, while having little negative impact on tree productivity (Werner, 2005; Prior *et al.*, 2006; this study). It is important to note that several authors have raised concerns that high frequencies of early dry season fires may also have negative long-term consequences for both savanna tree populations (Prior *et al.*, 2006) and fauna (Andersen *et al.*, 2005), so maximizing the effectiveness of early dry

season burning, and, hence, minimizing its extent, should also be an objective of savanna fire management.

A negative relationship between severe fire frequency and tree growth may have important consequences for the size and structure of tree populations in savannas. The most obvious consequence is that reduced growth rates will increase the time required for trees to escape the 'fire-trap' (i.e. reach sufficient size to survive fires), hence accentuating the negative impact of frequent severe fires on tree populations. Several authors have pointed out that knowledge of tree growth rates are critically important to predicting savanna tree demography (Higgins *et al.*, 2000; Liedloff & Cook, 2007), yet mechanistic demographic models do not currently assume that growth rates are affected by fires (e.g. Higgins *et al.*, 2000; Holdo, 2007; Liedloff & Cook, 2007). For this reason, such models may underestimate the detrimental long-term effects of frequent moderate and severe fires. It is also important to point out that some authors have argued that average growth rates may be relatively unimportant to tree population dynamics, and it is the growth rates of only the fastest growing individuals that play a crucial role in tree population dynamics (Clark & Clark, 1999; Prior *et al.*, 2006). Resolving the importance of tree growth rates will be a critical step in understanding, and predicting, savanna tree demography.

Conclusion

We have demonstrated that high frequencies of moderate or severe fires substantially reduce tree growth throughout a large area of mesic savanna in northern Australia, and it is likely that this reduction in growth is due directly to the negative effects of canopy damage on productivity. The effects of fire on tree growth have not previously been examined at such a large scale, nor utilizing such a varied, ambient fire regime. Clearly the effects of fire on tree growth need to be taken into account by models of savanna biomass dynamics if the long-term consequences of fire management is to be predicted. A reduction in tree growth by frequent moderate or severe fires implies that NPP will also be reduced, and supports recent reports that the negative indirect effects of savanna fires on the strength of carbon sequestration (e.g. reduction in tree NPP due to canopy damage) are relatively important. Our results suggest that the indirect losses of carbon associated with canopy damage and lost productivity are equivalent to around 25–85% of the direct losses of carbon through combustion. Clearly, both the direct and indirect effects of fire need to be accounted for when predicting the effects of fire management on the strength of carbon sequestration by savannas. These findings lend further support to the notion that the carbon sequestration potential of savannas can be increased by reducing the frequency of severe fires.

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