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Tree recruitment dynamics in fire-prone eucalypt savanna

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Abstract. Savanna sites are idealized as exhibiting a demographic "bottleneck" physiognomy comprising a lower stratum of abundant resprouting persistent "juveniles" (albeit of indeterminate age), a mid-stratum comprising relatively few released "saplings," and a canopy-layer cohort of "adults." The magnitude and frequency of disturbance is considered to influence the critical transition from juvenile into adult phases. Under fire-prone Australian savanna conditions, an extensive suite of both observational and manipulative studies have explored the responses of tree recruitment to fire disturbances. These studies oftentimes have produced seemingly highly disparate responses, particularly with respect to the differential responses of relatively fast-growing eucalypts versus non-eucalypts under different fire regime, and overstory competition, conditions. This study contrasts the responses of tree recruitment height classes to (1) the effects of total canopy removal from severe Cyclone Monica in 2006 over a subsequent 10-yr period, (2) with observations from long-term monitoring sites under relatively stable overstory conditions at Litchfield National Park over a six-year period, (3) under ambient, frequent fire occurrence (mean > 0.5 fires/yr) at both locales including relatively severe late dry season fires. Recruitment at both study sites was represented mostly by resprouting, clonally reproducing juvenile trees <2 m tall, around half of which died over respective assessment periods. At post-cyclone assessment plots, there was substantial release of eucalypts, including within the first five years, into the >5 m height class, with negligible corresponding release of non-eucalypts. At Litchfield plots, there was negligible release of both eucalypts and non-eucalypts. In discussion, we contrast these results with findings from relevant regional studies. We contend that collective disparate observations feasibly can be reconciled as reflecting significant interactions between fire regime characteristics and variable site overstory competition effects, such that the rate of recruitment of fast-growing savanna eucalypt individuals into the midstory is relatively independent of the fire regime, but is significantly regulated by resource competition interactions especially with the overstory, whereas recruitment of non-eucalypts is relatively independent of overstory competitive effects, but is suppressed under fire regimes dominated by frequent, especially severe fires.

Key words: Australia; canopy competition; cyclone disturbance; density dependence; eucalypt; fire disturbance; fire regime; juveniles; recruitment dynamics; resprouts; saplings; savanna.

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INTRODUCTION

Interactions between site productivity and grass and woody species competition, disturbances such as herbivory, trampling by large animals, recurrent fire, and infrequent severe wind events exert significant impacts on woody species demographic processes in savanna systems. Individual savanna sites typically are idealized as exhibiting a demographic "bottleneck" physiognomy comprising a lower stratum of abundant resprouting persistent "juveniles" (albeit of indeterminate age), a mid-stratum comprising few released "saplings" or "sub-adults," and a canopy-layer cohort of "adults" that may be more numerous than sub-adults. The magnitude and frequency of disturbance influences especially the critical transition from juvenile into adult phases (Bond and van Wilgen 1996, Scholes and Archer 1997, Higgins et al. 2000, 2007, Bond and Midgley 2001, Hoffmann and Solbrig 2003, Lehmann et al. 2009, Midgley et al. 2010, Prior et al. 2010, Bond et al. 2012, Werner and Prior 2013). At broader landscape scales, however, savanna tree populations may exhibit regionally stable structures despite significant variability in individual stands (Lehmann et al. 2009).

Most Australian studies of savanna vegetation dynamics have focused on fire regimes as a critical disturbance process given the absence of large native grazers or browsers. Key studies have included observations derived from (1) experimental manipulative fire treatments undertaken at Munmarlary (Hoare et al. 1980, Bowman et al. 1988, Russell-Smith et al. 2003) and Kapalga (Williams et al. 1998, 1999, 2003, Prior et al. 2006, Werner and Franklin 2010, Werner 2012, Werner and Prior 2013), both sites in present-day Kakadu National Park; (2) non-manipulative studies addressing structural changes mostly over decadal scales (Fensham and Bowman 1992, Woinarski et al. 2004, Lehmann et al. 2008, 2009, Prior et al. 2009, Murphy et al. 2010, Russell-Smith et al. 2010); and (3) investigations of the relative importance of bark thickness for survival of juvenile and sub-adult stems (Lawes et al. 2011*a*, *b*).

Studies of interactions between fire regimes and large introduced herbivores on savanna woody dynamics have included effects of (1) browsers, especially Asian water buffalo (Werner 2005, Werner et al. 2006, Petty et al. 2007), and (2) domestic cattle (Cowley et al. 2014). Studies of the effects of cyclonic or more localized tornado events on stand structure and resprouting processes have included Wilson and Bowman (1987), Bowman and Panton (1994), Franklin et al. (2010), and Hutley et al. (2013). All the above studies, with one exception (Cowley et al. 2014), were undertaken in mesic savanna (>1000 mm mean annual rainfall [MAR]; sensu Williams et al. 2017) on typically infertile (e.g., skeletal, sandy) to, less commonly, moderately fertile (loamy) substrates.

Responses of juvenile trees

The observed responses of juvenile trees to fire regime components (frequency, seasonality, intensity) have often varied between different regional studies, especially the effects of experimental treatments versus ambient observational studies.

The first long-term experimental study, conducted at the Munmarlary site in present-day Kakadu National Park between 1973 and 1996, found that under low (<1000 kW/m)-to-moderate (<2500 kW/m) intensity frequent burning, woody vegetation dominated by mature eucalypts was structurally stable, whereas in the absence of burning for at least five years, there was release of the non-eucalypt, woody component into the midstory (Russell-Smith et al. 2003). No treatment effects (annual early dry season fires; annual late dry season fires; biennial early dry season fires; unburnt) were observed in the population responses of juvenile (<2 m tall) and midstory (2–8 m tall) eucalypts—supporting findings from an experimental canopy removal study reported by Fensham and Bowman (1992) that mature eucalypt root competition plays a significant role in suppressing smaller eucalypt size classes. The competitive effects of mature overstories on the densities of recruiting size classes are widely documented in other Australian mesic savanna studies (Prior et al. 2006, 2009, 2010, Lehmann et al. 2009, Werner and Prior 2013).

The generality of the above findings is supported also by a study comparing fire exclusion over 23 yr with a contiguous mostly annually burnt site, in structurally intact savanna (Woinarski et al. 2004). Hence, while there was a fourfold increase in stem density (mostly attributable to rainforest taxa and *Acacia*) in unburnt relative to annually burnt quadrats, there was only weak relative increase of eucalypts in annually burnt quadrats of the smallest stem class (<1 cm diameter), and no differences in larger eucalypt stem classes. With the notable exception of the lack of response in eucalypts, it is widely observed in tropical savannas that release from fire pressures results in a significant increase in woody cover and stem density (e.g., Trapnell 1959, Rose-Innes 1972, San Jose and Farinas 1991, Swaine et al. 1992, Bond 2008, Hoffmann et al. 2009).

Other north Australian studies, however, have reported differential effects of fire regime treatments on recruitment classes, including eucalypts (Prior et al. 2006, 2009, 2010, Russell-Smith et al. 2010, Bond et al. 2012, Werner and Prior 2013). These studies have mostly, but not exclusively, been conducted at the Kapalga site, also in present-day Kakadu National Park, where fire intensities in respective treatments were typically substantially greater than at Munmarlary (Russell-Smith and Edwards 2006). For example, combining available growth, mortality, and recruitment data from two Kapalga datasets (Williams et al. [2003], 4 yr of observations; Werner [2005], 7 yr of observations), Prior et al. (2006) reported differential effects of fire treatments (early dry season, late dry season, extreme severity, unburnt) on juveniles (<1.5 m tall) and saplings (≥1.5 m to ≤5 cm dbh), where for juveniles, annual early and infrequent extreme fires had large adverse effects on height growth compared with late fires and unburnt treatments, and for saplings, annual late and infrequent extreme fires resulted in negative diameter growth increments.

Based on the same Williams et al. (2003) dataset, Prior et al. (2010) observed that significant stem accession occurred into size classes above 3 m for eucalypts and non-eucalypts in unburnt treatments, and to a lesser extent for eucalypts alone in late dry season fire treatments, whereas Bond et al. (2012) observed that accession above 4 m was especially prominent for eucalypts in five years of late dry season treatments followed by eight years under the ambient regime, and for non-eucalypts in unburnt treatments. The latter authors proposed that release of eucalypt recruitment might be especially responsive to the availability of canopy gaps.

The relative height growth competitiveness of eucalypt vis-à-vis non-eucalypt juveniles in fire-prone settings is attributed to the possession by eucalypts of deeply protected epicormic buds on the stem, whereas non-eucalypts need to expend more resources on developing bark protection for their buds (Burrows et al. 2008, 2010, Lawes et al. 2011*a*).

Reminiscent of schema reconciling contrasting demographic-bottleneck and competition-based models in savanna tree-grass coexistence contexts (Sankaran et al. 2004, O'Connor et al. 2014), the above observations suggest that interactions between site disturbance (fire, wind) and resource competition effects invoke strong and differential responses on the recruitment dynamics of eucalypt and non-eucalypt tree juveniles in Australian savannas (Fig. 1). For eucalypts (Fig. 1a), assembled observations indicate that recruitment is promoted under less competitive, increasingly open-canopied and more severe fire regime conditions, whereas for non-eucalypts generally (Fig. 1b), recruitment is promoted under variable canopy, but low fire regime severity conditions. These relationships may be expressed generally in mesic north Australian savannas, although the relative competitiveness and species diversity of non-eucalypts has been observed to be highest on high-rainfall sites especially under low fire frequency conditions (Lawes et al. 2011*c*).

Here we report on two complementary studies illustrating recruitment dynamics of woody taxa in frequently burnt eucalypt-dominated mesic savanna under contrasting overstory conditions: (1) the decadal regrowth response of tree juveniles following the devastating and regionally extensive impact of severe tropical Cyclone Monica on coastal and sub-coastal eucalypt-dominated mesic savanna in April 2006; and (2) the recruitment dynamics of tagged tree species juveniles over the six-year period 2011–2016, at long-term monitoring plots in more or less structurally mature savanna in Litchfield National Park. Ambient (non-manipulative) fire regimes in both studies were observed to comprise fires mostly in the early dry season (EDS, before August), and also lesser frequencies of typically more severe late dry season (LDS) fires.

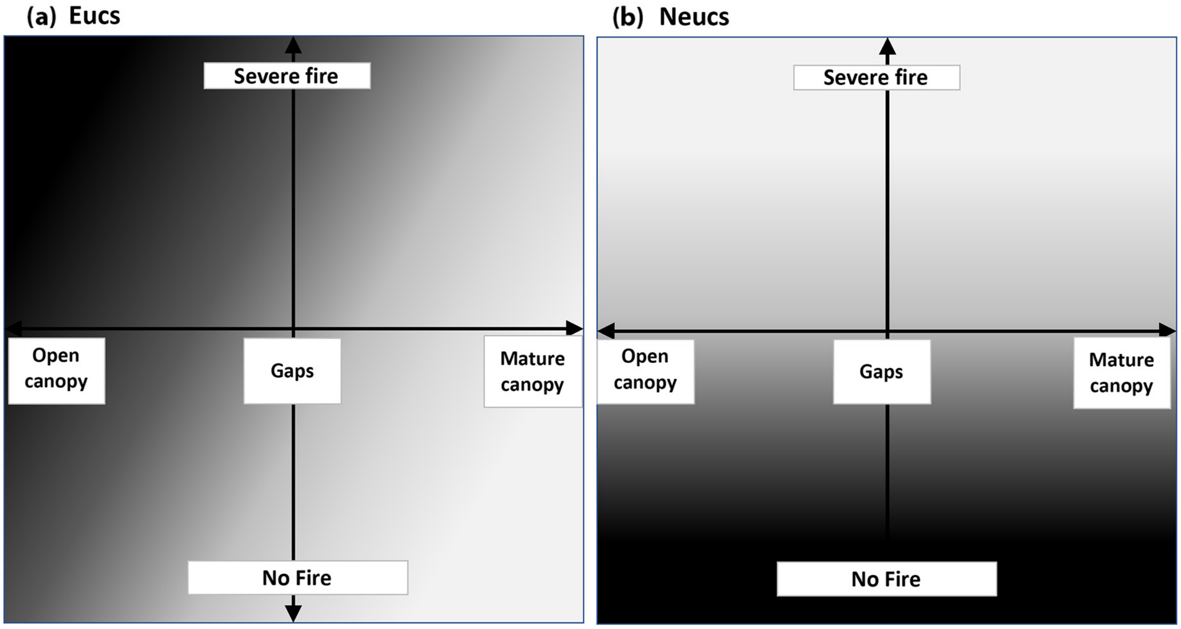

Fig. 1. Schematic summarizing observations from available studies illustrating interactions between fire regime and canopy competition effects on differential responses of (a) eucalypt (Eucs) and (b) non-eucalypt (Neucs) juvenile tree recruitment into the "tall sapling" class, defined in this paper as achieving a canopy height of 5 m. Darker shading represents increased recruitment response.

As a natural experiment test of the proposed recruitment framework presented in Fig. 1, we predict that (1) the absence of overstory competition at post-Cyclone Monica sites, in combination with frequent burning, would promote significant release of eucalypts but not non-eucalypts; and (2) under relatively stable stand structure and frequent fire conditions at Litchfield NP plots, there would be either negligible release of both non-eucalypts and eucalypts or accession by eucalypts only in the event of increased availability of canopy gaps. The study has significant long-term implications for biodiversity conservation and carbon stock management in fire and increasingly cyclone-prone northern Australia.

METHODS

Study area

The two study areas were located in frequently burnt savannas of coastal and sub-coastal regions of the Northern Territory, Australia (Fig. 2a). Based on available records from the closest (<50 km) long-term weather recording stations, mean annual rainfall exceeds 1500 mm at Litchfield and 1200 mm at Cyclone Monica sites, with >90% occurring in the wet season months November–March. Fire regimes in these locations are representative generally of north Australia's 426,000-km^2 mesic savannas where, for example, over the five-year period 2008–2012, an annual mean of 53% was burnt with two-thirds of fires occurring in the LDS period (Edwards et al. 2015).

Vegetation at both sites comprised eucalypt (*Eucalyptus*, *Corymbia*)-dominated open-forest (30–70% foliage projective cover: FPC) grading into woodland (10–30% FPC) savanna, with lesser components of other typical regional savanna tree and shrub taxa over a variable ground stratum of perennial (e.g., *Eriachne* spp., *Heteropogon* spp., *Sorghum plumosum*, *Themeda australis*, *Triodia microstachya*) and annual (e.g., *Eriachne* spp., *Sorghum* spp.) grass species. This mesic savanna vegetation is widespread across northern Australia (Fox et al. 2001, Williams et al. 2002, 2017).

Tropical Cyclone Monica was a Category 5 system (gusts > 280 km/h, as defined by the Australian Bureau of Meteorology) when it crossed the coastline (Fig. 2b) on 24 April 2006, with

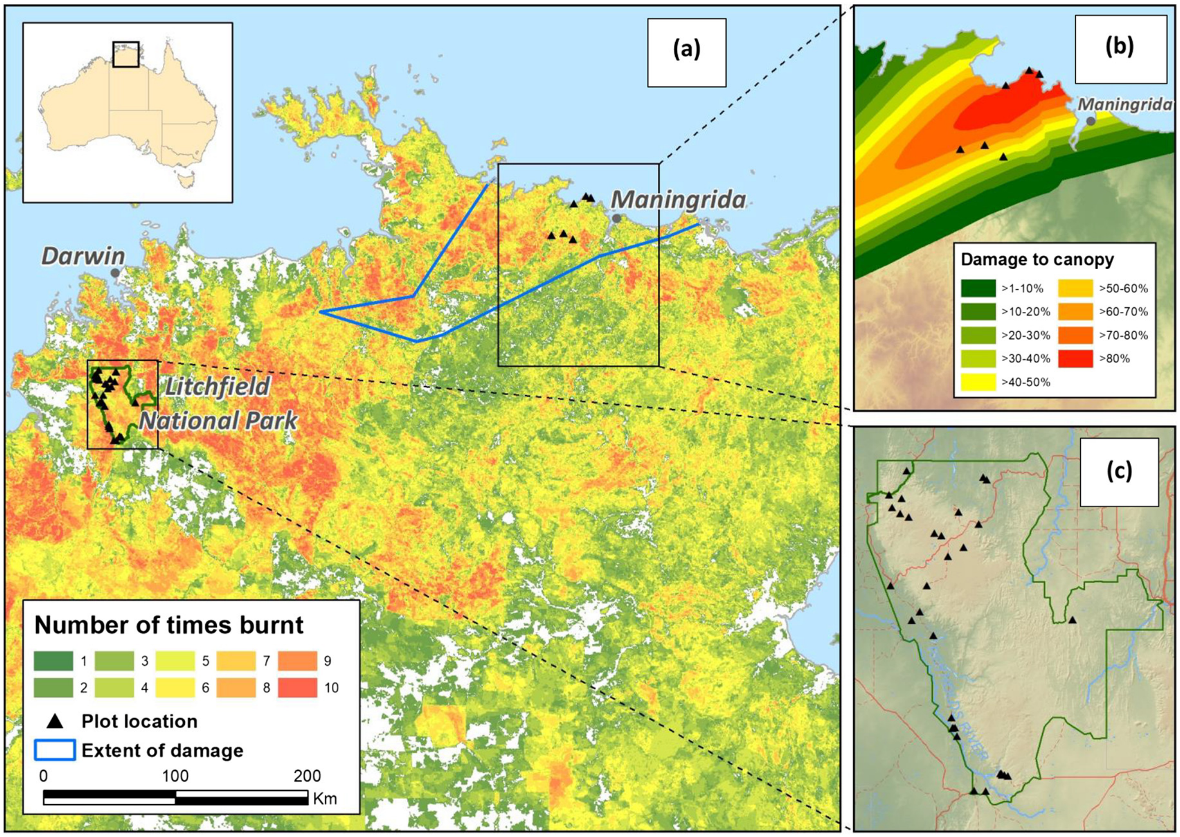

Fig. 2. Location of Cyclone Monica and Litchfield National Park study sites: (a) overlaid on regional fire history 2006–2016 derived from MODIS imagery; (b) distribution of Cyclone Monica study plots overlaid on swath of Cyclone Monica and modeled intensities (after Hutley et al. 2013); and (c) detailed distribution of Litchfield National Park plots.

estimated maximum wind gusts of 350–360 km/h at the point of landfall. After landfall, the cyclone moved WSW at 15 km/h and dissipated to a Category 1 system after about nine hours and traveling 140 km, impacting an area of 10,400 km^2 (Cook and Goyens 2008, Hutley et al. 2013). It remains the strongest recorded cyclonic event to have impacted the Australian mainland.

Cyclone Monica sites

Two sets of plots were established in different cyclonic impact zones in July 2016. A first set, comprising seven plots, was established in coastal savanna at the site of landfall (Fig. 2b). Post-cyclone damage to trees in this location was estimated as being >85% (Hutley et al. 2013). A second set of nine plots was established ~30 km from the coast, in an area with estimated tree damage of between 40% and 70% (Fig. 2b; Hutley et al. 2013).

At each coastal plot, a permanently marked transect 1 m wide and of variable length (74–90 m, depending on post-cyclone debris accessibility) was established. At sub-coastal plots, permanently marked transects were each 1 × 100 m. The identity, measured maximum height of living leaves or stems (to 0.1 m), recruitment type (seedling, resprout), and location along the transect (to within 0.1 m) of every tree juvenile were recorded along each transect. Obvious seedlings (e.g., with cotyledons attached, immature leaves) were distinguished from resprouts (typically multi-stemmed) in order to assess the relative contributions of these distinct recruitment modes. In instances where multiple stems arising from one genet were observed, the height of the tallest stem was recorded—along with notes concerning the areal extent of clonal "individuals" to inform subsequent sampling. All recruitment transects were established in 2006 within 3 months of Cyclone Monica and resampled annually between 2007 and 2011 (with the exception of one plot in 2007), and again in July 2016.

The diameter at breast height (dbh, 1.3 m) of all tree-sized stems (≥5 cm dbh) was measured in 2006 and 2016 in association with the above juvenile transects, but at widths varying from 10 to 20 m depending on minimum stem density sampling requirements (20 stems per transect). At both coastal and sub-coastal transects, dbh measurements were made on fallen or remnant stems. Although the reliability of stem sampling in 2006 is likely to be prone to (small) error, especially at coastal transects and for small-sized stems given the extent of treefall, we do not consider that this materially affects our assessment.

The annual occurrence and seasonality (EDS, LDS) of fires at each plot was assessed with reference to the available dry season time series of Landsat 7 ETM + (30×30 m^2 pixels)-derived color composites highlighting burned areas, augmented by fire occurrence observations made at the above sampling periods.

Litchfield National Park sites

Juvenile tree recruitment dynamics were assessed at 32 eucalypt-dominated savanna plots (Fig. 2c), originally established in 1995 as part of a long-term fire effects monitoring program (Russell-Smith et al. 2014). Juvenile trees were tagged at each plot in March 2011 and resampled annually at the start of the ensuing wet season (October–December), from 2011 to 2016. Tagged individuals were located within two fixed 1×40 m transects at each plot. The same data as per Cyclone Monica sample sites were recorded for each juvenile tree. Where respective genets comprised multiple stems, height and stem diameter data were recorded for the tallest living stem in each sampling period. dbh measurements of all tagged tree-sized stems (≥5 cm dbh) were undertaken in each 40×20 m plot both at the start and at the end of the study period.

The annual occurrence and severity of fires was recorded at each plot based on on-ground site visits in November–December. As for the cyclone study sites, fire seasonality (EDS, LDS) was checked with reference to available dry season Landsat derived satellite imagery. Following Russell-Smith and Edwards (2006), fire severity was categorized as mild (scorch height <2 m), moderate (scorch height >2 m but not affecting the canopy), or severe (canopy scorch). Leaf scorch height is closely related to measured Byram fire-line intensity in regional savannas ($R^2 = 0.85$; Williams et al. 1998), where mild fires imply Byram fire-line intensities of <1 MW/m, moderately severe fires intensities of 1–2 MW/m, and severe fires intensities of >2 MW/m. In regional studies, EDS fires are predominantly of low severity, and LDS fires are mostly of moderate and high severity (Russell-Smith and Edwards 2006, Murphy and Russell-Smith 2010).

Height class and taxonomic group definitions

For this assessment, tree taxa are defined here as those which typically can attain a canopy height of at least 8 m and a diameter at breast height (dbh, 1.3 m) of at least 5 cm. Our assessment focuses on the responses of all juvenile tree individuals <5 cm dbh. In regional studies, "juveniles" typically are categorized with reference to somewhat variable height classes which, for convenience and as referred to subsequently, are described here as:

1. "juveniles," typically multi-stemmed to single-stemmed in taller individuals, characterized by seasonal loss of most leaves by the mid-dry season—≤1.4 m (Werner et al. 2006), <1.5 m (Prior et al. 2006, 2010, Werner and Franklin 2010, Werner 2012, Werner and Prior 2013), and <2 m (Fensham and Bowman 1992, Russell-Smith et al. 2003, 2010); in some studies divided into "small" (<50 cm) and "tall" sub-classes.
2. "saplings," sometimes referred to as "small adults" or "small trees," typically single-stemmed, with smaller individuals often water-stressed and leafless by the LDS (Prior and Eamus 2000)—juvenile maximum height to ≤300 cm (Prior et al. 1997, 2010), ≤500 cm (Werner and Franklin 2010, Werner 2012), <5 cm dbh (Prior et al. 2006, 2010, Lehmann et al. 2009, Russell-Smith et al. 2010, Werner and Prior 2013); in some studies divided into "smaller" and "taller" sub-classes.

3. "poles," single-stemmed, taller individuals evergreen and not water-stressed—up to 8 m (Russell-Smith et al. 2003); juvenile maximum height to ≤10 m (Werner 2012); <10 cm dbh (Fensham and Bowman 1992).

Our assessment also focuses on the responses of tree juveniles in three broad taxonomic groups: Eucalypts ("Eucs") comprising *Eucalyptus* and *Corymbia*; *Acacia*; and Non-eucalypts ("Neucs") comprising a broad range of genera other than Eucalypts and *Acacia*. In other regional studies, non-eucalypts are sometimes referred to as "pantropics" (Williams et al. 1999, Prior et al. 2009, 2010), and *Acacia* spp. may be included in a separate grouping with other "fast-turnover" taxa (Prior et al. 2010). Although both the pandan, *Pandanus spiralis*, and palm, *Livistona humilis*, can attain tree-size status, these taxa were omitted from both analyses involving tree-sized stems and juvenile trees.

Analysis

We present assembled data concerning the survivorship and height responses of tree-sized taxonomic groups, and changes in tree stem demography and basal area (m^2/ha), over 10- and 6-yr assessment periods, at post-Cyclone Monica and Litchfield National Park plots, respectively.

While we consider our untagged field-based sampling procedure at post-cyclone plots enabled us to reliably re-locate previously sampled, and subsequently recruited, individuals (mostly ramets and/or genets), for conservative statistical assessment purposes we present linear or logistic models based on plot-level data. Post-cyclone recruitment (total recruitment, recruitment into 5 m height class) and mortality (count dead, proportion dead) plot-level data, and measured height increment (change over time) of individual stems, were linearly modeled in relation to initial plot basal area, fire history (total fire frequency, total LDS fire frequency), and vegetation type (coastal, sub-coastal) using the "stat" package of R 3.4.4 (R Core Team 2018). The validity of all linear models was assessed visually using quantile–quantile residual plots and statistically using the Shapiro-Wilks tests. We also assessed individual stem mortality in relation to the above predictors using logistic models from the "glm" function of R 3.4.4 (R Core Team 2018). Logistic models were tested for over-dispersion and model reliability was assessed using the "binnedplot" function of the "arm" package (Gelman and Su 2016) in R 3.4.4 wherein 95% of binned model residuals are expected to fall within confidence bounds (±2 SE). All models were conducted on data subsetted by (1) sampling period (t1 = 2006–2011; t2 = 2011–2016) and (2) taxonomic group, while logistic models were also conducted on subsets taken according to (3) taxonomic group and initial size class.

For statistical assessment of Litchfield National Park data, height increment of tagged juvenile trees was linearly modeled in relation to initial plot basal area, fire history (total fire frequency, total LDS fire frequency), taxonomic group, and initial height size class. Linear model validity was assessed as per models of post-cyclone data. Stem mortality at Litchfield National Park was modeled and diagnosed as per models of post-cyclone data. Linear and logistic models of Litchfield National Park data were conducted on data subsetted by (1) taxonomic group, (2) initial height size class, and (3) taxonomic group and initial height class.

RESULTS

Fire history

*Post-cyclone plots.—*Over the 10-yr observation period, the mean fire frequency at all 16 assessment plots was 0.71, comprising 0.4 in the EDS period and 0.31 in the LDS period (Appendix S1; Fig. 3a). Sub-coastal plots (n = 9) burnt at greater mean frequency (annual = 0.83; EDS = 0.51; LDS = 0.32) than coastal plots (n = 7; annual = 0.56; EDS = 0.26; LDS = 0.3). The range of annual fire frequency was from 0.7 to 0.9 at respective sub-coastal plots and from 0.4 to 0.8 at coastal plots.

*Litchfield NP plots.—*Over the six-year observation period, the mean fire frequency experienced at 32 assessment plots was 0.61, comprising 0.46 in the EDS and 0.15 in the LDS (Appendix S1). Mean fire frequencies were slightly less than at Cyclone Monica plots, especially in the LDS. Most fires at Litchfield plots were of low (mean frequency = 0.35) or moderate (mean frequency = 0.1) severity in the EDS, whereas LDS

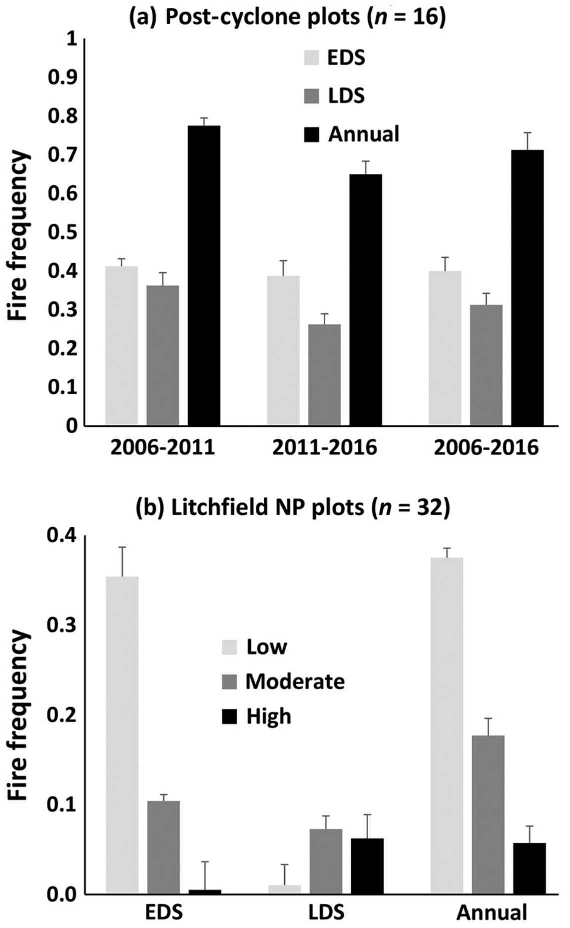

Fig. 3. Fire regimes experienced at (a) post-cyclone and (b) Litchfield National Park plots over respective study periods (EDS, early dry season [pre-August]; LDS, late dry season). Fire severity classes in (b): low, leaf scorch <2 m; moderate, leaf scorch not affecting canopy; and high, canopy scorch.

fires were typically of moderate (mean frequency = 0.07) or high (mean frequency = 0.06) severity (Fig. 3b).

Stand structure

*Post-cyclone plots.—*Based on sampling three months after Cyclone Monica (refer to Methods), it is estimated that mean tree stem density over all plots was 261 ha^{-1}, of which 29% were ≤10 cm dbh (Appendix S1). In 2016, mean tree stem density was 742 ha^{-1}, of which 75% were ≤10 cm dbh and 96% were ≤20 cm dbh (Fig. 4a). Stem densities at coastal plots were on average 2.3 times greater than those at sub-coastal plots prior to the start of the observation period and 1.5 times greater at the end.

Stem basal area at the time of Cyclone Monica was estimated to be 9.8 ± 1.6 m^2/ha over all plots (mean ± SE; Fig. 4b; Appendix S1), with coastal plots supporting 2.6 times greater basal area than at sub-coastal plots. Extensive structural devastation was evident in the aftermath of the cyclone (Fig. 5a). By 2016, mean basal area had recovered to ~6.5 m^2/ha at both coastal (Fig. 5b) and sub-coastal plots—but including very substantial increase in basal area at one sub-coastal plot between 2011 and 2016, from 5.3 to 11.8 m^2/ha associated with massive (eucalypt) stem recruitment. At 2006 and 2016 sampling periods, eucalypt basal area comprised 77.5% and 73% of the total, respectively, with the remainder comprising mostly non-eucalypt basal area in 2006, and an equivalent relatively large *Acacia* proportion in 2016 (Fig. 4b; Appendix S1).

*Litchfield NP plots.—*The mean stem size-class distributions at Litchfield inventory plots in 2011 and 2016 are given in Fig. 4c, and the basal area of eucalypt, non-eucalypt, and *Acacia* stems for the same sampling times is given in Fig. 4d. There were no significant differences in either of these distributions over the assessment period. Total mean tree stem densities at the 32 assessment plots were 384.4 ± 29.7 ha^{-1} in 2011 and 395.3 ± 31.7 ha^{-1} in 2016, of which ~50% were ≤10 cm dbh in both sampling times. Mean stem densities were very similar to those at pre-Cyclone Monica coastal plots (Appendix S1), but included 170% greater tree stems, ≤10 cm dbh. Mean basal area was 7.8 ± 0.8 m^2/ha in 2011 and 7.7 ± 0.9 m^2/ha in 2016, comprising mostly eucalypt (57%), then non-eucalypt (41%) and *Acacia* (1.5%) basal area at respective sampling times (Appendix S1). Mean basal area at Litchfield plots was ~20% less than that on average at pre-Cyclone Monica plots, but comprised a substantially greater proportion of non-eucalypt basal area.

Responses of juvenile trees

*Post-cyclone plots.—*Total densities of 5363, 6671, and 4187 juvenile trees/ha were sampled along permanent transects in 2006, 2011, and 2016, respectively (Fig. 6d). In 2006, 69.8% were

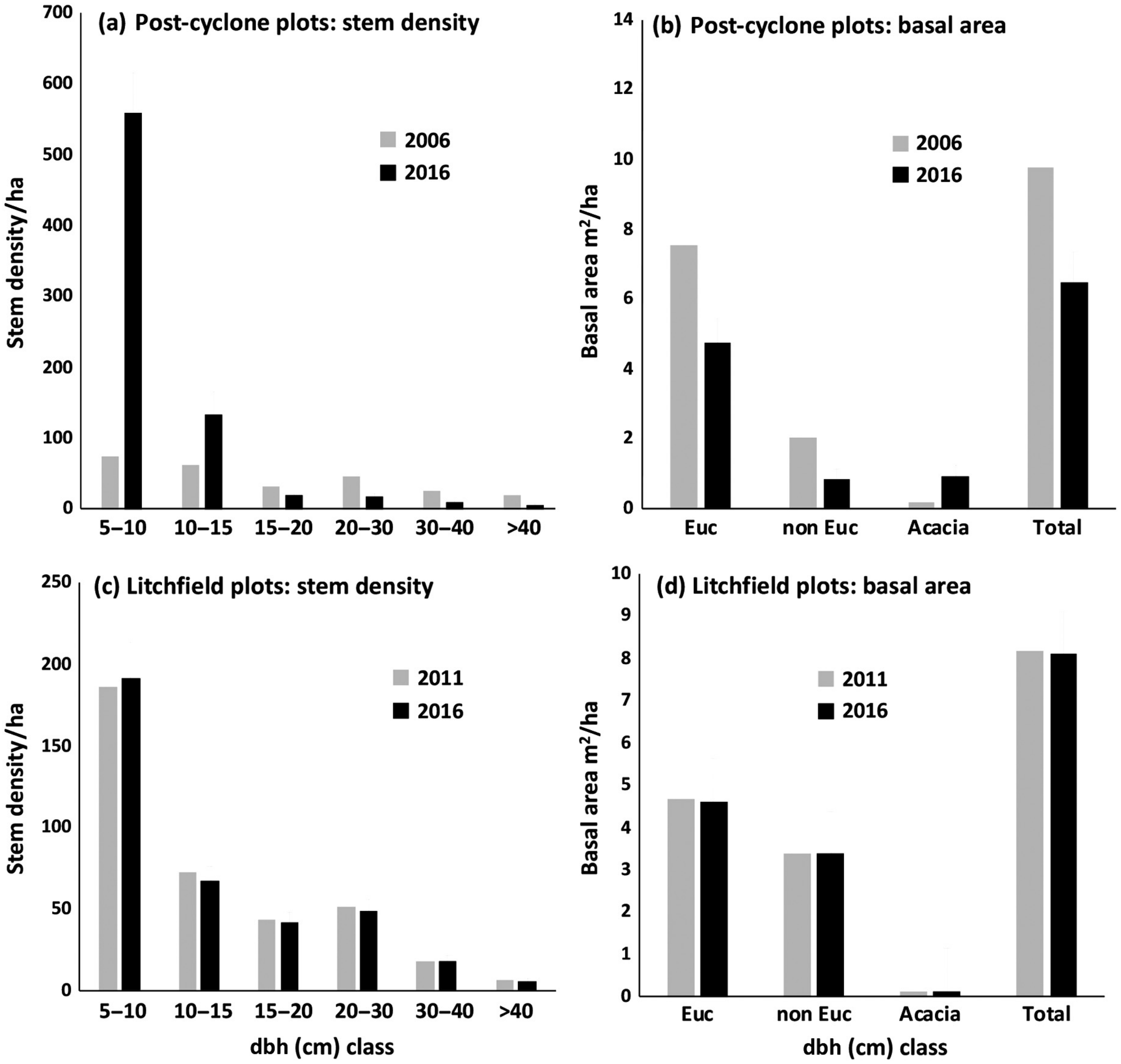

Fig. 4. Change in stem density and basal area at post-cyclone and Litchfield National Park plots over respective study periods.

<50 cm tall, and 35 individuals (0.3%) were >2 m. By 2016, 20.8% were <50 cm and 6.2% were >2 m. Between 2006 and 2011 and 2011 and 2016, respectively 391 and 74 new juvenile stems were recruited across all sample sites. The great majority of these recruits were from clonally reproducing species; over the full assessment period, 70.4% of all recruits represented just four clonal taxa: *Acacia mimula* (15.3%), *Buchanania obovata* (17%), *Erythrophleum chlorostachys* (19.6%), and *Eucalyptus tetrodonta* (18.5%). Just 16 individuals were unambiguously seedlings, all *Acacia* spp.

Between 2006 and 2011, mortality overall was 26.1%, with the highest proportion (30.5%, $n = 541$ initially) occurring in the smallest (<50 cm) height class. Between 2011 and 2016, juvenile stem mortality was 45.5%, with the largest proportion occurring in the >5 m height class (81.3%, $n = 16$ initially), and largest numerically in the <50 cm height class (55.6%, $n = 324$ initially) (Appendix S2: Fig. S1).

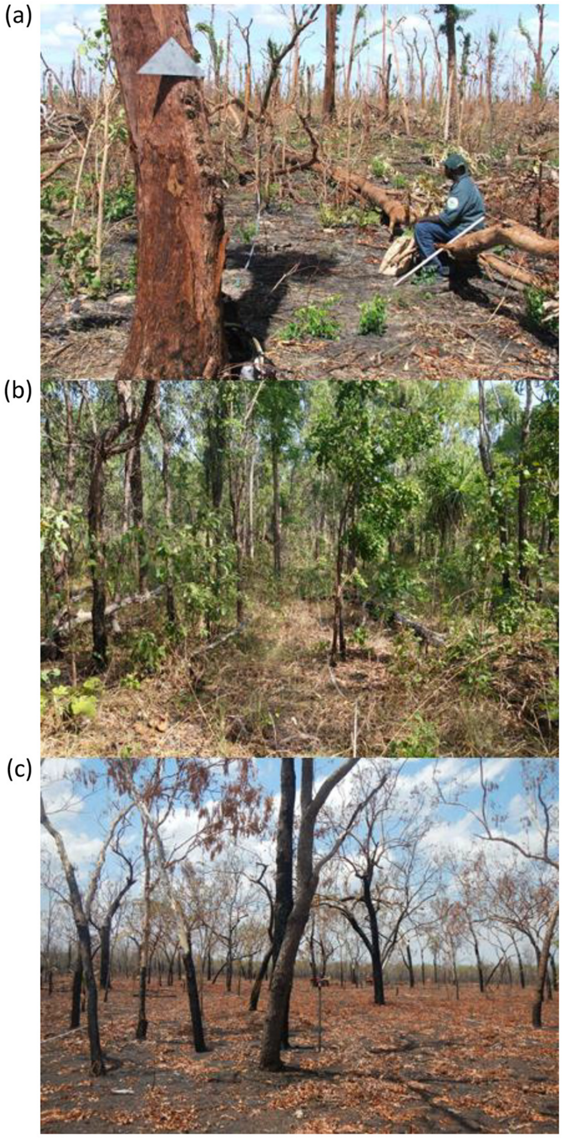

Fig. 5. Assessment plots: (a) four months after Cyclone Monica in 2006, with the plot having already been burnt by low-severity early dry season fire; (b) the same location in August 2016, unburnt in that year; and (c) immediate effects of late dry season canopy-scorching fire, Plot 6 (basal area = 7.2 m^2/ha) in Litchfield NP. Panel (a) shows evident epicormic regrowth on some remnant stems. This regrowth, and stems generally, typically subsequently died most likely associated with roots having been sheared from shaking stems during the height of the storm (Franklin et al. 2010; G. D. Cook, *personal communication*). Note in panel (c) the very sparse remnant understory and coarse woody debris.

Most juveniles comprised non-eucalypts (range: 50.2% in 2006 to 54.5% in 2011), followed by eucalypts (range: 31.2% in 2006 to 26.9% in 2011), then *Acacia* (range: 18.7% in 2011 to 18.3% in 2016). For all taxonomic groups, numbers of juveniles were greatest in 2011, and substantial declines were observed for juveniles <50 cm in successive periods after 2006. Juvenile stem mortality in all three taxonomic groups was greatest in the second assessment period, 2011–2016 (eucalypts 40.5% vs. 29.3% 2006–2011; non-eucalypts 47.4% vs. 24.7% 2006–2011; *Acacia* 47.2% vs. 24.3 2006–2011), occurring numerically mostly in smaller height classes (Appendix S2: Fig. S1).

Height responses of surviving juveniles in different height classes and sample periods varied between the three taxonomic groups: generally increasing in eucalypts, except for juveniles >2 m tall in the first period (but $n = 2$); generally increasing in height for non-eucalypts <50 cm and declining in those initially >2 m, over both assessment periods; and generally increasing in height for *Acacia* in all three height classes over both assessment periods, but especially those >2 m in the first period (Appendix S2: Fig. S2).

Over the 10-yr observation period, 57 eucalypt individuals of 239 originally sampled (24%) attained ≥5 m height: nine in the first 2006–2011 period, and a further 48 in the second assessment period. In 2006, the tallest sampled eucalypt was 170 cm. Conversely, by 2016, just five *Acacia* individuals and one non-eucalypt had attained 5 m height.

The mean annual rate of height increment for any eucalypt individual which attained ≥5 m over the assessment period was 62.5 ± 4.9 cm ($n = 57$). In the first assessment period, seven stems exhibited rates of height increment >1 m/yr, and 15 in the second period. One stem was recorded as 50 cm tall in 2006, 95 cm in 2011, and 10 m in 2016—an annual rate of height increment in the second period of 181 cm/yr.

*Litchfield NP plots.—*A total of 69 species of juvenile trees were tagged at the establishment of the trial, representing five *Acacia* spp., 13 eucalypts (8 *Corymbia*, 5 *Eucalyptus*), and 41 non-eucalypts. All but four taxa (*Acacia plectocarpa*, *Callitris intratropica*, *Calytrix arborescens*, *Grevillea pteridifolia*) were resprouters. In 2011 (t1), 819 juvenile trees were tagged, comprising 81 (9.2%) *Acacia*, 184 (20.9%) eucalypts, and 614 (69.9%) non-eucalypts. By

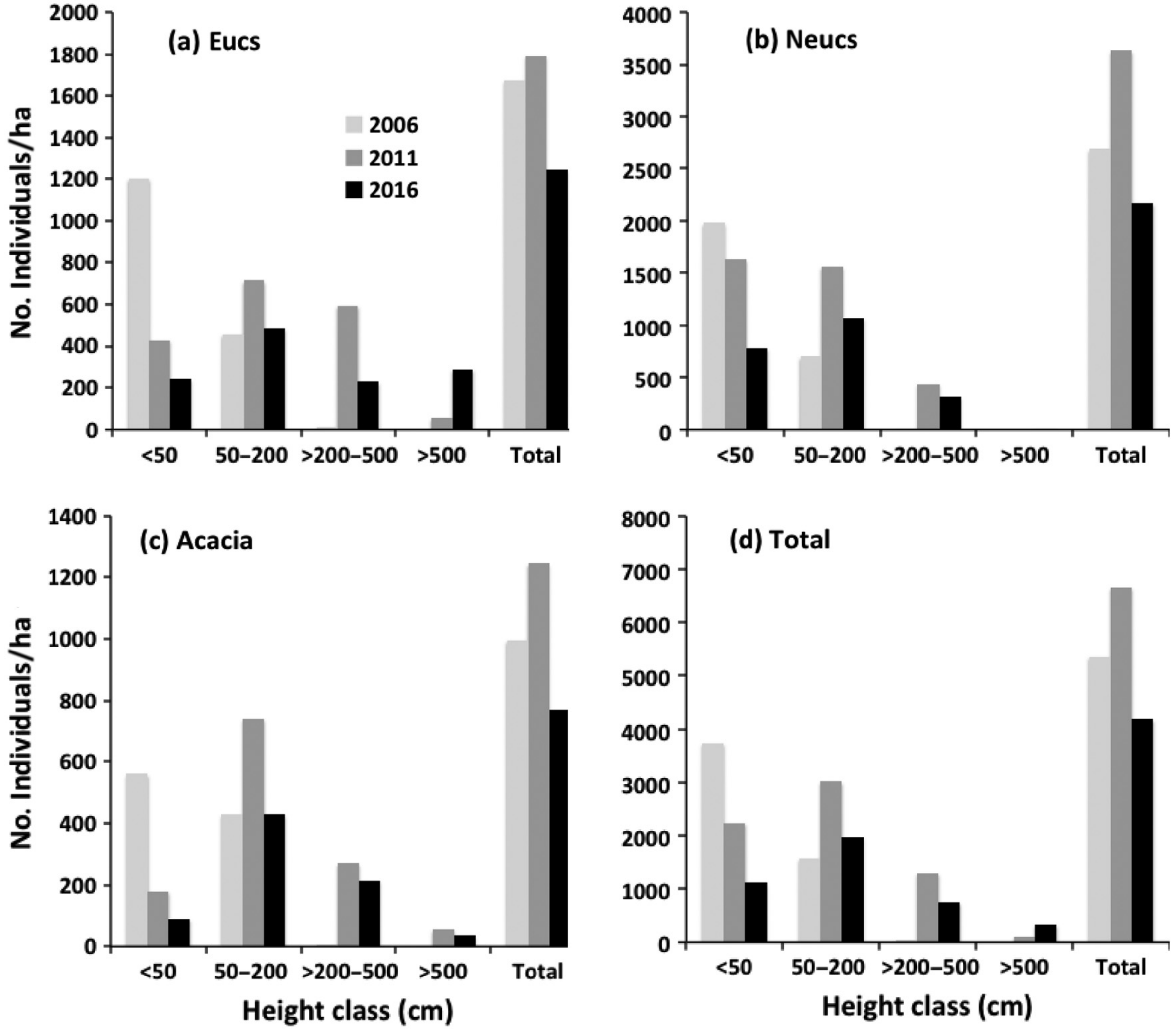

Fig. 6. Total sampled density (sum of all 16 plots) of (a) Eucs, (b) Neucs, (c) Acacia, (d) Total tree species juveniles at post-cyclone plots in different height classes in 2006, 2011, and 2016. Note different scales on *y*-axes; Eucs = eucalypts; Neucs = non-eucalypts.

height class at t1, 31.1% were <50 cm tall, 56% were 50 to <200 cm tall, 12.6% were 200 to <500 cm tall, and 0.3% were >500 cm tall. At the end of the observation period in 2016 (t7), there were 450 (−49%) remaining live tagged individuals, comprising 17 (−79%) *Acacia*, 94 (−48.9%) eucalypts, and 339 (−44.8%) non-eucalypts. By height class at t7, 32.2% were <50 cm tall, 41.6% were 50 to <200 cm tall, 24% were 200 to <500 cm tall, and 2.2% were >500 cm tall.

Height responses of tagged juveniles varied between the three taxonomic groups, but especially with *Acacia* where the majority of individuals initially in the smaller height classes died. For eucalypts and non-eucalypts, generally similar patterns were observed with the fates of height classes, with most individuals <200 cm dying, whereas individuals >200 cm mostly remained in that height class (Fig. 7).

Only one eucalypt, initially 400 cm tall at trial establishment in 2011, attained a height ≥5 m over the assessment period, growing at mean height increments of 20 cm/yr. By contrast, four *Acacia* and five non-eucalypts attained ≥5 m, growing at mean height increments of 65.4 ± 8.4 cm/yr and 35.5 ± 14.8 cm/yr, respectively.

Summary of comparative responses between post-cyclone and Litchfield plots

The height-class distributions of juvenile trees at respective study sites were initially markedly dissimilar, comprising mostly (61.5%) individuals <50 cm tall at Cyclone Monica sites, and mostly (56%) individuals 50 to <200 cm tall at Litchfield inventory plots. By the end of respective observation periods, (1) despite significant recruitment of predominantly clonal ramets at Cyclone Monica plots especially in the first five-year observation period, most (54.8%) of those originally censused had died; (2) similar levels of mortality (48.8%) of tagged individuals were observed over six years of observations at Litchfield plots; and (3) there was substantial proportional accession into taller 2 to <5 m and ≥5 m classes at Cyclone Monica plots, especially of eucalypts into the ≥5 m class (Fig. 8b), whereas (4) for tagged individuals at Litchfield, there was very limited accession into the ≥5 m class, proportionally most notably by fast-growing *Acacia* (Fig. 8d).

Modeled responses of juvenile trees

In general, statistical modeling of the responses of juvenile tree demographic characteristics at

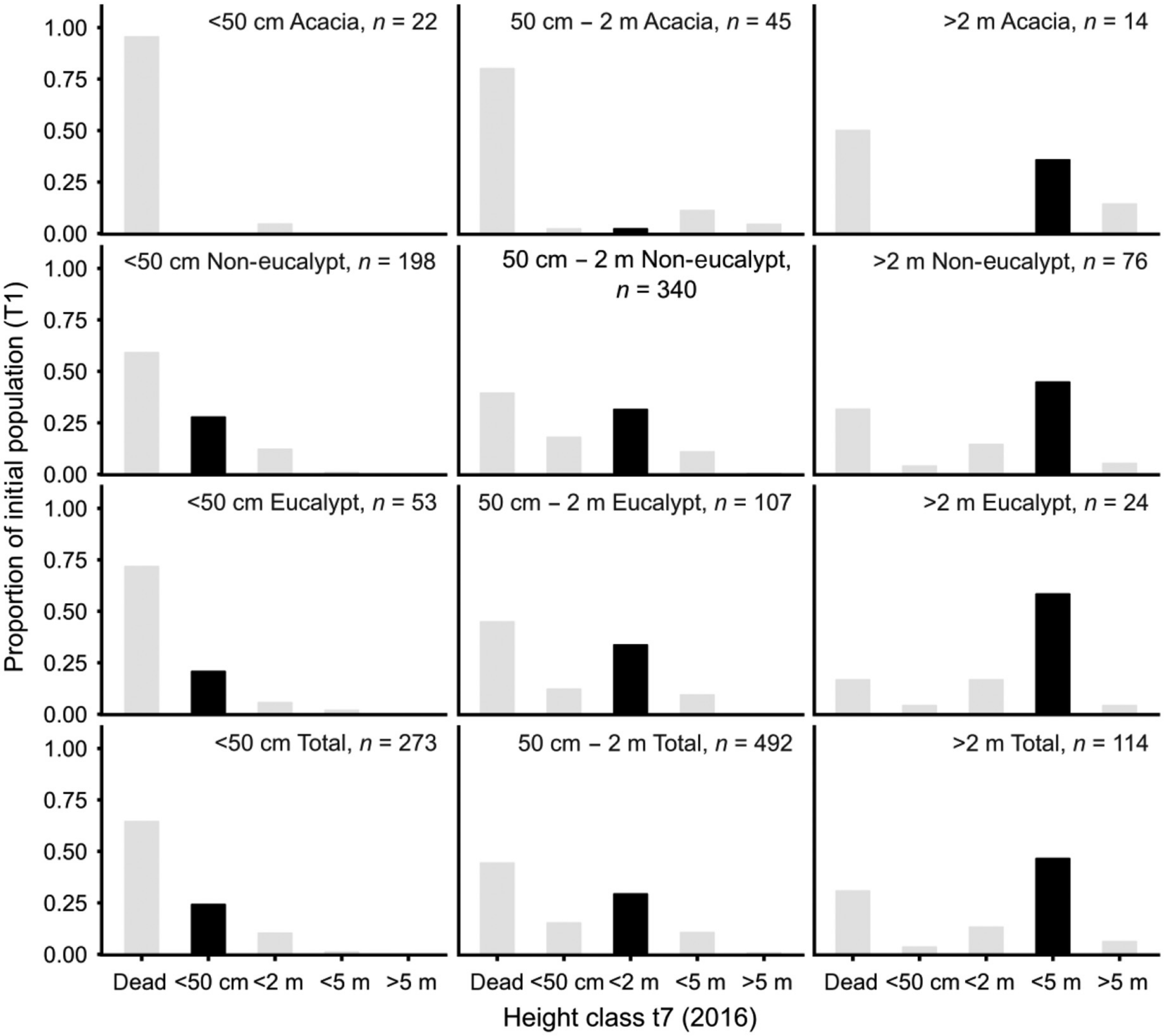

Fig. 7. Proportional change (%) in fate of tagged juvenile trees in three initial height classes (<50 cm, 50 cm to 2 m, >2 m) over the period 2011–2016, summed for all 32 Litchfield National Park observation plots. Black bars represent the initial height classes of respective taxonomic groups; *n* = *n*umber of initial tagged individuals.

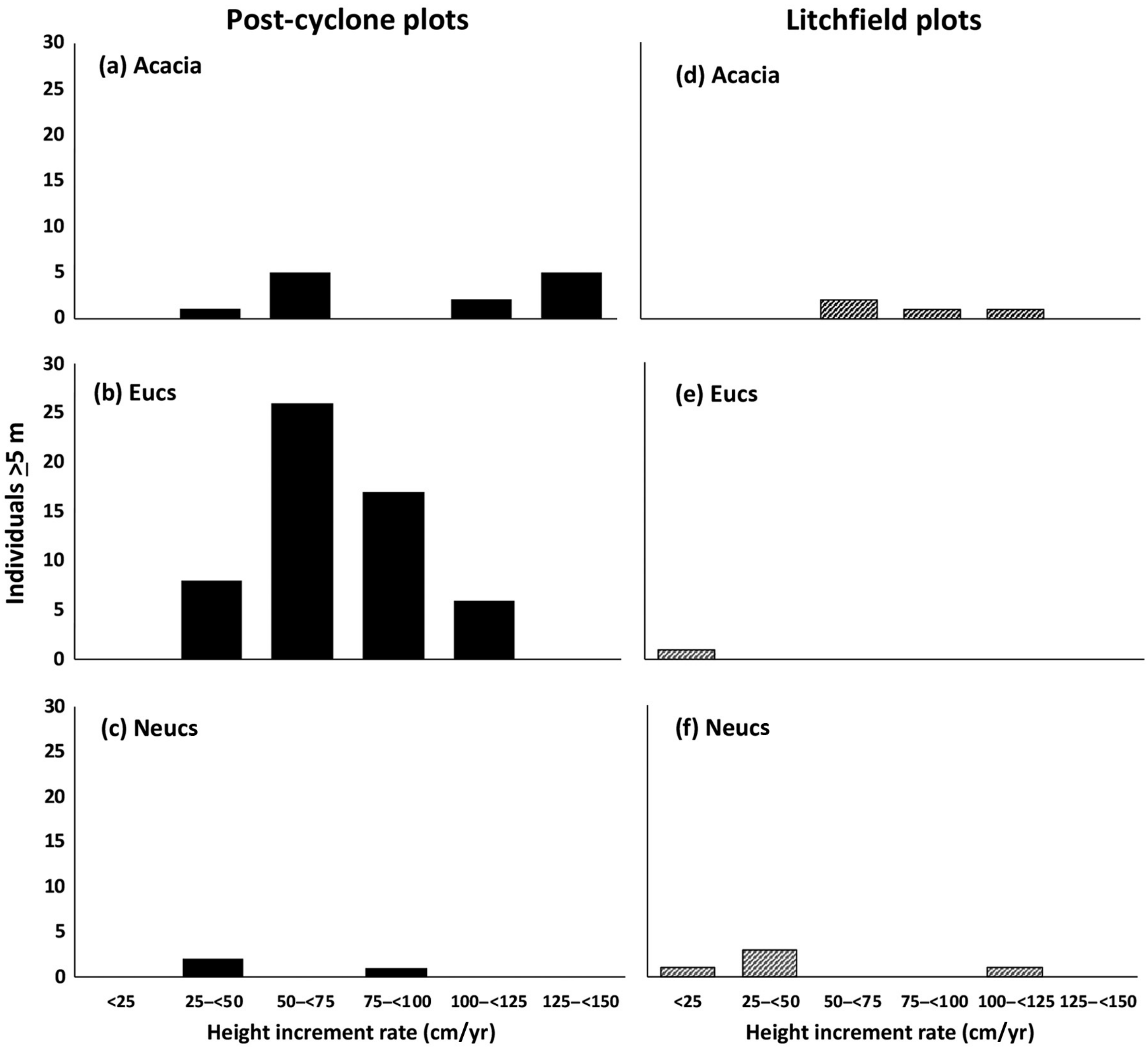

Fig. 8. Height growth increment rate of all individuals which attained ≥5 m height at respective post-cyclone (a–c) and Litchfield (d–f) study plots.

both post-Cyclone Monica and Litchfield sites was not effectively described by fire regime and other explanatory variables. The limited variability in fire regimes experienced at respective site plots is likely to have been contributory. Fire regime variables were included as significant terms in six (of 12) statistically explanatory models describing post-Cyclone Monica data, and none (of three) for Litchfield data. The relative importance of initial basal area as an explanatory variable was indicated by its inclusion as a significant term in three post-Cyclone Monica and all three significant Litchfield explanatory models (Table 1).

Post-cyclone plots.—A total of 162 separate linear and 66 logistic models (Appendix S1: Table 1a) were run to assess relationships between response variables (total recruitment, recruitment into 5 m height class, mortality) with initial plot basal area, fire history (total fire frequency, total LDS fire frequency), and vegetation type (coastal, sub-coastal), subset by sampling period (t1 = 2006–2011; t2 = 2011–2016), and taxonomic group. All but 12 models (Table 1a) either did not meet model assumptions (e.g., normality of residuals) or were not statistically significant (α = 0.05).

For juvenile eucalypts, three valid models were derived: For recruitment, in t2 only, total recruitment was observed to be negatively affected by both initial basal area and fire frequency; for mortality, the proportion of those dying over the entire t1–t2 assessment period was negatively associated with initial basal area, and the number of individuals which died was observed to be negatively related to fire frequency in t2 only.

The proportional mortality of juvenile non-eucalypts was observed to differ significantly between coastal and sub-coastal plots over the entire t1–t2 sampling period (coastal: 0.63 ± 0.07; sub-coastal 0.30 ± 0.07), and in t2 alone (coastal: 0.52 ± 0.05; sub-coastal: 0.28 ± 0.07), in separate linear models including either fire frequency or LDS fire frequency. Survivorship of juvenile non-eucalypts <50 cm tall was found to be negatively affected by both severe and especially frequent fires.

The total number of *Acacia* recruited into the 5 m height class across the entire monitoring period was positively associated with initial plot basal area. In t2, the height increment of *Acacia* 50–200 cm tall was found to be negatively influenced by both severe and frequent fires (Table 1a).

Litchfield NP plots.—A total of 34 separate linear and 20 logistic models (Appendix S3: Table 1b) were run to assess relationships between response variables (stem height recruitment, stem mortality), with predictive variables (initial plot basal area, initial stem height class, fire history [total fire frequency, total LDS fire frequency]), and taxonomic group. Modeling was not undertaken for *Acacia*. All but three models either did not meet model assumptions (e.g., normality of residuals) or were not statistically significant (α = 0.05).

For juvenile eucalypts, two valid logistic models described the effects of initial basal area on mortality of stems <50 m height, with separate significant models including fire frequency and the frequency of severe fires, respectively (Table 1b). For non-eucalypt juveniles >200 cm tall, initial basal area was observed to have negative effects on stem height increment.

DISCUSSION

This study takes advantage of the effects of near-complete woody canopy removal at sites severely impacted by Cyclone Monica in 2006, contrasted with the maintenance of woody canopy conditions at Litchfield National Park sites, on the demographic responses of juvenile trees in eucalypt-dominated savanna under ambient, regionally typical, high fire frequency conditions. As posited in the introduction, these observations add to a substantial body of literature addressing eucalypt-dominated savanna dynamics, derived from both manipulative fire treatment and ambient fire regime studies, under structurally mature woody canopy conditions.

Despite higher fire frequencies, including typically more severe LDS fires, experienced at post-Cyclone Monica plots, there was substantial release of small eucalypts into both tall juvenile and small-sized tree stem (5–15 cm dbh) classes. By contrast, at Litchfield plots, there was muted height release of juveniles and relatively little change evident in smaller tree stem size classes. Collectively these observations illustrate significant differential fire regime and overstory competition effects on eucalypt and non-eucalypt recruitment dynamics in fire-prone eucalypt savannas.

Responses of juvenile trees

The adaptive value of sprouting and clonality for persistence in fire-prone savanna environments is well recognized (e.g., Scholes and Archer 1997, Higgins et al. 2000, Bond and Midgley 2001, Williams et al. 2002, Werner 2012). Juvenile trees at both study sites were represented by mostly resprouting, clonally reproducing species, and by relatively small numbers of obligate seeders.

Resprouting traits were conspicuous at post-Cyclone Monica sites where clonal sprouts dominated both pre- and post-cyclone inventories, especially in the first five-year assessment period; seedling recruitment (of obligate seeding *Acacia* only) comprised <1% of the total. Seedling recruitment in regional savanna resprouting taxa, including eucalypts, is typically infrequently observed, sporadic, not episodic (Setterfield 2002, Williams 2004, Russell-Smith and

Table 1. Modeled relationships between response and predictive variables at (a) post-Cyclone Monica plots and (b) Litchfield National Park plots, where for post-Cyclone Monica plots, t1 = sampling period 2006–2011 and t2 = sampling period 2011–2016; minus (−) or plus (+) sign for significant predictive variables indicating negative or positive responses, respectively; $^{*}P < 0.05$, $^{**}P < 0.01$; response of Acacia not modeled for Litchfield National Park plots.

Model	Data subset	Response variable	Predictive variable/s in model	Description
(a) Post-Cyclone Monica plots				
Linear	Eucalypt, t2 only	Total recruitment	(−) Initial basal area* Vegetation type (−) Total fire frequency**	Total number of eucalypt recruits in t2 was negatively influenced by initial basal area ($F_{1,12} = 4.67$; $P = 0.05$) and total fire frequency ($F_{1,12} = 10.89$; $P < 0.01$)
Linear	Eucalypt, t2 only	Number dead	Initial basal area Vegetation type (+) Total fire frequency*	Fire frequency was found to be a strong positive predictor of the number of dead eucalypts in t2 ($F_{1,12} = 7.39$; $P = 0.02$)
Linear	Eucalypt, t1–t2	Proportion dead	(+) Initial basal area* Vegetation type LDS fire frequency	Initial plot basal area is a significant positive predictor of eucalypt mortality across the entire sampling period ($F_{1,11} = 6.95$; $P = 0.02$)
Linear	Non-eucalypt, t1–t2	Proportion dead	Initial basal area Vegetation type* LDS fire frequency	Non-eucalypt proportion dead differed significantly between vegetation types across the entire period ($F_{1,12} = 5.19$; $P = 0.04$) with coast being higher than sub-coastal
Linear	Non-eucalypt, t1–t2	Proportion dead	Initial basal area Vegetation type* Total fire frequency	Non-eucalypt proportion dead differed significantly between vegetation types across the entire period ($F_{1,12} = 5.80$; $P = 0.03$) with coast being higher than sub-coastal
Linear	Non-eucalypt, t1 only	Proportion dead	Initial basal area Vegetation type* LDS fire frequency	Non-eucalypt proportion dead differed significantly between vegetation types in t1 ($F_{1,12} = 5.95$; $P = 0.03$) with coast being higher than sub-coastal
Linear	Non-eucalypt, t1 only	Proportion dead	Initial basal area Vegetation type* Total fire frequency	Non-eucalypt proportion dead differed significantly between vegetation types in t1 ($F_{1,12} = 7.09$; $P = 0.02$) with coast being higher than sub-coastal
Logistic	Non-eucalypt (<50 cm), t2 only	Mortality	Initial basal area (−) Severe fire frequency* Vegetation type	Severe fire frequency negatively influenced survivorship in t2 ($F_{1,197} = 5.45$, $P = 0.02$)
Logistic	Non-eucalypt (<50 cm), t2 only	Mortality	Initial basal area (−) Fire frequency** Vegetation type	Fire frequency negatively influenced survivorship in t2 ($F_{1,197} = 7.08$, $P < 0.01$)
Linear	Acacia, t1–t2	5 m recruitment	(+) Initial basal area* Vegetation type LDS fire frequency	Statistically significant positive influence of initial plot basal area on 5 m recruitment ($F_{1,12} = 8.06$; $P = 0.02$)
Linear	Acacia (50–200 cm), t2 only	Height increment	Initial basal area (−) Severe fire frequency*	Vegetation type removed due to lack of variance. Severe fire frequency had a significant negative influence on survivorship in t2 ($F_{1,34} = 7.46395$, $P = 0.01$)
Linear	Acacia (50–200 cm), t2 only	Height increment	Initial basal area (−) Fire frequency*	Vegetation type removed due to lack of variance. Fire frequency had a significant negative influence on survivorship in t2 ($F_{1,34} = 7.46395$, $P = 0.01$)
(b) Litchfield National Park plots				
Logistic	Eucalypt (<50 cm)	Mortality	(−) Initial basal area** Severe fire frequency	Statistically significant negative influence of initial basal area ($F_{1,81} = 9.64$; $P < 0.01$)
Logistic	Eucalypt (<50 cm)	Mortality	(−) Initial basal area** Fire frequency	Statistically significant negative influence of initial basal area ($F_{1,87} = 8.65$; $P < 0.01$)

(Table 1. Continued.)

Model	Data subset	Response variable	Predictive variable/s in model	Description
Linear	Non-eucalypt (>200 cm)	Height increment	(−) Initial basal area* Severe fire frequency	Statistically significant negative influence of initial plot basal area ($F_{1,73}$ = 3.92; P = 0.05)

Setterfield 2006). By contrast, obligate seeder taxa, many possessing dormant seed banks (e.g., legumes), comprise significant components of less frequently burnt regional monsoon forest and sandstone heath assemblages (Russell-Smith et al. 2012).

Despite substantially greater numbers of non-eucalypt than eucalypt juveniles at post-Cyclone Monica assessment plots both initially and in subsequent assessment periods, the height increment of fast-growing eucalypts significantly outperformed that of non-eucalypts over the entire study period. The relative competitiveness of eucalypt juveniles with respect to non-eucalypts in frequently burnt savannas is held to be a consequence of the possession by eucalypts of epicormic buds arranged along the stem on meristematic strands deeply buried at the level of the vascular cambium, effectively meaning that eucalypts do not need to expend resources on thick bark to protect their buds (Burrows et al. 2008, 2010). At the juvenile stage, savanna eucalypts typically have relatively tall stems for a given stem diameter, whereas non-eucalypts tend to have relatively short stems for a given stem diameter (Lawes et al. 2011*a*). In fire-prone savannas, eucalypts can thus minimize loss of stem height to fire by resprouting from protected epicormic buds, facilitating escape from at least low-to-moderately severe fires through maximizing height growth (Lawes et al. 2011*a*). Fensham and Bowman (1992) posited that the vigor of aerial stem release in typical savanna eucalypts and non-eucalypts is likely related to the health of basal lignotubers and associated carbohydrate stores.

The relative release of eucalypts at post-Cyclone Monica plots under frequently burnt, but unrestricted canopy competition conditions supports observations made by Wilson and Bowman (1987) who documented significant release of eucalypts in fire-prone savanna a decade after severe Cyclone Tracy in 1974. Similarly, based on observations from experimental canopy removal studies at fire-prone sites on Melville Island, Fensham and Bowman (1992) demonstrated that eucalypt overstory root competition plays a significant role in suppression of eucalypt juveniles at distances up to 25 m from intact forest boundaries.

At Litchfield, limited accession into taller height classes over the assessment period was evident for all taxonomic groups with only one eucalypt, four *Acacia*, and five non-eucalypts attaining ≥5 m. This muted release of saplings into taller size classes conforms with observations from two decades of EDS and LDS fire treatments under mature canopy conditions at Munmarlary (Russell-Smith et al. 2003), but contrasts with observations from observations at Kapalga where, over five years of repeated burning, eucalypts were released into the "adult tree" class (≥3 m) at a rate of 11 individuals·ha^{-1}·yr^{-1} in EDS treatments and 20 individuals·ha^{-1}·yr^{-1} in LDS treatments, whereas non-eucalypts (referred to as "pantropics") were released at substantially reduced rates especially in LDS treatments (Prior et al. 2010).

Likewise, based on data derived initially from the same experimental treatments as reported by Prior et al. (2006, 2010), but followed by eight years of ambient fire regime effects where fire frequency and seasonality were not described, Bond et al. (2012) observed that by the end of the first five-year treatment period, those individuals which had attained a "fire escape height" of >4 m comprised a majority of non-eucalypts (74%, n = 61) on unburnt plots, compared with a majority of eucalypts (59%, n = 97) on burnt treatments. These patterns were amplified over the full 13-yr term—where the majority of non-eucalypts attaining >4 m were located on originally unburnt plots (64%, n = 42), and the majority of released eucalypts were located on originally burnt (94%, $n = 91$), especially LDS (76%, $n = 74$), plots. In explaining the release of eucalypts, Bond et al. (2012:682) surmised that "canopy gaps may be essential for shade-intolerant eucalypt saplings to achieve maximum growth rates."

Synthesis

Despite considerable variability in the responses of tree juveniles and saplings in north Australian savanna studies, assembled observations support the following generalizations:

Juveniles (generally <2 m tall; see Methods*).—*

1. typically low-to-moderate intensity EDS fires have larger impacts on still actively growing stems than do typically more intense LDS fires on stems which are physiologically inactive (Prior et al. 2006)
2. fire impacts are greater under conditions of more intense herbaceous understory competition (Werner et al. 2006, Werner and Franklin 2010, Werner 2012)
3. under ambient burning regimes (combining frequent EDS and LDS fires), both eucalypts and non-eucalypts may be released into the sapling class (>2 m) in mature-canopied vegetation (Russell-Smith et al. 2010; Table 1), whereas eucalypts are preferentially released under open-canopied conditions (Fig. 8).
4. in the absence of burning, whereas non-eucalypts may be substantially released into the sapling class within five years (Russell-Smith et al. 2003, Prior et al. 2010), the observed responses of eucalypts vary from being substantially released (Prior et al. 2010) to more generally being strongly inhibited under mature canopy conditions (Fensham and Bowman 1992, Russell-Smith et al. 2003, Woinarski et al. 2004, Lehmann et al. 2009)

Saplings (generally > 2 m tall to <5 cm dbh; see Methods*).—*

1. significantly greater impacts of LDS than EDS fires on sapling stem diameter and height growth are attributable to stems being more water-stressed in the LDS period (Prior et al. 2006, 2010, Werner and Franklin 2010)
2. limited topkill impact on saplings in the EDS occurs under reduced herbaceous understory competition conditions, but very significant topkill impact on saplings occurs in the LDS regardless of competitive understory conditions (Werner and Franklin 2010)
3. under conditions of frequent burning, observed responses vary from (1) muted release of both eucalypts and non-eucalypts into the small tree class (>5 cm to <10 cm dbh) under mature canopy conditions (Russell-Smith et al. 2010; Table 1); and (2) relatively high densities of eucalypts being released, especially in LDS treatments (Prior et al. 2010, Bond et al. 2012, Werner 2012) and under open-canopy (Fig. 8) conditions, whereas (3) non-eucalypts are released at substantially reduced rates, especially under LDS fire (Prior et al. 2010, Bond et al. 2012) conditions
4. in the absence of burning, observed responses vary from substantial release of both eucalypts and non-eucalypts at Kapalga treatments (Prior et al. 2010, Bond et al. 2012) to very limited response of eucalypts and very substantial release of non-eucalypts in two twenty-year studies under mature canopy conditions (Russell-Smith et al. 2003, Woinarski et al. 2004)

These oftentimes seemingly disparate responses, for example, the different responses of juveniles and saplings observed under fire regime treatments at Kapalga and at other sites, feasibly can be reconciled as reflecting significant interactions between fire regime characteristics and variable site overstory competition effects (e.g., Bond et al. 2012). Hence, whereas long-term data from the Munmarlary and Solar Village sites strongly implicate the role of mature canopy conditions on inhibition of eucalypt recruitment, the relative release of eucalypts in the absence of burning at Kapalga suggests that variable, less competitive canopy conditions (e.g., the general availability of adequate-sized gaps) have facilitated sapling release at that site. Similarly, the relative substantial release of eucalypts at Kapalga under frequent burning, especially in LDS treatments, effectively mirrors the response of eucalypts at frequently burnt, open-canopied post-Cyclone Monica sites but stands in stark contrast to the response of eucalypts at fire-prone, more mature-canopied Litchfield sites. Considerable spatio-temporal variability and dynamism in regional savanna canopy cover conditions, predominantly driven by fire regime effects, have been demonstrated over four decades at Kapalga by Lehmann et al. (2008).

At savanna-wide scales, it is self-evident that resource limitation, especially seasonal water availability, asserts significant control on site productivity and hence the upper bound of woody biomass along continental rainfall gradients (Sankaran et al. 2005, Fensham et al. 2009, Lehmann et al. 2014). The very considerable biomass variability observed at sites under this upper bound is often attributed to disturbance effects, especially fire disturbance. At the stand level under Australian conditions, Murphy et al. (2015) argue that water resource limitation rather than fire disturbance is the primary driver of eucalypt biomass whereas non-eucalypts are more vulnerable to fire regime impacts. Although this proposition resonates generally with our proposed schema (Fig. 1) and findings, we note that fire effects on savanna woody biomass have been shown to be considerable at local scales (Lehmann et al. 2008, 2009), especially on non-eucalypts (Lawes et al. 2011*c*), in the instance of severe fire regimes (Murphy et al. 2010), following very severe fires (Lonsdale and Braithwaite 1991, Williams et al. 1999, 2003), and especially extensive (>1000 km^2) severe fires under more precarious lower rainfall savanna conditions (Edwards et al. 2018).

The above discussion illustrates the challenges inherent in disentangling disparate observations and findings associated with complex fire response datasets. Higgins et al. (2007:1124) concluded similarly that the variable results of African fire manipulation experiments “make it difficult to generalize about the influence of fire.” In a previous assessment of vegetation responses to ambient fire regimes based on ten years of observations from 122 north Australian savanna plots, the authors posed an extended challenge: “How do effects of experimental fire treatments. . .in different landscape settings relate to the complexity and generality of ambient fire regimes?” (Russell-Smith et al. 2010:1628).

Such questions can have significant ramifications—for example, the generally contrasting perspectives on fire regime-driven savanna tree carbon dynamics afforded respectively by empirically based assessment of extensive ambient fire regime data, contrasted with more process-based modeling and associated assumptions derived from restricted manipulative treatments (Cook et al. 2015). We do not have a simple solution for this conundrum. However, as illustrated here, while observations derived from a diversity of observational and manipulative studies clearly are instructive, their interpretation evidently requires a broader appreciation of the site-based historical vegetation dynamics and disturbance context.

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