

Resprouting and mortality of juvenile eucalypts in an Australian savanna: impacts of fire season and annual sorghum

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Abstract. In northern Australian savannas, canopy tree species often have juvenile tree banks that are composed mainly of small individuals of indeterminate age that have resprouted repeatedly after fire. Little is known about their demography. We report the initial responses (mortality, topkill and resprouting type) of 3133 marked juvenile eucalypts to set fires of different seasons (early dry season, late dry season, wet season, unburnt) in a 32 400 m² field experiment. Fire treatments were repeated in plots dominated by a native annual grass (sorghum) that becomes senescent before the early dry season and provides the main fuel of savanna fires, and in others with little or no sorghum, but instead other native grasses and forbs that remain green well into the dry season. Most juvenile eucalypts <150 cm high were topkilled but resprouted from underground tissues regardless of fire season or understorey (86–100% vs <5% in unburnt plots). Few saplings 200–500 cm high died or were topkilled, but impacts of fire were harsher in sorghum than in non-sorghum vegetation. The response of eucalypts 150–199 cm high was intermediate, suggesting a ‘tactical’ transition from suppressed persistence to growth toward maturity. Counter-intuitively, genet death of juvenile trees was >22% in the low-intensity early dry season fire in plots with little or no annual sorghum, compared with <2% in all other fire/understorey combinations. We suggest results are related to fire behaviour, seasonal carbohydrate storage dynamics and competition with ground-layer plants.

Introduction

In the world’s savannas, resprouting of individual trees after disturbance is a major mechanism of persistence of tree populations (Abrahamson 1984; Olson and Platt 1995; Hoffmann 1998, 1999; Menges and Hawkes 1998; Bond and Midgley 2001; Drewa *et al.* 2002; Hoffmann and Moreira 2002; Hoffmann and Solbrig 2003; Werner *et al.* 2006; Nefabas and Gambiza 2007; Hoffmann *et al.* 2009; Franklin *et al.* 2010; Midgley *et al.* 2010). The high fire frequencies of savannas select for trees that resprout from stems or underground tissues. Indeed, fire is generally recognised as a primary ecological determinant of the physiognomy of the world’s savannas, as well as the population dynamics of their constituent species (e.g. references in Bond and van Wilgen 1996; Scholes and Archer 1997; Hoffmann 1999; Higgins *et al.* 2000; Hoffmann and Moreira 2002; Miranda *et al.* 2002; Hoffmann and Solbrig 2003; Sankaran *et al.* 2004; Bond 2008; Lehmann *et al.* 2009a; Williams 2009; Midgley *et al.* 2010).

Studies of tree population size structures or of fire frequency and woody cover in northern Australian savannas have suggested that frequent fire is the fundamental cause of bottlenecks in the replacement of canopy trees (Werner 1986; Russell-Smith *et al.* 2003a; Werner *et al.* 2006; Lehmann *et al.* 2009a, 2009b; Williams 2009; Prior *et al.* in press), but little is known about potential mechanisms that might produce such bottlenecks. The >200 000 km² wooded savanna of Australia’s Top End (north central region) has a very strong cycle of

precipitation where an average of only 16% of the 1290–1580 mm annual precipitation falls in the 7-month period from April to November and the remaining 84% in a distinct wet season from approximately December to May (Andersen *et al.* 2003). These savannas are considered mesic with a relatively dense (typically >60% projected ground cover) canopy of trees 15–25 m height and a sparse shrub or small tree mid-layer. The savanna also experiences a very high frequency of fire, often occurring two years out of three, or even annually, at any given location (Russell-Smith *et al.* 1997, 2003b; Cook *et al.* 1998). Since the mid-1980s, ~55% of the savanna woodlands in World Heritage Kakadu National Park have been burnt annually, mainly as deliberately set, management fires, with a shift toward a relatively greater area of ground burnt by early dry season fire compared with late dry season fire (Russell-Smith *et al.* 1997, 2003b). Little is known about the impact of fires set at different seasons on juvenile stages of the canopy tree species.

Few, if any, of the canopy tree species in Australian savannas have been demonstrated to have seed banks (Setterfield 2002), but juvenile tree banks are very common (Werner *et al.* 2006). Such banks are composed mainly of suppressed plants <150 cm tall and of indeterminate age (for convenience, termed ‘juveniles’) that have survived for years in a suppressed state, most often as resprouts that have emerged from underground tissues whenever aboveground portions are burned, eaten or damaged. These suppressed juveniles can be composed of one to several stems arising from a large underground lignotuber. If left unburnt

or uneaten, one stem will eventually become dominant, usually after several years (Werner *et al.* 2006), which then will grow rapidly in height, called hereafter 'saplings', similar to the 'gullivars' in African savannas (Bond and van Wilgen 1996). The juvenile tree banks and subsequent bolting saplings form the potential source of recruits of adults into the canopy layer.

The main fuel for the northern Australian savanna fires is a 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), commonly called spear grass or simply 'annual sorghum'. These grasses have single stems, often >2 m height, which become senescent late in the wet season, forming into a dry, perched, aerated and easily ignited fuel before the start of the dry season. Sparse patches of sorghum several metres in diameter are very common in otherwise dense stands (Andrew 1986). Because this annual grass lacks a persistent seed bank (Andrew and Mott 1983), if a population is eliminated (e.g., by an early wet season fire that destroys seedlings), the species will not recolonise for at least 4–5 years (Andrew 1986; Press 1987; Miles 2003). In the absence of sorghum (or introduced African grasses), the understorey is a mixture of forbs with rosettes and/or single to a few branching stems, small annual grasses and perennial grasses 20–150 cm in height that remain green well into the long dry season (Williams *et al.* 2003). Although it is known that the burn patterns of fires are different in the two types of understorey (Werner 2010), there have been no reports of potential impacts of understorey type on juvenile canopy trees.

Young savanna trees are known to recover from topkill caused by fire much better than do mesic forest trees in other savannas (Hoffmann *et al.* 2009; Williams 2009), but whether they resprout from underground tissues and/or suffer aboveground damage and resprout from stems is generally unquantified. Further, in all of the world's savannas, little is understood about the extent to which responses might differ with season of fire, or other co-factors such as rainfall, herbivory or understorey type, that would permit or enhance the transition of a young tree to canopy size (Midgley *et al.* 2010).

We report on a large-scale (32 400 m²) field experiment examining the role of fire season and understorey type on juvenile tree dynamics in a northern Australian savanna. Specifically, we present the initial responses (topkill, resprouting, genet death) of juvenile and sapling trees of canopy species to the seasonal timing of fire (early dry season, late dry season, wet season and unburnt) and two understorey types (annual sorghum vs little or no sorghum). More than 3100 juvenile trees were individually marked and measured before fires and reassessed post-fire.

Although conceptually, the term 'juvenile' is often used to refer to any individual of a tree population that has not yet made the transition to canopy height, for purposes of analyses and discussion, we use the term 'juveniles' for all trees initially <150 cm in height (because multi-stem forms persist for years to approximately this height before a single stem becomes dominant); 'small saplings' for trees initially 150–199 cm in height (approximate heights when a single stem has become dominant), and 'large saplings' for trees initially 200–500 cm in

height. Juveniles were further divided into 50-cm height classes for some analyses. The aim of our study was to examine post-fire morphological responses and demography of juvenile trees of canopy species in order to better understand the relative roles of fire season and grass abundance in determining juvenile tree dynamics.

Methods

Background: fire seasons

Three major types of fires are commonly identified in the Top End of the Northern Territory (Gill *et al.* 1996; Williams *et al.* 1998; Andersen *et al.* 2003; Russell-Smith *et al.* 2003b; Russell-Smith and Edwards 2006). The seasons are defined relative to 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 and Tulloch 1986). Typical calendar months are May–July for early dry season fires, September–November for late dry season fires and December–January for wet season fires when rains do not occur every day, permitting vegetation to dry sufficiently to carry a fire.

- Early dry season fires: generally slow-moving, trunk-scorching, ground fires of low intensity, almost entirely set by humans, both historically by Aboriginal peoples and today by a wide range of land managers;
- Late dry season fires: generally rapidly moving, canopy-scorching fires of high intensity as a consequence of greater leaf litter, drier fuels and more severe fire weather, mainly human-set but also caused by lightning; and
- Wet season fires: during early wet season when precipitation may not fall over a span of several days, allowing vegetation to dry; generally rapidly moving fires of high intensity but may be of lower intensity than those of the late dry season, depending on fuel, weather and the amount of recent rainfall. These fires are rare, sometimes started by lightning but more often by humans for management purposes.

As in many savannas, almost all fires are ground (not canopy) fires although some may attain high intensities, depending on the amount, type and moisture content of grassy fuel. Large fuel loads (1–6 tonnes ha⁻¹; Cook *et al.* 1998; Williams *et al.* 1998, 1999; Werner *et al.* 2006; Bowman *et al.* 2007) are a consequence of high annual rainfall and strong seasonality of rainfall with subsequent annual drying of understorey plants.

Study area

The study was conducted in 1988–1989 in Kakadu National Park (KNP) 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 Williams *et al.* (2003) and Andersen *et al.* (2003). The experiment was set up in the southern half of Kapalga where buffalo had been excluded for 6 years after a period of heavy grazing for some 30 years previously. 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. All study sites had similar woody canopy cover and size

structure of mature trees. The study pre-dated, and was not part of, the Kapalga fire experiment (Andersen *et al.* 2003).

Experimental design and plots

The experiment examined the initial response of juvenile trees to four fire seasons (early dry, late dry, wet, none) and to the abundance of sorghum (heavy, little or none) in a 4×2 design with plot replication. Responses included death of genet (entire individual), topkill (death of stems) and type of resprouting.

Both early dry season and late dry season fire treatments were set up in Compartment J which is $\sim 20 \text{ km}^2$ in size (see map of Kapalga in Andersen *et al.* 1998). For the early dry season fire treatments, eight different plots, each $30 \times 30 \text{ m}$ (total area 7200 m^2) were identified for monitoring. Four selected plots were visually dominated by sorghum (hereafter 'sorghum plots' or 'heavy sorghum') and four other selected plots had no or little sorghum (hereafter 'plots with little or no sorghum'). Similarly, for the late dry season fire treatment, eight other plots were identified, each $30 \times 30 \text{ m}$ (total area 7200 m^2), four visually dominated by sorghum and four with little or no sorghum.

For wet season fire treatments, 10 plots, each $20 \times 50 \text{ m}$ (total area $10\,000 \text{ m}^2$), were established; six were visually dominated by sorghum and four had little or no sorghum. Plots were located outside Kapalga compartments but adjacent to Compartments E, F, G, H, L and P. For the unburnt comparisons, eight plots, each $20 \times 50 \text{ m}$ (total area 8000 m^2), were set up, half in Compartment C where ground cover was dominated by sorghum and half in Compartment S where there was little or no sorghum. For all fire treatments, care was taken to pair the sorghum and little or no sorghum plots were in close proximity to each other wherever possible. Further, pairs were sited across the perceived gradual topographic gradient so that any differences would not be attributable to location on the gentle slope.

Understorey vegetation

The projective ground cover (%) of sorghum, all other herbaceous species and woody stems $< 2 \text{ m}$ high were recorded in each of the 34 study plots in the early dry season of 1988 before the first fire treatment, using 20 m^2 subplots within each plot (five randomly placed subplots along four 30-m transects). Details are reported in Werner (2010) and summarised below.

All species were natives; there were no exotic plants in the study plots (Werner 2010). In sorghum plots, annual sorghum was by far the most abundant species, ranging from 40–80% (mean = 70%) projected ground cover, compared to a range of 0–20% (mean = 7%) projected cover of sorghum in little to no sorghum plots. Conversely, the projective ground cover of herbaceous dicotyledonous species, considered collectively, tended to be greater in plots with little or no sorghum compared with plots dominated by sorghum; means = 15% versus 22%, respectively. These forb species were mainly plants with single or multi-stems and/or basal rosettes, including *Mitrasacme* spp., *Stylidium* spp. and *Spermacoce* spp.

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 plots

with little to no sorghum, but all other perennial grasses collectively, including *Chrysopogon* spp. and *Mnesithea rottboeljhoides* (R.Br.) de Konig & Sosef., were $< 3\%$. Annual grasses (excluding sorghum) collectively registered 11% of total ground cover in either type sorghum plots; these included *Pseudopogonatherium contortum* (Brongn.) A. Camus, *Panicum mindanaense* Merr., *Setaria apiculata* (Schribn. & Merr.) K. Schum. and *Thaumatocloa major* (S. T. Blake). Overall, the total ground cover of vegetation tended to be greater in sorghum plots (50–85% total cover) compared with plots with little or no sorghum (30–65% total cover). The projective ground cover of woody stems of shrubs and trees $< 2 \text{ m}$ in height, collectively, was 10% regardless of understorey type (Werner 2010).

Permanent marking of trees and initial measurements

The permanent marking of trees occurred during the 1988 growing season so that the young trees could be located with confidence, even after the smallest juveniles became dormant and lost their leaves later in the dry season. Within each plot that was to be burnt, young trees ($\leq 500 \text{ cm}$ high) of the dry-fruited sub-family Leptospermoideae 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 juveniles ($< 150 \text{ cm}$ high) were encountered. All juveniles $< 150 \text{ cm}$ in height and saplings up to 300 cm in height were marked using galvanised steel fence droppers (0.6 m long) and numbered heavy-duty aluminium tags, to assist in relocating stems that had lost leaves and/or been burnt to the ground. Trees $\geq 300 \text{ cm}$ in height and 5 cm in diameter at breast height (dbh) were marked only with heavy-duty aluminium tags. In the unburnt plots, all trees were marked for monitoring.

The number of trees marked and measured ranged from 237–479 per treatment combination across the eight ($4 \text{ fire} \times 2 \text{ sorghum}$) treatments (Table 1), totalling 3133 young trees across nine eucalypt canopy species. Of these, 94% were of just three species: *Eucalyptus tetradonta* (stringybark), *E. miniata* (woolybutt) and *Corymbia porrecta* (Table 1).

The height and number of stems of all marked trees were determined at the end of the growing season, once both juveniles and saplings had lost leaves and/or become dormant in August–September. Wherever there were multi-stemmed trees, the height of the tallest stem was deemed to be the height of the tree. Multiple stems of individual genets were easily identified as individuals were widely distributed from each other with coppiced stems of an individual tree within a 20 cm radius. The end of the growing season was chosen for pre-fire measurements in order to provide a common calibration point, since all trees would have attained their maximum height for the year's growing season before the setting of fires.

Prescribed fires

The wet season fire, early dry season, and late dry season fires were lit in late December 1988, late May 1989 and late September 1989, respectively. The fires were set using drip cans and multiple ignition spots across a transect upslope of the

Table 1. Species and number of young trees marked in heavy sorghum plots (S) and plots with little or no sorghum (NS) in each fire treatment

Species names	Season of fire								Total per species
	Early dry		Late dry		Wet		No fire		
	S	NS	S	NS	S	NS	S	NS	
<i>Eucalyptus tetradonta</i> F. Muell.	265	133	231	120	174	128	186	226	1463
<i>Corymbia porrecta</i> (ST Blake)	97	193	97	167	113	45	77	104	893
K.D. Hill and L.A.S. Johnson									
<i>E. miniata</i> A.Cunn. ex Schauer	32	74	149	70	125	63	25	42	580
<i>Xanthostemon paradoxus</i> F. Muell.					3	1	86	35	125
<i>C. bleeseri</i> (Blakely) K.D Hill and L.A.S. Johnson	4		2	7	25		2		40
^A <i>C. polysiada</i> (F.Muell.) K.D. Hill and L.A.S. Johnson				13			1		14
<i>C. confertiflora</i> (F.Muell.) K.D Hill and L.A.S. Johnson				5	2				7
<i>C. foelscheana</i> (F.Muell.) K.D Hill and L.A.S. Johnson				3	2				5
<i>E. tectifera</i> F.Muell.					3				3
<i>Eucalyptus</i> unknown	1						2		3
Total number	399	400	479	385	447	237	379	407	3133

^Aformerly *Eucalyptus clavigera* Cunn. ex Schauer.

relevant compartment sections, on a day with little wind. They were set more than 100 m away from the plots so that whereas the fires were set as ‘fronting’ fires, they behaved in a more realistic, natural landscape pattern by the time they 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 season fire was judged as ‘low intensity’ with char heights <2 m and scorch heights <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 leaf canopies. These are commonly accepted criteria of fire severity in these wooded savannas (Gill *et al.* 1987, 1996; Williams *et al.* 2003; Russell-Smith and Edwards 2006).

The late dry season fire created a ‘scorched earth’ regardless of understorey type, with little probability that any juvenile tree would escape being burnt (Werner 2010). Similarly, in the wet season fire plots, grass abundance made little difference as to

whether juvenile trees experienced fire (99% and 93% were burnt in heavy sorghum vs plots with little or no sorghum, respectively). In both these fires, almost all sizes of burnt areas were ≥30 m in size (Werner 2010). Alternatively, early season fire produced patchy burns (on a 10-cm linear scale), resulting in a mosaic of both large and small areas of burnt and unburnt vegetation, but with differences between understorey types (Werner 2010). Overall, the percentage of total area burnt was 95% in sorghum plots versus 53% in plots with little or no sorghum. Moreover, in sorghum plots, the patches were larger, with more than half of the patches ≥10 m (linear scale) and only a third <3 m in size, in contrast to plots with little or no sorghum where only <1% of the patches were ≥10 m in size and 41% were <50 cm in size (Werner 2010).

Assessments of trees after fires

Two to three months following any fire, a time interval considered sufficient to determine the fate of individuals, each young tree was assessed for microsite (burnt/not burnt) and tree condition (Table 2). New stems emerging from the ground occurred within 15 cm of the old stem and were considered resprouts.

Table 2. Relationship between condition of plant and its microhabitat recorded in the field and the response classes used in the analyses

Microsite condition	Tree condition	Response class
Not burned	Alive or dead or dormant	Unaffected by fire
Not burned	New stems from below ground (main stem unaffected)	Sprouting from lignotuber
Burned	Main stem shows no sign of fire damage; little or no resprouting	Unaffected by fire
Burned	Leaves and/or main stem scorched and/or charred; new growth from above ground only	Resprouting from stem
Burned	Leaves and/or main stem scorched and/or charred; new growth from both above and below ground	Resprouting from stem and lignotuber
Burned	Main stem dead (topkill), new growth from both below ground only	Resprouting from lignotuber
Burned	Stems present but dead (topkill); no living tissue above ground	Dead or dormant
Burned	No part of plant was found above ground, dead or alive	Dead or dormant
Missing tag or cannot locate plant	For time 1, plant died between initial pegging and first measurement. For time 2, cannot find peg or no name on tag.	Missing data

They originated from lignotubers (P.A. Werner and J.S. Cusack, pers. obs.).

The length of time between the fire and the second assessment varied with fire treatment because these eucalypts generally grow new tissues only when there is sufficient soil moisture. At the risk of confounding 'length-of-time-since-fire' (cf. Streng *et al.* 1993; Midgley *et al.* 2010) with a true biological (morphological) response to the fire, we chose to err on the side of the biological clock, and assessed the initial response of the juvenile trees to fires as soon as the dominant herbaceous plants were judged to have recovered from the fire, using them as a 'marker' of soil moisture and potential site productivity. Trees in unburnt plots were assessed 1 year following the initial measurement in order to obtain an estimate of annual topkill and mortality without fire, for comparative purposes.

The condition of the trees varied greatly when remeasured; we identified nine conditions as well as two microsite types (burnt and not burnt) (Table 2). Here, we have condensed these to five response categories (Table 2). Approximately 1% of the individual tree markers could not be relocated or else the tag number was obliterated and the relevant trees were classified as 'missing data'. Plants showing total destruction of stem(s) (topkill) were classified as either 'dead' (only if obvious) or 'dead or dormant' if they failed to produce new stems (Table 2). This was done because it is known that young juvenile trees can become dormant for a year or more (Werner *et al.* 2006). Of the 'dead or dormant' trees, only a small proportion emerged from the ground after a second full growing season (P.A. Werner, unpubl. data) and were then reclassified as having resprouted from underground tissues. Missing data (<1% of trees) were ignored and not assigned 'zeros' in any calculations.

Results

Topkill and resprouting

Overwhelmingly, juveniles <150 cm in height were topkilled by fire and resprouted only from underground tissues (60–100%; Fig. 1). In the unburnt plots, <5% of the juvenile stems died back to ground level.

In late dry season and wet season fires, >97% of juveniles <150 cm in height were topkilled regardless of understorey type. This is in contrast to the impact of early dry season fire where overall, ~80% of juveniles were reduced to ground level, with differences depending on both tree size and understorey type. In sorghum plots, 10–20% of trees resprouted from existing stems and in plots with little or no sorghum, ~24% of the trees died (described below) (Fig. 1).

Of the small saplings (150–199 cm high), >97% were topkilled and resprouted from lignotubers after the late dry season fire, as did >85% after wet season fire, regardless of understorey type. Early dry season fire was less harsh overall, but impacts on trees differed greatly with sorghum abundance: in sorghum plots, 70% of the small saplings were topkilled and resprouted from lignotubers compared with only 40% in plots with little or no sorghum, with the remainder of the trees either unaffected or resprouting from existing stems (Fig. 1).

No large saplings (200–500 cm high) were left unaffected by late dry season fire, and almost all resprouted from existing stems and/or lignotubers. An exception was in sorghum plots, where 6% of the large saplings died (see below). In wet season fire, ~12% were unaffected and 86% resprouted from existing stems and/or lignotubers; none died. Early dry season fire was less harsh overall, but understorey type made a difference: in sorghum plots, only 22% of large saplings were unaffected by the fire, 50% resprouted only from existing stems and the remainder resprouted from lignotubers, in contrast to large saplings in plots with little or no sorghum where 70% were unaffected by fire and 30% resprouted from existing stems and/or lignotubers (Fig. 1).

Mortality

Early dry season fire in plots with little or no sorghum killed outright >20% of the juveniles (<150 cm high); another 10% were deemed either dead or dormant at the end of the study (Fig. 1). The proportion of deaths were related to size of juvenile: e.g., for juveniles <50 cm, 50–99 cm, and 100–149 cm in height, 26%, 22% and 19% juveniles died, with an additional 14%, 7% and 5% 'dead or dormant', respectively (Fig. 2). In contrast, <2% of the juvenile trees died in sorghum plots with early dry season fire, a similar death rate to the 0–3% after fires in other seasons regardless of understorey type. Confirmed deaths of juveniles in unburnt plots was <2% (Fig. 2).

Late dry season fire in sorghum plots killed 6% of large saplings (200–500 cm high), but none in plots with little to no sorghum. No large saplings died in early dry season or wet season fires, and <1% died in unburnt plots.

Discussion

The massive topkill of juvenile trees and resprouting after fire of any season is consistent with casual observations by field researchers but which was not documented previously in eucalypt savanna woodlands. The persistent juvenile tree banks of these eucalypts are similar to those of tree species in other mesic savannas of South America or Africa where intervals between disturbance are also very short (e.g., Hoffmann 1998, 1999; Menges and Hawkes 1998; Bond and Midgley 2001; Hoffmann and Solbrig 2003; Chidumayo 2004; Hoffmann *et al.* 2009; Wigley *et al.* 2009). They are prime examples of species occupying a 'persistence niche' (Bond and Midgley 2001).

Mechanism(s) that allow young savanna trees to survive and resprout include anatomical features and growth form (cf. Miambo and Mapaure 2006; Midgley *et al.* 2010). The fact that juvenile (<150 cm high) eucalypts were nearly always burnt to the ground and then resprouted would indicate that they had not achieved sufficient bark to avoid being topkilled but generally had sufficient underground carbohydrate stores to produce new stems. Juvenile eucalypt trees burnt in late dry and wet season fires most likely used stored underground reserves to support respiration and build aboveground tissues which in turn functioned to replenish reserves, as has been demonstrated by tissue assays and isotope tracking in the coppiced stems (<100 cm height) of the canopy tree *Acacia*

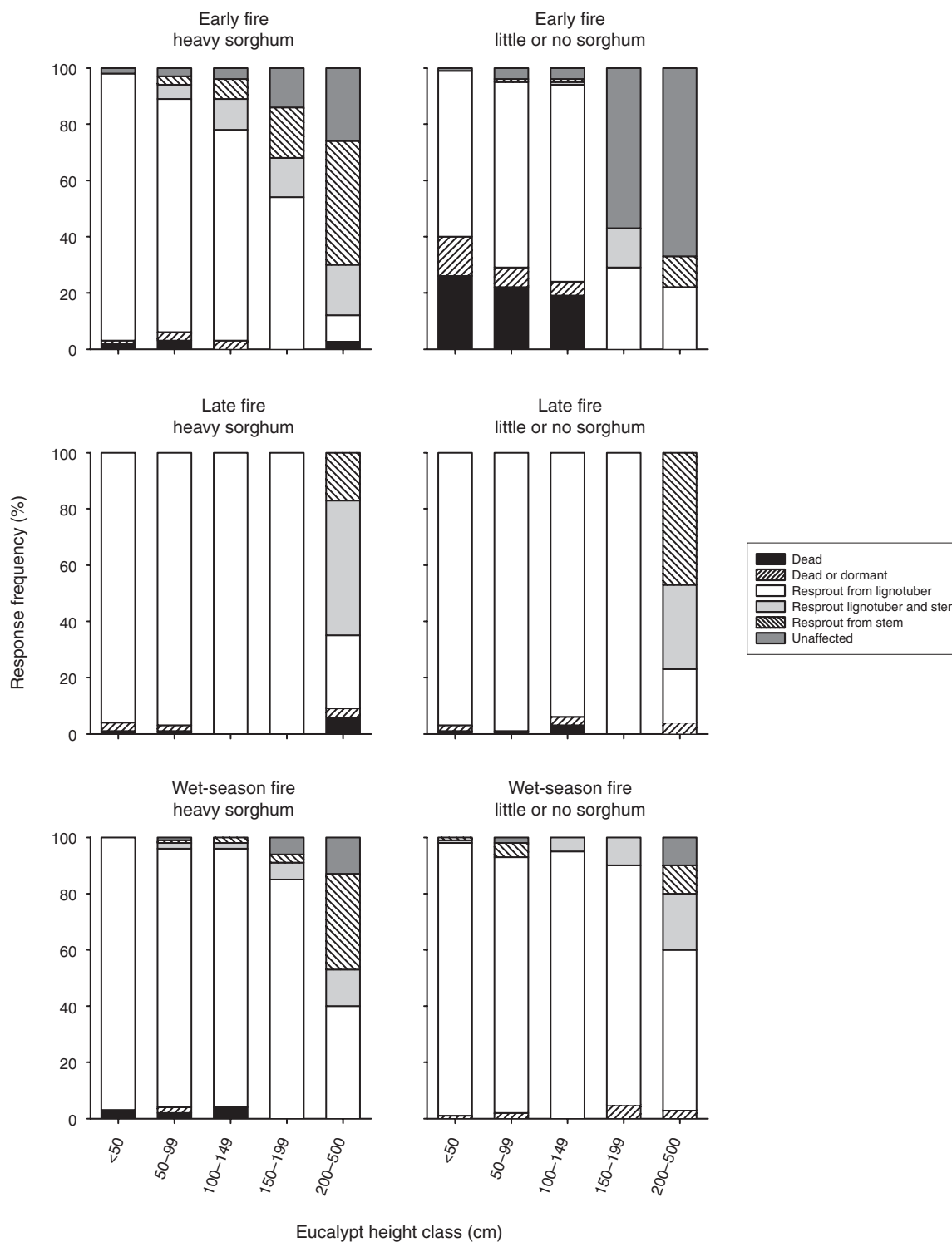


Fig. 1. Initial responses of young eucalypts (<500 cm high) of various height classes to fires at different seasons and abundance of sorghum.

karoo Hayne (adults 12 m height) following late dry season fire in the drier savanna of Hluhluwe-iMfolozi Park in South Africa (average precipitation of 780 mm per annum) (Schutz *et al.* 2009; Wigley *et al.* 2009). An important exception to resprouting by juvenile eucalypts is the >20% deaths of genets

(entire individuals) following early dry season fire in plots with little or no sorghum; discussed below).

Small saplings (150–199 cm high) generally withstood early late season fire but did not do well in late dry season or wet season fires. They responded to the less intense early dry season

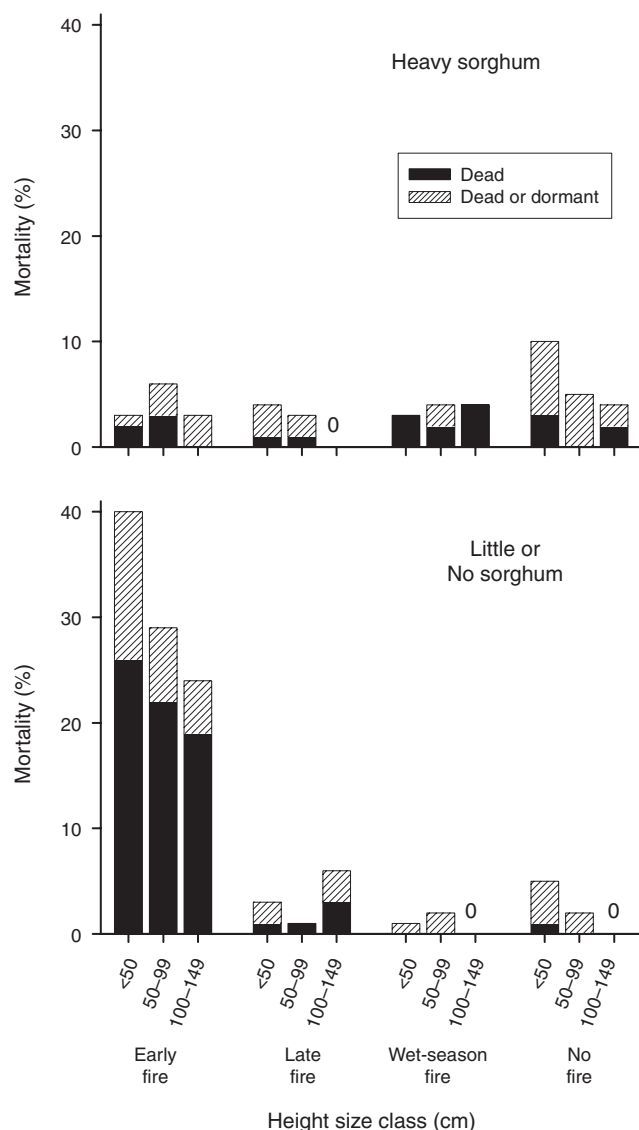


Fig. 2. Initial mortality of those juvenile eucalypts by height class, season of fire and abundance of sorghum. Mortality of unburnt trees over 1 year is included for comparison.

fire much like large saplings – that is, bark thickness and carbohydrate stores were sufficient for the tree to be unaffected or to resprout from existing stems or lignotubers. However, in late dry season and wet season fires, small saplings responded much like the larger juveniles (100–149 cm high), being topkilled with subsequent resprouting from lignotubers, indicating that they had not yet attained sufficient bark thickness to withstand these more intense fires.

The fact that the majority of large saplings (200–500 cm high) were unaffected or resprouted from existing stems in early dry season fire reflects the acquisition of thicker bark with age (McArthur 1968). However, in late dry season fire, ~22% of the large saplings were topkilled and resprouted only from lignotubers, indicating that the thickness of bark was not yet sufficient to protect these trees after particularly intense fire. In

general, for saplings both the degree of impact and the type of restoration depended on the season of fire or type of understorey.

Although bark thickness of juveniles (<150 cm high) of these eucalypt species has not been measured, bark thickness of large saplings of two of the species has been reported. In saplings of 5–10 cm diameter (>200 cm high), bark averaged <10 mm and <4 mm for *E. tetradonta* and *E. miniata*, respectively, at <2 m above the ground (Werner and Murphy 2001). Furthermore, the bark of *E. miniata* was twice as thick again in trees 10–20 cm in diameter, although in *E. tetradonta* further thickening of bark did not occur until the trees reached 20 cm diameter (Werner and Murphy 2001). Interestingly, these values for Australian eucalypts are far less than the 18 mm threshold for bark thickness necessary for trees in seasonally dry forest in Bolivia to withstand lethal cambial temperatures during low intensity fires (Pinard and Huffman 1997).

Small eucalypt trees allocate a great deal of biomass to underground tissues (Werner and Murphy 2001), producing lignotubers that allow them to produce new shoots from stored carbohydrates (Lacey 1974). This characteristic is similar to trees in Brazilian savannas where Hoffmann *et al.* (2003) showed that it is the greater allocation of total biomass to underground tissues by savanna trees, and not carbohydrate concentration, that confers a greater capacity to persist under a high fire regime compared with forest trees. Underground stores of carbohydrate and shifts in biomass allocation following fires also have been demonstrated as important to post-fire recovery by resprouting in species also in Africa (e.g., Bowen and Pate 1993; Verdaguer and Ojeda 2002; Schutz *et al.* 2009; Wigley *et al.* 2009) but little is known about underground carbohydrate dynamics in Australian savannas and their roles in resprouting and/or response to fire.

The seasonality of carbohydrate storage and its interaction with the timing of fire can play a critical role in responses of young savanna trees to any disturbance that removes biomass (Bowen and Pate 1993; Chidumayo and Frost 1996; Drewa *et al.* 2002; Miambo and Mapaura 2006). This may be particularly true for trees in the Australian wet-dry tropics where, as Williams *et al.* (1997) have suggested, the mechanisms underlying patterns of physiology relative to leaf phenology are largely endogenous. The eucalypt species in this study are classified as evergreen or semi-deciduous based on their adult habit (Williams *et al.* 2003). However, juveniles (<150 cm high) are all seasonally leafless, losing their leaves in the mid- to late dry season, with the smallest juveniles becoming leafless earlier than the larger ones (P. Werner and J. Cusack, unpubl. data). During the following wet season, the juveniles have produced new leaves and begin storing new carbohydrate, but if fire occurs early in the new dry season and destroys all aboveground tissues, the trees may not have yet stored sufficient carbohydrate to resprout new stems and leaves and therefore they die. Indeed, we proffer that this is the reason that early dry season fire in our study was able to kill ~22% of the juveniles (<150 cm high), with highest mortality rates in the very smallest size class (<50 cm high) in plots with little or no sorghum, even though early dry season fires are, in general, of lower intensity than late dry or wet season fires.

That the deaths of these juvenile trees in early season fires occurred in plots with little or no sorghum, not in the

sorghum that provides the main fuel of these savannas, is an important finding. Previously, a field experiment in Kapalga had demonstrated that herbaceous vegetation *per se* had a negative effect on juvenile tree survival and dormancy (Werner *et al.* 2006), but the present study indicates there is also a difference between understorey types.

The phenologies of growth of the two understorey types differ greatly, and this in turn affects both fire behaviour and competitive regime of the young trees. By the early dry season, the non-sorghum understorey is still green and physiologically active (P.A. Werner and J.S. Cusack, unpubl. data) in contrast to the annual sorghum which has already set seed and died, producing a very flammable aerated fuel (Andrew 1986; Lazarides *et al.* 1991). Sorghum grass fires are relatively fast-moving in either early or late dry season, whereas in plots with little or no sorghum, early dry season fires are usually very slow-moving and produce patchy burns (on a 10-cm scale; Werner 2010). The longer residence times in the greener vegetation of non-sorghum plots may contribute to the death of juvenile eucalypts. Further, by remaining green well into the dry season, the non-sorghum understorey most likely creates a higher competitive regime during this time, causing delayed or lower annual carbohydrate storage by the juvenile trees, compared with those trees growing in the senescent sorghum which would be released from competition by the time the early dry season fire occurred. The suggestion that sorghum provides a less competitive environment for juvenile trees is further supported by experimental evidence that juvenile trees grow relatively faster in the presence of annual sorghum (P. A. Werner, unpubl. data.).

Given that stems of the large saplings (200–500 cm high) generally survived fires (either being unaffected entirely or resprouting from existing stems or from lignotubers, depending on the timing of fire and understorey type), the 6% deaths in late dry season fire in sorghum plots is a somewhat unexpected result. The saplings may be particularly vulnerable to late dry season fire due to the fact that, unlike smaller juveniles that become dormant, they retain their leaves well into the dry season and exhibit water stress, unlike either juveniles or adult eucalypts (Prior *et al.* 1997; Eamus *et al.* 1999; Eamus and Prior 2001). Further, judging from percentage of topkill, they also have insufficient bark thickness to withstand the damaging temperatures of a sorghum-fueled, late dry season fire.

Resprouting of young trees, no matter how successful, will not sustain a eucalypt canopy. Individuals must be able to grow tall enough to escape loss of foliage and buds in the 'fire zone', and acquire bark thick enough to prevent loss of stems. Height and stem growth must be 'traded' against storage of carbohydrate underground, and the tactical timing of this transition doubtless reflects fire histories and past selection pressures. Our study shows that eucalypts >200 cm in height have generally acquired the necessary resources to survive being topkilled when burnt, but that responses to the season of fire depend on whether annual sorghum or other herbaceous plants dominates the understorey. A combination of early dry season fire and little or no sorghum understorey, while producing a 22% mortality of the smallest trees in our study, burnt only 53% of the ground (Werner 2010). Unburnt patches provide the

necessary 'windows of escape' required for juveniles and saplings to use scarce resources to build larger carbohydrate reserves, to develop bark thick enough to withstand subsequent fires without being topkilled, and to grow in height, eventually to reach canopy level.

The implications of the interaction of season of fire and understorey type for population dynamics of canopy trees and for physiognomy of savannas, as well as the mechanisms relating to phenology of growth, carbohydrate stores, threshold bark thicknesses and threshold heights, warrant further investigation.

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