

Growth of juvenile and sapling trees differs with both fire season and understorey type: Trade-offs and transitions out of the fire trap in an Australian savanna

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Abstract Canopy tree populations in mesic savannas are often bimodal with few saplings but many smaller individuals of indeterminate age that repeatedly suffer topkill and regenerate from underground tissues. Little is known about growth rates or mechanisms that allow subadult trees to reach the canopy. The wooded savannas of northern Australia have high frequencies of dry-season fires. In a 32 400-m² field experiment, 2405 juveniles (<150-cm height) and saplings (150–499 cm) of the eucalypt canopy species were individually marked and measured the year prior to fires set in three different seasons and again at the end of the growing season (without fires) a year later. Trees in unburnt plots served as controls. All fire treatments were repeated in plots dominated by the most common understorey, a native annual grass (sorghum) and in plots dominated by perennial native species; these produce different fuels for fires and competitive regimes for young trees. After early dry-season fires, height growth of larger juveniles and all saplings was significantly enhanced, especially in sorghum. After late dry- or wet-season fires, juvenile trees grew well, but all of the small saplings (150- to 299-cm height) were reduced to ‘juveniles’ and did not recover pre-fire heights but, instead, produced many new basal (coppice) stems. Late, dry-season fires reduced more than 80% of large saplings (300–499 cm) to juvenile size in sorghum, whereas in non-sorghum, 60% of the trees grew to poles (500–999 cm). The results demonstrate that juvenile and sapling growth responses to fire and the probability of subadult trees reaching the canopy are related to fire–understorey interactions, and suggest that the mechanisms include morphological and carbohydrate storage dynamics which vary with tree size and life history stage. The key to successful management of a sustainable woody canopy lies in the understorey.

Key words: *Eucalyptus* population dynamics, fire: effect of fire season, fire–understorey interaction, savanna woodland: tree: height growth, tree: canopy replacement.

INTRODUCTION

Canopy tree species in wooded mesic savannas of the world generally have bimodal population size distributions with very few saplings but a large number of suppressed small trees (usually <1.5 m tall) of indeterminate age (for convenience termed ‘juveniles’), usually with one, but up to several, stem arising from a large underground lignotuber or other storage organ. The distribution reflects a disturbance-mediated bottleneck preventing young trees from reaching the canopy. When the bottleneck is caused by repeated fires, a ‘fire trap’ continually kills or topkills juvenile trees which then recover mainly from underground carbohydrate stores. Saplings often have not yet produced bark sufficiently thick to protect buds and vascular cambium that would allow them to avoid being topkilled by low-intensity fires (cf. references in Lawes

et al. 2011) or avoid being killed outright by high-intensity fires. Furthermore, saplings are too large for their biomass and original heights to be replaced rapidly from below-ground carbohydrate stores.

In effect, young trees of the canopy species in savannas occupy a ‘persistence niche’ (Bond & Midgley 2001) until some window of opportunity allows them to grow through the transition bottleneck and ultimately become mature canopy trees with high resistance to subsequent fires (Hoffmann 1999; Higgins *et al.* 2000; Bond & Midgley 2001; Chidumayo 2004; Hoffmann *et al.* 2009; Wigley *et al.* 2009; Midgley *et al.* 2010; Prior *et al.* 2010).

In spite of the fact that juvenile-tree survival and growth are critical for sustainable canopy tree populations, and even potentially determine savanna physiognomy, little is understood about the extent to which young savanna trees are directly affected by the season in which fire occurs, or other cofactors such as understorey type, herbivory, rainfall or overstorey and other

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mechanisms permitting or enhancing the transition of a young tree to canopy size (Midgley *et al.* 2010).

Mesic savannas are the most frequently burnt biome in the world (Chuvieco *et al.* 2008), and the highest recorded fire frequencies occur in the mesic savannas of tropical north Australia that extend 3000 km from eastern Queensland to western West Australia. In the >200 000-km² wooded savanna in Australia's 'Top End' (north-central region), fires commonly occur 2 out of 3 years at any given location. In World Heritage-listed Kakadu National Park, approximately 55% of the savanna woodlands have been burnt annually since the mid-1980s, mainly as deliberately set management fires (Russell-Smith *et al.* 1997, 2003a; Cook *et al.* 1998). The most common size distribution in populations of savanna canopy species consists of many large trees in the canopy, a dearth of saplings, an abundant ground layer of juvenile trees <1.5 m tall and no demonstrated seed bank (Werner 1986, 2005; Fensham & Bowman 1992; Bowman & Panton 1993; Setterfield 2002; Russell-Smith *et al.* 2003b; Prior *et al.* 2006, 2010; Lehmann *et al.* 2009a; Williams 2009). The juveniles are of indeterminate age with remarkable persistence, surviving year after year in a suppressed state, often regenerating from underground tissues whenever above-ground portions are burned, eaten or damaged, sometimes after a year or more of dormancy below ground (Lacey 1974; Fensham 1990; Wilson *et al.* 1996; Setterfield 2002; Werner *et al.* 2006; Werner & Franklin 2010).

To date, most research studies into the factors that create the transition bottleneck to the canopy in Australian savannas are landscape-scale studies and point increasingly to high fire frequency and/or the seasonal timing of fires as the major cause of transition bottlenecks (Russell-Smith *et al.* 2003b; Prior *et al.* 2006, 2009, 2010; Murphy *et al.* 2009; Lehmann *et al.* 2009a,b). Very little has been reported, however, on interactions between fire and understorey (e.g. Werner & Franklin 2010) or on potential mechanisms such as plant phenology, physiology or morphology (e.g. bark thickness or epicormic structures; Burrows *et al.* 2010; Lawes *et al.* 2011) that might aid our understanding of what prevents, permits or promotes a transition from the juvenile habit to sapling and canopy-sized trees.

I report the results of a large-scale (32 400 m²) field experiment examining the impact of fires set in different seasons and in different understorey types (presence/absence of sorghum) on growth and cloning of 2405 individually marked juvenile and sapling trees of the canopy species. The specific goal was to determine the maximum gain (or loss) in height and stem number of subadult trees of various sizes, as well as the proportional transitions of juvenile and sapling trees to other size categories, after a full growing season following fires and given that the trees did not suffer a repeat burn.

Furthermore, I explored potential mechanisms underlying the responses of subadult trees to fire season and understorey type using known morphological and phenological properties that vary with understorey type, tree size and life history stage. The overall object was to gain insights into the roles of fire timing, grassy understorey and fire-grass interactions in the transition of canopy trees from the juvenile pool, a process which determines the size structure of tree populations and ultimately the physiognomy of savannas.

METHODS

Definitions: juveniles and saplings

Although the terms 'juvenile' and 'sapling' are commonly used in other studies to refer to all subadult individuals of a tree population collectively, it is appropriate for the Australian setting to differentiate within this class because of known differences in behaviour, physiology and phenology of young trees, based on size and/or life history stage (e.g. Prior *et al.* 1997, 2004; Prior & Eamus 2000; Eamus & Prior 2001; Werner *et al.* 2006). The following terms and size categories are used:

- Juveniles: <150 cm tall (single stem most common, but also multi-stem forms; persisting for years at this height; usually seasonal loss of all leaves by mid-dry season)
- Small saplings: 150–299 cm tall (approximately the height at which a single stem has become dominant in a multi-stemmed juvenile; usually growing rapidly in height, water-stressed in the dry season and may be totally leafless by late dry season)
- Large saplings: 300–499 cm tall (evergreen; water-stressed late in dry season)
- Poles: 500–999 cm in height (evergreen; generally not water-stressed in dry season)

Juveniles were further divided into small and large size-classes (<50 cm and 50–149 cm tall respectively) for some analyses.

Background: precipitation and fire seasons

Precipitation in the Top End of the Northern Territory occurs in strong annual cycles with an average of only 16% of the 1290–1580 mm of annual rainfall occurring in the 7-month period from April to November and the remaining 84% in a distinct wet season extending from approximately December to May (Andersen *et al.* 2003) which strongly promotes grass curing and flammability. During the current study, wet-season rainfall was 1357 mm and 1029 mm, and dry-season rainfall was 21 mm and 33 mm in years when experimental fires were applied and trees remeasured respectively.

Three major types of fires are commonly identified in the region (Gill *et al.* 1996; Williams *et al.* 1998; Andersen *et al.* 2003; Russell-Smith *et al.* 2003a; Russell-Smith & Edwards 2006). They are described by recent weather, rather than calendar months, and thus naturally vary in start and duration

from year to year, by up to 10 weeks in extreme years (Taylor & Tulloch 1985). Typical calendar months are indicated in parentheses: early dry-season fires (May to early July); late dry-season fires (September to November); wet-season fires (December to January) only early in the wet season when precipitation may not occur for several days, allowing vegetation to dry sufficiently to carry a fire.

As in most savannas, almost all fires are ground (not canopy) fires although some may attain high intensities, depending on the amount, type and moisture content of fuel. Large fuel loads in these savannas (1–10 tonnes per hectare; Cook *et al.* 1998; Williams *et al.* 1998, 1999, 2003a; Bowman *et al.* 2007) are a consequence of high annual rainfall, absence of large grazing mammals and strong seasonality of rainfall with subsequent annual drying of understorey plants.

Background: understorey vegetation

The main fuel for the northern Australian savannas is a wide-spread and dominant native species of annual grass, *Sorghum brachypodium* Lazarides (formerly *Sorghum intrans* F. Muell. and *Sarga intrans* (F. Muell) Spangler) (Lazarides *et al.* 1991; Spangler 2003), hereafter termed 'sorghum'. Mature plants with mainly single stems form tall (often >1.5–3.0 m), thick stands of up to 200–400 stems per square metre (Andrew & Mott 1983; Watkinson *et al.* 1989) that die back at the end of the wet season, before most other grasses and herbaceous forbs, and crumple into a perched, aerated and easily ignited fuel by the time early dry-season fires begin (Andrew 1986). The seasonal growth of sorghum is determined endogenously and mature plants do not resprout if topkilled by a fire.

Within otherwise dense stands of sorghum, sparse patches of non-sorghum vegetation several metres in diameter are very common and often persistent (Andrew 1986). The non-sorghum understorey (in the absence of introduced African grasses, which occur elsewhere in the savanna) is made up of a mixture of forbs with rosettes and/or one to a few branching stems, small annual grasses and perennial grasses 20–150 cm in height (Werner 2010). These species remain green well into the long dry season, in contrast to the early drying off of the sorghum.

The two types of native understorey produce different fire behaviour and burn patterns (Cook *et al.* 1998; Werner 2010) as well as differences in juvenile-tree mortality in early dry-season fires and in sapling resprouting patterns after late dry-season and wet-season fires (Werner & Franklin 2010). The dominance of a tall single-stemmed annual grass in the Australian savanna landscape contrasts with the perennial tussock grasses that tend to dominate the American or African mesic savannas (e.g. Bond & Van Wilgen 1996).

Study area

The study was located in Kakadu National Park at the Kapalga Research Station (12°34'S, 132°22'E). Descriptions of the geology, climate and vegetation of the region are detailed in Press *et al.* (1995), Wilson *et al.* (1996) and Finlayson and von Oertzen (1996) and of Kapalga in Andersen

et al. (2003). The experiment was established in the southern half of Kapalga where buffalo had been excluded for 6 years after a period of heavy grazing for more than 20 years. Study plots were set up in mid-1988 (year 0) and experimental treatments applied in 1989 (year 1). The monitoring of trees extended from November 1988 (year 0) to November 1990 (year 2). There were no fires the year the experiment was established in 1988, but a high-intensity fire had burnt all study sites in 1987 so there was little previous-year litter on the ground. The study pre-dated the Kapalga fire experiment (Andersen *et al.* 1998, 2003).

Experimental design and plots

The experiment examined the response of juvenile trees to fire seasons (early dry-, late dry-, wet-, none) and to the abundance of sorghum (high, low) in a 4 × 2 design with plot replication. Responses recorded included morphological changes, mortality of main stems (topkill) and mortality of genets immediately after fires (as reported in Werner & Franklin 2010), incremental changes in height and number of stems and transitions to other size categories by the end of the first full growing season following fire the previous year.

Both the early dry-season and late dry-season fire treatments were established in Kapalga Compartment J which is approximately 20 km² in size (map in Andersen *et al.* 1998). For the early dry-season fire treatments, eight plots, each 30 × 30 m, were established for monitoring. Four of these plots were visually dominated by sorghum and four had little or no sorghum. Eight similar plots were established for the late dry-season fire treatment.

For the wet-season fire treatments, 10 plots, each 20 m × 50 m, were established; six were visually dominated by sorghum and four had little or no sorghum. Plots were located in firebreaks adjacent to nearby Compartments E, F, G, H, L and P. For the unburnt comparisons, eight plots, each 20 m × 50 m, were established, four in Compartment C where ground cover was dominated by sorghum and four in Compartment S where there was little or no sorghum.

As nearly as possible, all study sites had similar woody canopy cover, tree species, size distributions of trees, ground-level biomass and topographic positions. For all fire treatments, care was taken to pair the sorghum and non-sorghum plots in close proximity to each other wherever possible. Furthermore, pairs were sited across the perceived gradual topographic gradient so that any differences would not be attributable to location on the gentle slope. Apart from these two criteria, individual sorghum plots were randomly selected first within each of the larger sites. With the exception of the wet-season fire plots, there was some degree of pseudo-replication within single large Kapalga compartments, which was unavoidable due to the sheer size of compartments and fire treatments. One strength of the study was that individuals were measured before application of the treatment (fire), allowing the calculation of relative response, at minimum, if not absolute differences in responses, to the different fires.

Because wet-season fires effectively prevent regrowth of sorghum the following growing season, this fire treatment served as a check on any potential pre-existing site differences relative to initial sorghum abundance, strengthening

the case that any differences in growth of young trees among understorey types were due to the interactions of trees, vegetation and fire, and not due to inherent site differences.

Understorey assessment

In year 0, the projected ground covers (%) of sorghum, all other herbaceous species and woody stems <2 m in height were recorded in each of the 34 study plots, using 20 1-m square subplots for each plot (five randomly placed subplots along four 30-m transects). Details of the abundances of understorey species are reported in Werner (2010) and summarized below.

In sorghum plots, annual sorghum was by far the most abundant species, ranging 40–80% (mean = 70%) projected ground cover, compared to a range of 0–20% (mean = 7%) projected cover of sorghum in non-sorghum plots. Conversely, in non-sorghum plots, the projected ground cover of herbaceous, dicotyledonous species, considered collectively, tended to be greater than that of sorghum plots (means = 22% versus 15% respectively). The forb species were mainly plants with single- or multi-stems and/or basal rosettes including *Mitrasacme* spp., *Stylidium* spp. and *Spermacoce* spp. Annual grasses (excluding sorghum) collectively comprised 11% of total ground cover in either understorey type. Perennial grasses were of lesser importance. *Heteropogon* spp. averaged 8% projected ground cover in sorghum plots and *Alloteropsis semialata* (R. Br) Hitchc. averaged 9% in non-sorghum plots. The projected ground cover of woody stems of shrubs and trees <2 m tall, collectively, was approximately 10% regardless of understorey type. The total projected ground cover of understorey vegetation tended to be greater in sorghum plots (50–85% total cover) than in non-sorghum plots (30–65% total cover) (Werner 2010), although there was very little difference in total biomass (P. A. Werner & J. S. Cusack 1988, unpubl. data). All species were natives to Kakadu National Park (Werner 2010).

Permanent marking of trees and pre-fire measurements (year 0)

Trees were permanently marked early in the 1988 growing season so that the young trees could be relocated after the smallest juveniles became dormant and lost their leaves later in the dry season. Within each plot scheduled to be burnt, juveniles and saplings of the dry-fruited subfamily Lepidospermoideae of Myrtaceae (*Eucalyptus*, *Corymbia*, *Xanthostemon*; hereafter referred to as 'eucalypts' although the term is not normally applied to *Xanthostemon*) were located by walking along 1-m-wide transects, marking all trees until 100 individuals were encountered. Numbered heavy duty aluminium tags were attached to a stem of each of the juveniles and saplings. Furthermore, the positions of all trees <300 cm tall were marked using galvanized steel fence droppers (0.6 m long) to assist in relocating plants that would lose leaves and/or have been burnt to the ground in subsequent fires. In unburnt plots, all trees were so marked for monitoring.

The number of trees marked ranged from 237 to 479 per treatment combination (four fire seasons × two understorey types), totalling 3133 young trees across nine eucalypt canopy species. Ninety-four per cent of the individuals were of just three species: *Eucalyptus tetrodonta*, *Eucalyptus miniata* and *Corymbia porrecta* (totals of 1463, 580 and 893 respectively), with each of these species distributed relatively evenly among the treatment combinations. Adults of these species formed the majority (more than 95%) of the canopy layer. Numbers of individuals of each species for each fire season × understorey treatment are detailed in Werner and Franklin (2010).

The heights and numbers of stems of all marked trees were determined at the end of the 1988 (year 0) growing season, once both juveniles and saplings had lost leaves and/or become dormant in August–September. Multiple stems of individual genets were easily identified and located within a 25-cm radius. The end of the growing season was chosen for pre-fire measurements in order to provide a common calibration point because all trees would have attained their maximum height for the season prior to the setting of fires.

Prescribed fires (year 1)

The wet-season, early dry-season and late dry-season fires were lit in late December 1988, late May 1989 and late September 1989 respectively. They were set using drip cans and multiple ignition spots across a transect upslope of the relevant compartment sections, on a day with little wind. They were set >100 m away from the plots so that the fires were 'fronting' or 'line' fires and behaved in a realistic, natural landscape pattern by the time the fire front arrived at the monitored plots.

After the fires, the heights of charring (dark discolouration of bark) and scorching (withering of leaves due to heat) were assessed along four 30-m transects within each plot. The early dry-season fire was judged as 'low intensity' with char heights of <2 m and scorch heights of <3.5 m above ground level and no scorching of the canopy leaves of the tallest trees, whereas the late dry-season and wet-season fires were judged 'high intensity' producing charred tree trunks at heights of 2–7 m and scorched and/or burnt canopy leaves (Werner 2010). These are commonly accepted criteria of fire severity in these wooded savannas (Gill *et al.* 1996; Williams *et al.* 2003a; Russell-Smith & Edwards 2006).

Details of the burn patterns produced by fire season and understorey are reported in Werner (2010). Essentially, the late dry-season fire and wet-season fires burnt 93–100% of the area of any plot, regardless of understorey type, with a low probability that any juvenile tree would escape being burnt. In contrast, in early-season fires, the total area burnt differed with understorey type, with 95% burnt in sorghum plots versus 53% in non-sorghum plots. Furthermore, in non-sorghum plots, burns were very patchy, producing a fine mosaic of burnt and unburnt areas; 41% of the patches were <50 cm in size and less than 1% were ≥10 m in size (as measured on a 10-cm linear scale; Werner 2010).

Assessments of trees after fires (year 2)

After fires, all individually marked trees were relocated within weeks with the exception of the less than 1% where tag

numbers were missing or obliterated; these trees were classified as 'missing data'. Initial responses (topkill, resprouting and mortality) of trees to the seasonal fires were assessed at time intervals sufficient to determine initial mortality and the mode of recovery of 3133 individual plants and reported by Werner and Franklin (2010).

Half of the original plots of each treatment combination were reassessed for tree growth at the end of a full growing season (year 2) after fires the previous year and without a repeat fire. Plots were selected randomly within each treatment combination. Within each selected plot, all of the originally marked trees were remeasured for height and stem number for a total of 2405 trees.

At the risk of confounding 'length of time since fire' with a true biological response to fire, I chose to err on the side of the biological clock (Streng *et al.* 1993; Midgley *et al.* 2010), calibrating measurements not to the fires per se, but to the juvenile trees' strong annual growth cycle, taking both pre-fire and post-fire measurements at the end of each growing season when the young trees would have accrued maximum resources and been at seasonal maximum heights prior to entering their annual late dry-season senescent period. Thus, a positive value for height increment indicated that the individual plant had regained, and even surpassed, its initial height the following growing season whereas a negative value indicated that the plant had not recovered its initial height, even given the opportunity of a full growing season after experiencing fire.

Data analyses

Because the trees were individually marked and monitored, measurements of growth and calculation of parameters required for population dynamics studies (such as transitions of individual juveniles and small saplings to other size-classes) were direct and explicit. They were not inferred from extended regressions from measurements on mature trees, or from the 'appearance' of trees into larger size categories, a common and logically practical technique in landscape-scale studies (e.g. Prior *et al.* 2010).

In all cases, the analysis of height and number of stems explicitly compared values before fires with the values in year following the set fires, as described above. The height of the tallest stem was used, should a plant have more than one basal stem. Missing data were ignored and not assigned 'zeros' in any calculations. In calculations of growth increments, changes in number of stems and proportional numbers of trees that changed from one size-class to another size-class, only data from living plants with above-ground tissues were used; that is, no zeros due to death or dormancy were used.

No correction for background mortality was made, as it was considered trivial relative to treatment effects. In unburnt control plots, 0–2% of the young trees died per year, which compares favourably to values for unburnt trees in other studies in Kapalga: less than 3% for juvenile trees (Werner *et al.* 2006) and approximately 1% for saplings or mature trees (Werner 1986, 2005; Williams *et al.* 1999, 2003b; Prior *et al.* 2006).

The basic experiment was set up in an orthogonal design, allowing *a priori* statistical tests. A single over-arching

ANOVA was inappropriate, however, given the structure of the data (i.e. general lack of variance homogeneity, including some distributions not amenable to simple mathematical transformation). For analyses, the appropriate highest-order test was used within subsets of data. Two-tailed *t*-tests were used to examine subsets of height increments and an *F*-test, in conjunction with negative exponential regression analysis, was used to examine the relationship of summary data on incremental changes in height and number of stems. Chi-squared tests were used where non-parametric tests were appropriate. Model selection and multi-model inference techniques were developed elsewhere which revealed the relative strengths of various explanatory variables on tree responses (P.A. Werner & L. D. Prior 2011, unpubl. data) but they did not explore biologically important relationships (e.g. trade-offs) presented in this report.

Because the study measured the growth of young trees over the growing season that followed fires set the previous year, without repeat fires, the growth increments may be higher than growth increments in other studies which have used averages of trees growing in repeat annual or biennial fires (e.g. Williams *et al.* 1999; Russell-Smith *et al.* 2003b; Prior *et al.* 2006, 2010). Repeat fires are known to reduce growth, at least of mature trees, in these savannas (Murphy *et al.* 2009).

RESULTS

Height increment

Dry-season fire (early *vs.* late dry season) and understorey type (sorghum *vs.* non-sorghum) significantly affected the growth of small juveniles ($\chi^2 = 4.9005$; $P < 0.05$) and large juveniles ($\chi^2 = 7.9401$; $P < 0.01$).

Small juveniles (<50 cm tall) increased in height in all treatment combinations (Fig. 1). The greatest average height increment was in unburnt sorghum plots, where trees grew significantly faster than in unburnt non-sorghum plots ($t = 1.858$; $P < 0.05$) (Fig. 1). This difference cannot be attributed to inherent site differences responsible for the abundance of sorghum in the first place, judging by the fact that the height increments in wet-season fire plots which removed the previous heavy sorghum were actually the reverse – less in the (former) sorghum plots than in non-sorghum plots (Fig. 1). Following early dry- or late dry-season fires, small juveniles gained height over the previous year, but generally less than those in unburnt sorghum or in wet-season burned non-sorghum plots (Fig. 1).

For large juveniles 50–149 cm tall, understorey type affected height increment. Average height increments were positive after early and late dry-season fires and generally greater than for trees in unburnt plots. The greatest height increment occurred in sorghum plots after early dry-season fires, significantly greater than in non-sorghum plots ($t = 1.969$; $P < 0.05$). After

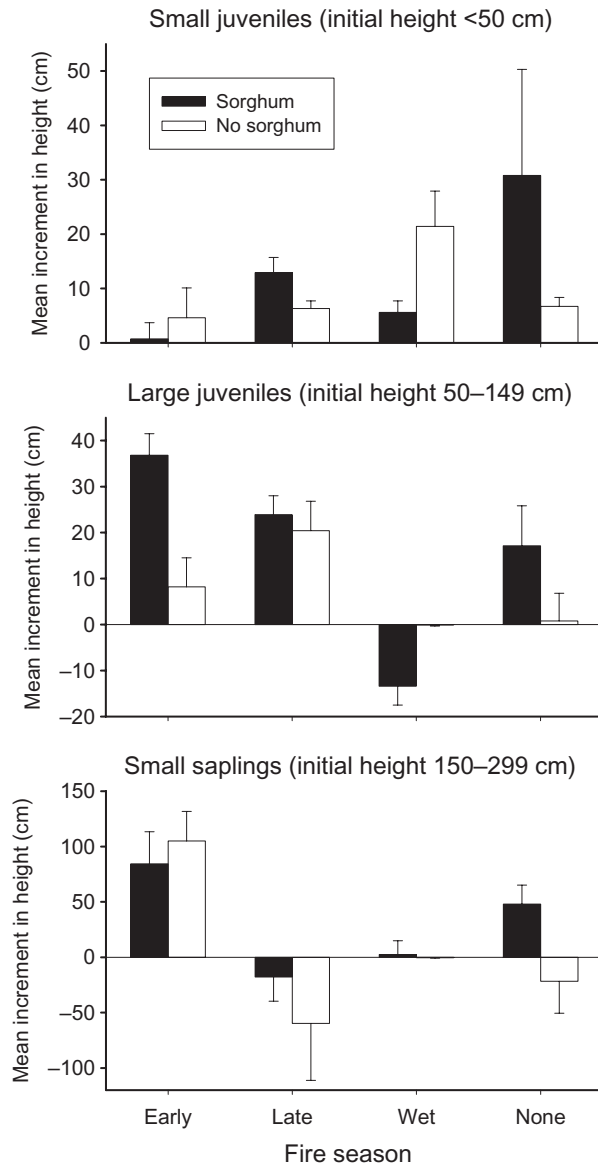


Fig. 1. Mean height increment (cm) of small juveniles, large juveniles and saplings (initial heights of <50 cm, 50–149 cm and 150–299 cm respectively) of eucalyptus trees, collectively, one growing season after fire by seasonal timing of fires and abundance of sorghum. Standard errors are also shown.

wet-season fires, however, large juveniles did not recover pre-fire height. In sorghum, large juveniles lost an average of 13.4 cm in height and in non-sorghum they neither gained nor lost height, similar to results for unburnt large juveniles in non-sorghum, although variances were high (Fig. 1).

For small saplings (150–299 cm tall), height growth was markedly affected by season of fire, regardless of understory type. Whereas early dry-season fire significantly enhanced height growth of small saplings, on average, compared to unburnt small saplings, late dry-

season fire was particularly harmful, producing large negative growth increments, on average (but with large variances) (Fig. 1). In wet-season fires, small saplings neither gained nor lost height, on average; again, variances were high (Fig. 1).

Unfortunately, for large saplings (≥ 300 cm tall) there were too few individuals available for marking within the study plots to estimate the significance of the average height increment for each of the eight fire season \times understory-type treatment combinations. Nevertheless, for the late dry-season fire only, the growth responses differed sufficiently between understory types that further analysis was warranted. In plots with heavy sorghum, all but one (24/25) of the saplings and poles 400–1400 cm tall were reduced to <150 cm in height. Conversely, in non-sorghum vegetation, most trees grew in height after the late dry-season fire and only 20% (3/15) were reduced to juvenile size (Fig. 2). The relationship between pre-fire and 1 year post late dry season fire heights of all saplings and poles combined (150- to 1400-cm initial height) are described by different linear regressions (Fig. 2).

Number of stems

Following fires, 60–100% of the juvenile trees were topkilled and then resprouted from underground tissues, depending on fire season and understory type, whereas in unburnt plots, less than 5% of juveniles died back to ground level (Werner & Franklin 2010). In unburnt sorghum plots, the number of stems per individual small juvenile or small sapling did not change (mean \pm SE = 0.0 ± 0.42 and 0.10 ± 0.28 respectively), although stem numbers of large juveniles increased somewhat (mean \pm SE = 0.81 ± 0.55). In unburnt non-sorghum understory, however, stem numbers per individual declined in all tree size categories (averages ranged from -0.11 to -0.40 , with variances ranging from 0.12 to 0.26).

Among all treatment combinations, the changes in stem numbers per individual tree were not significantly different due to large variances, especially after wet-season fires. Although the average increment was less than two for most treatment combinations, in individual cases the field effect was often dramatic, with up to 15 or more new basal stems (coppice) in the growing season following a late dry-season or wet-season fire, but never with early dry-season fires or in unburnt plots (P. A. Werner 1990, unpubl. data).

Trade-offs: height growth versus coppice

By considering only those plants that had positive responses in growth (an increase in either height or

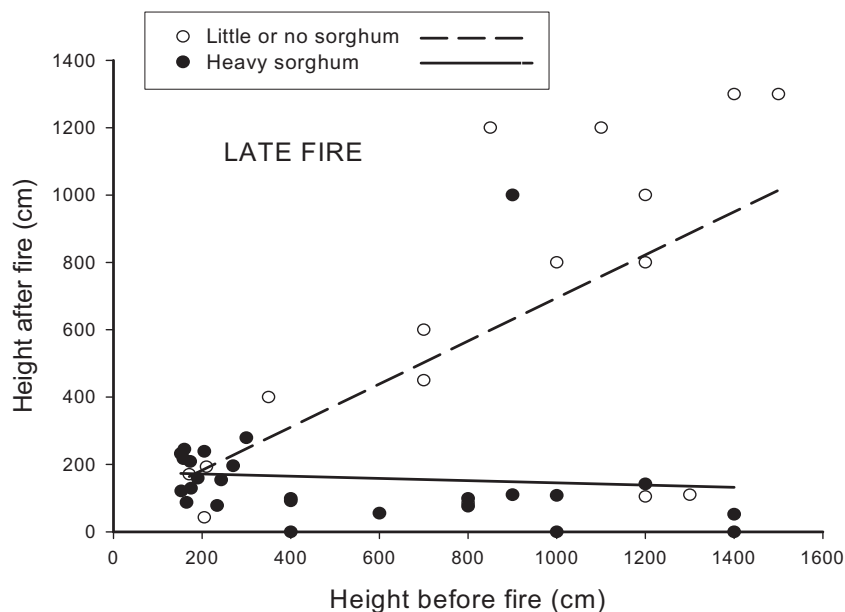


Fig. 2. Height of sapling, pole and mature trees at start of study (x -axis) and at the end of one growing season after a single late dry-season fire (y -axis), in plots with heavy sorghum *versus* plots with little or no sorghum. For trees in non-sorghum plots, height increment is described by $y = 124.6 + 61.6x$, and in sorghum plots by $y = 166.8 - 20.39x$.

number of stems) over the growing season following fires, a pattern emerged suggesting a possible biological trade-off, at least for saplings, between producing new coppiced basal stems (persistence) and growing in height (moving towards canopy), and that these two options varied with treatment combination.

Among saplings, there was a significant negative relationship between the percentage of trees that increased in stem height and the percentage that produced new basal stems (Fig. 3, bottom). Assuming a negative exponential form and a two-parameter model, the regression $y = 84.0658 \times e^{-0.0205x}$ describes the relationship between x , the proportion of plants that increase their number of stems, and y , the proportion of plants that increase in height ($F_{1,6} = 6.83$, $P = 0.04$). The greatest proportion of saplings that increased in height (as opposed to number of stems) was found after early dry-season fire and among unburnt trees. In contrast, the greatest percentage of saplings that increased their number of stems (as opposed to height) was after late dry-season or wet-season fires. Understorey type made little difference, except for late dry-season and wet-season fires; for example, only 23% of saplings growing in sorghum grew in height after suffering a late dry-season fire, but 70% increased their number of stems (Fig. 3, bottom).

Among juvenile trees, the percentage that increased in stem height was not strongly related to the season of fire but the percentage that increased stem number differed with both fire season and abundance of sorghum (Fig. 3, top). For each fire treatment, the percentage of juveniles that increased their number of

stems was greater in the sorghum plots ($P = 0.06$; Fig. 3). The greatest percentage of juveniles producing new stems occurred in sorghum plots after late dry- or wet-season fires, whereas the lowest percentage was in non-sorghum plots after early dry-season fires or when left unburnt (Fig. 3, top).

Transitions among all height classes

In general, the greatest proportion of young trees to make the transition to a larger size-class occurred after early dry-season fire and/or in sorghum understoreys. In sorghum plots, approximately the same proportion (approximately 50%) of juvenile trees remained in their original size-class, or grew to a larger size-class (approximately 20%), in early dry-season fire and unburnt plots. Among large juveniles and small saplings, however, the unburnt trees had a wider range of variation of responses than did the trees exposed to early dry-season fire – as many unburnt trees lost height as gained height (Fig. 4).

In non-sorghum plots, the transition probabilities in early dry-season and unburnt plots also tended to be similar for juvenile trees, but there were vast differences for saplings. After early dry-season fires, more than 50% of saplings grew into the next size category, but more than 40% of the unburnt trees declined in height or died (Fig. 4).

Late dry-season fires were beneficial only to the transition of the smallest juveniles to large-juvenile size. None of the small saplings made the transition to

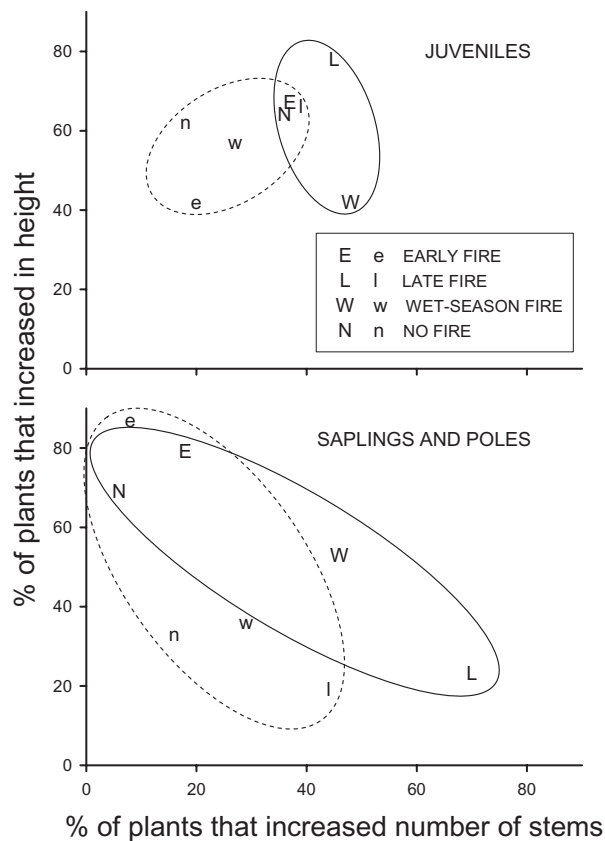


Fig. 3. The percentages of juvenile trees (<150-cm initial height) (top) or saplings and poles (150- to 999-cm initial height) (bottom) that increased in height *versus* increased in number of stems, by seasonal timing of fire and understorey type. Upper case letters = sorghum; lower case letters = non-sorghum. N & n = unburnt plots; E & e = early dry-season fires; L & l = late dry-season fires; W & w = wet-season fires.

larger size-classes in either understorey type (Fig. 4). Of large saplings in non-sorghum plots, more than 50% grew to pole size but, in sorghum plots, nearly all large saplings decreased in size and 10% died (Fig. 4).

Wet-season fires in sorghum tended to hinder juvenile transitions to larger size-classes whereas in non-sorghum, that transition was enhanced (i.e. more than 40% of the juveniles made the transition to larger sizes, compared to approximately 20% for all other treatment combinations). Sapling transitions to larger or smaller size categories were similar to those for unburnt saplings, regardless of understorey types (Fig. 4).

Three critical transitions

Three critical transitions are required for a young tree to become part of the canopy layer. These are described by height, although they also reflect, to a

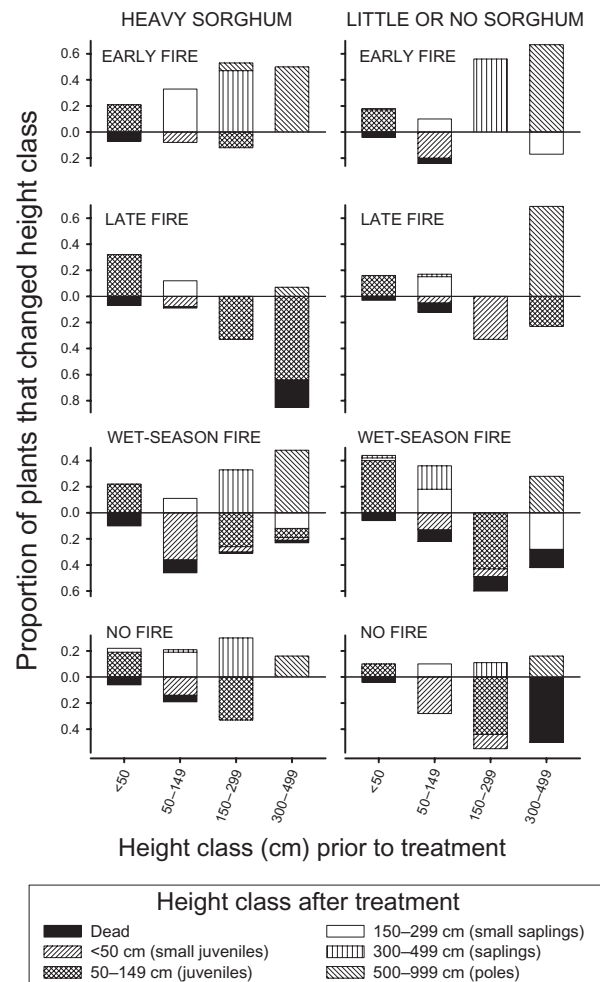


Fig. 4. The proportion of plants that changed height class, comparing pretreatment heights with heights one growing season after a fire. All bars above the 0.0 line show the proportion that transitioned into a larger (taller) height class. All bars below the 0.0 line show the proportion that transitioned into a smaller (shorter) height class. The proportion that remained in the same height class during this period is not shown.

great extent, life history stages which have different physiologies and seasonal phenologies.

1. From juvenile pool to small-sapling size. The proportion of unburnt trees that grew out of the juvenile pool to small-sapling size (3–5%) serves as a baseline for comparisons with experimental treatments (Table 1). After early dry-season fires, the proportion of juveniles that grew out of the juvenile pool was enhanced threefold in sorghum, but not in non-sorghum. Conversely, after late dry-season or wet-season fires, the proportion of juveniles that grew to sapling sizes was enhanced in non-sorghum, but not in sorghum (Table 1).
2. From small-sapling size to large-sapling size. The proportion of unburnt small saplings that grew to

Table 1. Critical transitions

Size-class	% Transition to size-class (or larger)	Fire season	Sorghum understorey	Non-sorghum understorey
Juveniles (<150 cm)	Small saplings (150–299 cm)	Unburnt	5	3
		Early dry	22	6
		Late dry	11	4
Small saplings (150–299 cm)	Large saplings (300–499 cm)	Unburnt	24	10
		Early dry	>50	>50
		Late dry	0	0
Large saplings (300–499 cm)	Poles (500–999 cm)	Unburnt	15	15
		Early dry	45	60
		Late dry	3	60

Comparisons of the percentage of trees of various size-classes that grew sufficiently within one growing season to make the transition to the next larger size-class (or larger) following fires of various season and comparing those located in sorghum *versus* non-sorghum understorey. Furthermore, after late dry-season fires in sorghum, 100% of small saplings were reduced to the juvenile pool, and 10% of large saplings died.

large-sapling height was 24% in sorghum and only 10% in non-sorghum. Early dry-season fires greatly enhanced these proportions, to more than 50%. After late dry-season fires, however, no small saplings made the transition to large-sapling size, regardless of understorey type (Table 1) – in fact, nearly 100% were reduced to juvenile height (Fig. 4).

- From large saplings to poles or greater. When unburnt, only 15% of large saplings made the transition to poles in each understorey type. Early dry-season fires, however, greatly enhanced this proportion regardless of understorey type. By contrast, after late dry-season fires this transition was greatly hindered, but only in sorghum (where only less than 3% grew to larger sizes, more than 60% were reduced to juvenile height and 20% died). In non-sorghum, 60% of the large saplings grew to pole size or larger and none died (Fig. 4; Table 1).

DISCUSSION

Growth, trade-offs and mechanisms

Whereas fires tend to be landscape-scale phenomena, the fate (growth and survival) of an individual tree is always a local phenomenon. In order to gain insights into the mechanisms responsible for the effects of fires on young savanna trees, one has to be aware of both the local environment (Grace & Platt 1995; Menges & Hawkes 1998) and the various attributes of the young trees that determine how they respond to the local environment.

No other published study of fire season effects on northern Australian canopy trees has specified under-

storey type but, as shown here, sorghum and non-sorghum can produce very different outcomes for height growth, coppicing and transition to other size categories, especially for juvenile trees in early dry-season fires and saplings in late dry-season fires. I suggest that these different outcomes are firstly related to the different seasonal growth patterns and morphology of the two types of understorey which affect both fire behaviour (Werner 2010) and the competitive regime experienced by young trees.

That competition pressure on young trees during the dry season is greater in non-sorghum understorey than in sorghum is evidenced by the lower growth rates of juveniles and small saplings in non-sorghum vegetation, as well as the enhanced height growth of large juveniles after early dry-season fires when sorghum is senescent but non-sorghum vegetation is still green. Further evidence comes from the high mortality rates of large saplings in non-sorghum plots when left unburnt (Fig. 4) and of juveniles in non-sorghum plots after early dry-season fires (Werner & Franklin 2010), compared to those trees growing in sorghum.

Juvenile and sapling biology determines, to a great extent, a tree's responses to its local fire environment and competitive regime. Morphological attributes such as total height, bark thickness and meristem (bud) placement are known correlates of tree responses to fire (cf. references in Werner & Franklin 2010; Lawes *et al.* 2011). Physiological responses, such as shifts in carbohydrate or biomass allocation following fires, have been shown to be as important for post-fire recovery of savanna trees in Africa and South America (cf. Schutz *et al.* 2009; references in Werner & Franklin 2010). Unfortunately, little is known about carbohydrate dynamics in Australian savanna trees after fire, but inferences can be drawn from photosynthetic and water use studies of various life history stages of canopy trees,

as well as from the timing of leaf flush, stem growth and seasonal changes in morphology.

For example, mature trees of the two major canopy species, *Eucalyptus tetradonta* and *Eucalyptus miniata*, flush new leaves throughout the year with a major peak in the late dry season as a result of endogenous mechanisms, rather than environmental controls such as soil moisture, and are physiologically active through the entire dry season, avoiding water stress by adjusting leaf area (Williams *et al.* 1997). Juvenile trees, however, have seasonal physiologies different from those of mature trees. Juveniles produce new leaves early in the wet season, increase bark thickness and store carbohydrate underground until mid-dry season when they shed all or nearly all their leaves and become dormant. Furthermore, the smaller the juvenile tree, the earlier it sheds its leaves (P. A. Werner & J. S. Cusack 1988, unpubl. data). Saplings are intermediate between juveniles and mature trees, retaining leaves well into the end of the dry season whereupon they may or may not become leafless. The sapling stage is the only life history stage where water stress has been recorded during the dry season in these eucalypts (Prior *et al.* 1997, 2004; Prior & Eamus 2000; Eamus & Prior 2001).

If an early dry-season fire occurs, juveniles may respond immediately with new above-ground growth but generally they do not recover their original height in the same year (Werner & Franklin 2010; Lawes *et al.* 2011; P. A. Werner 1989, unpubl. data) before losing their leaves in the mid-dry season and flushing new leaves the following wet season. If a late dry-season fire occurs, juveniles are leafless and dormant, and new growth does not begin until the next wet season (P. A. Werner & J. S. Cusack 1989, unpubl. data). Saplings may respond immediately to fires (Werner & Franklin 2010), although after a late dry-season fire, many wait to restore leaves or produce new stems the following wet season (P. A. Werner & J. S. Cusack 1989, unpubl. data). The general vulnerability of the saplings to fire is most likely due firstly to insufficient bark thickness compounded to some degree by water stress, especially in the late dry season.

I suggest that the reason that smallest juveniles grow best, by far, in unburnt sorghum plots is that not only have they avoided having to replace tissues lost to a fire, but there is little competitive pressure from the senescent sorghum during the early dry season. After early dry-season fires, the 'fertilization effect' on growth of large juveniles and small saplings is made possible by sufficient underground carbohydrate stores that allow a rapid response to the release of nutrients and/or reduced competitive pressure. A similar 'fertilization' response after early dry-season fires has been reported for mature trees (Werner 2005; Prior *et al.* 2006; Murphy *et al.* 2009).

Wet-season fires occur just when juveniles are breaking dormancy and have their lowest stores of

carbohydrates. Hence, juveniles are limited in their ability to use sparse carbohydrate stores to rebuild previous leaf area, stem and bark and cannot recover original height entirely in just one growing season. Instead, they produce many coppiced basal stems, each with prolific leaf tissue, a response which, in effect, increases photosynthetic surface and the capacity to replenish underground carbohydrate stores.

Bark thickness in these eucalypts increases with tree height, diameter and distance above the ground but the increases are not linear (Werner & Murphy 2001; Lawes *et al.* 2011). Saplings seemed to have gained bark thick enough to avoid being severely damaged by at least some early dry-season fires, but they do not have bark thick enough to withstand late dry-season fires, especially in sorghum. The reasons why late dry-season fire in non-sorghum does not harm large saplings and poles to the same extent as do fires in sorghum is unknown but most likely is related to differences in bark thickness interacting with fuel properties, fire intensity and/or other behaviour of fire in the two types of understorey.

The trade-off between height growth and production of new coppiced stems by subadult trees is mainly a response to season of fire, not to understorey type. When large juveniles, saplings or poles are burned to the ground in late dry-season fires, they seem to revert to a 'persistence' mode, producing many coppiced basal stems, rather than rebuilding a single taller stem. By way of contrast, after early dry-season fires, the same-sized trees tend to use their 'released' status to build even taller stems, shedding multiple stems and 'reaching' for the canopy. This response is similar to that of small trees in longleaf pine savannas of south-eastern North America, which produce large numbers of resprouts only after late dry-season (dormant-season) fires, attributed to the physiological status of the plants at the time of fires (Drewa *et al.* 2002). Similarly, burnt or cut stems of saplings in African savannas concentrate on coppice regrowth and underground storage for a number of years prior to producing a taller stem (Chidumayo & Frost 1996; Miambo & Mapaire 2006; Gignoux *et al.* 2009 and references therein).

Remarkable persistence in the face of repeated fires is, of itself, an ecological and evolutionary 'dead-end', however. For the individual, it is necessary that there be some transition point where storage of carbohydrate underground is used for height growth, and the timing of this transition is critical. A tree's 'dash for the canopy' begins when a large juvenile simultaneously decreases stem number and rapidly increases the height of one stem in a single growing season (P. A. Werner 1990, unpubl. data), even at the risk of suffering severe water deficits by late dry season as a sapling. The 'bolters' include both 'winners' and 'losers' (Fig. 4) whose fates depend on both their local environments as well as their own abilities to grow bark

thick enough and to place leaves at a height sufficient to meet the challenges of potential competitors and subsequent fires.

Fire traps and sapling bottlenecks

Late dry-season fires keep young potential canopy trees in a 'fire trap', but the height at which the trap operates depends on the understorey type. A very strong bottleneck occurs at a height of 150–299 cm (i.e. the small-sapling size) whenever late dry-season fires occur, but it extends up to 500 cm if the understorey is sorghum. The difference in 'escape height' between sorghum and non-sorghum vegetation is most likely related to differences in fire intensity, fire behaviour and seasonal patterns of curing of the two understorey types. In any case, the bottleneck inhibiting progress of trees towards the canopy is due almost entirely to the very high vulnerability of saplings to late dry-season fires and the failure to recover original height in the year following (and most likely for some years thereafter) topkill.

The bottleneck is not caused in the first instance by the death of juvenile trees, or by failure of juvenile trees to grow into saplings after a late dry-season fire. Although more than 95% of the juveniles are topkilled in late dry-season fires, almost all resprout from underground tissues (Werner & Franklin 2010). Furthermore, as shown here, the average juvenile tree more than recovered its original height with about 20% of juveniles growing into small saplings the year following a late dry-season fire (with the absence of repeat fires).

None of the small saplings in this study made the transition to larger size-classes after the late dry-season fire. This is consistent with the 1% per year and 3% per year (modelled and field data respectively) 'proportional recruitment' reported by Prior *et al.* (2010). The Prior *et al.* (2010) analysis used data from a landscape-scale fire experiment in Kapalga (Andersen *et al.* 2003; Williams *et al.* 2003b), where fires were repeated annually over 5 years, understorey type was not an experimental variable and estimates of 'proportional recruitment' were made by counting the appearance of new saplings 1.5–2.99 m and small adults 3–5 m in height.

Early dry-season fires did not cause a bottleneck to young trees growing towards the canopy in the present study. In fact, after early dry-season fire, about half the saplings of all sizes made the transition to larger size-classes regardless of understorey type, a much greater proportion than for trees growing in unburnt plots. This finding runs counter to that of Prior *et al.* (2010) who reported a bottleneck after early dry-season fires, with only 7% per year (actual field data) and 1% per year (modelled value, described above) 'proportional recruitment' of trees into height category ≥ 300 cm.

The data used for the Prior *et al.* (2010) analysis originated from repeated early dry-season fires which were of unusually high intensity, especially in the first year, perhaps due in part to weather conditions on the day of fire as well as to accumulated fuel over the previous 2 years during which time the site had not been burnt (Williams *et al.* 2003a). Furthermore, the 'ring fire' technique used in that experiment yielded early dry-season fires estimated to have been, on average, of some 2.5–5 times more intense than the 'line ignition' fires used in another long-term study at nearby Munmarlary (Russell-Smith & Edwards 2006), the technique also used in the present study. These differences underscore the fact that fire season alone is not a strict predictor of absolute fire intensity, especially in the early dry season (cf. Williams *et al.* 2003a).

That an early dry-season fire does not necessarily reinforce a 'fire trap' for young canopy trees but indeed can enhance the progress of saplings towards the canopy is a significant finding of this study. Unless fire intensity is unusually high (due to fuel build-up and/or certain fire management practices), an early dry-season fire can provide a more 'open door' to the canopy for these eucalypt species, in contrast to remaining unburnt.

Although, by definition, trees in unburnt plots cannot be caught in a 'fire trap', the results of the current study suggest that many young trees, nevertheless, can be caught in a 'natural sapling bottleneck'. Only very small juveniles grow best in unburnt plots but, on average, large juveniles and small saplings grow more slowly in unburnt plots than trees that have been burnt by early dry-season fire. In fact, the larger the tree, the greater the percentage of 'losers' in unburnt plots, so that eventually, more of the large saplings lose height than gain height and, in non-sorghum vegetation, many die.

This suggests that in unburnt plots, other inhibiting factors operating at a local scale (e.g. underground, understorey and overstorey competition; Fensham 1990; Menaut *et al.* 1990; Fensham & Bowman 1992; Werner *et al.* 2006) become the most important factors determining the probability that any particular individual young eucalypt tree will reach the canopy. Variability in local environments might be expected to be greater in unburnt sites than in burnt sites, as fires tend to 'homogenize' an area. The result would be more variable growth rates (and transition probabilities) in unburnt sites, which is what was found in the present study.

Even given a natural sapling bottleneck in unburnt areas that reduces the percentage of trees making the transition to the canopy compared to that of early dry-season fires, it may be that there are enough absolute 'winners' to replace lost canopy trees. For example, the 15% of large saplings that became poles in a single year in unburnt plots of the present study, or

the 8–14% per year reported by Prior *et al.* (2010; described above) for the appearance of new saplings in unburnt plots, may provide more than enough replacements for lost canopy trees. However, the number (or proportion) of young trees required to pass through the sapling bottleneck to ensure a sustainable canopy is unknown. Furthermore, fire exclusion for an extended time could lead to an increase in competing non-sorghum understorey as sorghum declines (Lazarides *et al.* 1991; Cook *et al.* 1998), as well as an increase in more fire-sensitive tree species (Woinarski *et al.* 2004), ultimately reducing the proportional representation of eucalypts in the canopy.

Implications of understorey type for management

In a mixed-fire regime, where fires occur in any season, a sorghum understorey can be 'mixed blessing' with respect to young trees reaching the canopy. When early dry-season fires occur in sorghum, juvenile trees grow much faster than they do if left unburnt or if growing in non-sorghum, but the relative advantage is entirely lost if a late dry-season fire occurs before they reach pole size (9 m). Furthermore, because late dry-season and wet-season fires encourage coppicing after topkill of main stems, too frequent fires in these seasons also could lead to a 'thickening up' of woody vegetation made up of small (<3 m high), coppiced stems with low probability that the former tall canopy could be recovered and/or maintained. Fortunately, in areas where suppression of the late dry-season fires cannot be guaranteed (and assuming no thick stands of introduced grasses), management can ameliorate the influence of sorghum on canopy recruitment by the judicious use of a wet-season fire (Andrew & Mott 1983; Andrew 1986; Press 1987) and thus producing a local environment more conducive to the survival and growth of trees through the sapling bottleneck.

The key for management to long-term sustainability of the woody canopy in the northern Australian savannas is not only an understanding of the effects of the frequency and season of fires, but also of the dynamics of the understorey. It is vitally important to understand how both landscape and local environmental factors interact with the physiology, morphology and phenology of the early life history stages of the canopy species which collectively influence the long-term sustainability of the savanna canopy.

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