Austral Ecology (2009) 34, 120-131

# Contrasting demographics of tropical savanna and temperate forest eucalypts provide insight into how savannas and forests function. A case study using *Corymbia clarksoniana* from north-eastern Australia

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Abstract Eucalypts (Eucalyptus spp. and Corymbia spp.) dominate many communities across Australia, including frequently burnt tropical savannas and temperate forests, which receive less frequent but more intense fires. Understanding the demographic characteristics that allow related trees to persist in tropical savannas and temperate forest ecosystems can provide insight into how savannas and forests function, including grass-tree coexistence. This study reviews differences in critical stages in the life cycle of savanna and temperate forest eucalypts, especially in relation to fire. It adds to the limited data on tropical eucalypts, by evaluating the effect of fire regimes on the population biology of Corvmbia clarksoniana, a tree that dominates some tropical savannas of north-eastern Australia. Corymbia clarksoniana displays similar demographic characteristics to other tropical savanna species, except that seedling emergence is enhanced when seed falls onto recently burnt ground during a high rainfall period. In contrast to many temperate forest eucalypts, tropical savanna eucalypts lack canopy-stored seed banks; time annual seed fall to coincide with the onset of predictable wet season rain; have very rare seedling emergence events, including a lack of mass germination after each fire; possess an abundant sapling bank; and every tropical eucalypt species has the ability to maintain canopy structure by epicormically resprouting after all but the most intense fires. The combination of poor seedling recruitment strategies, coupled with characteristics allowing long-term persistence of established plants, indicate tropical savanna eucalypts function through the persistence niche rather than the regeneration niche. The high rainfall-promoted seedling emergence of C. clarksoniana and the reduction of seedling survival and sapling growth by fire, support the predictions that grass-tree coexistence in savannas is governed by rainfall limiting tree seedling recruitment and regular fires limiting the growth of juvenile trees to the canopy.

Key words: Corymbia, demography, Eucalyptus, fire, temperate forest, tropical savanna.

## INTRODUCTION

The processes that control the coexistence of grasses and trees, which is a feature of tropical savannas, have been widely debated (Walker 1985; Scholes & Archer 1997; Higgins *et al.* 2000). Initial discussions focused on resource competition and the division of soil resources between shallow-rooted grasses and deeprooted trees (Walter 1971; Walker & Noy-Meir 1982). More recently, Higgins *et al.* (2000) argued that rainfall governs tree seedling establishment, while increasing grass density promotes fire, which in turn limits the growth of tree saplings to the canopy by keeping them within the 'fire-trap' (Bond & Midgley 2001). Evidence supporting this model includes seedling recruitment studies of some South American savanna trees

Accepted for publication February 2008.

© 2009 The Author Journal compilation © 2009 Ecological Society of Australia (Hoffmann 1996) and African *Acacia* spp. (Wilson & Witkowski 1998) and the role of regular fire in keeping saplings and trees stunted in South American (Hoffmann & Solbrig 2003) and African savannas (Higgins *et al.* 2007).

Savannas across each continent are dominated by their own suite of related tree taxa, such as the acacias of Africa and eucalypts of Australia, and this pattern may be evidence of the rapid evolution of trees tolerant of increased fire frequencies following the appearance of C4 grasses in the late Tertiary (Bond *et al.* 2005). Eucalypts (*Eucalyptus* spp. and *Corymbia* spp.) dominate not only savannas, but also temperate and sub-tropical forests and mallee shrublands across Australia. Tropical eucalypt savannas are densely grassed and regularly burnt, whereas temperate eucalypt forests possess comparatively little grass biomass and receive less frequent but more intense fires. Contrasting the demographic processes that govern eucalypt populations of tropical savannas and temperate forests can provide an insight into ecosystem function, including how trees coexist with grasses in savannas.

In contrast to many eucalypts of temperate forests of southern Australia, such as C. maculata (Pook et al. 1997), Eucalyptus delegatensis (O'Dowd & Gill 1984) and E. regnans (Ashton 1979), tropical eucalypts do not store seed in the canopy for several years as serotinous seed banks (Dunlop & Webb 1991). Mature seed and capsules of eucalypts of tropical savannas fall to the ground annually in the late dry season and wet season (Burrows & Burrows 1992; Brennan 1996; Setterfield & Williams 1996; Williams et al. 1999a; Williams 2003). This absence of a serotinous seed bank may reflect the general absence of broad-scale, intense crown fires that can trigger mass seed drop in temperate serotinous Eucalyptus species (Ashton 1979), but which are rare in savannas of northern Australia (Craig 1997).

Fire can influence seed production in tropical eucalypts. Setterfield (1997) demonstrated that the seed production of *E. miniata* and *E. tetrodonta*, which co-dominate many tropical savannas across the Northern Territory and Western Australia, can be reduced by both early and late dry season fires, owing to the death of flower buds and seed within immature capsules. Flower production is also reduced as a result of the re-allocation of resources to replace leaves lost through leaf scorch during dry season fires (Setterfield 1997).

Seedling emergence of tropical eucalypts is typically irregular and does not occur after most fires (Lacey 1974; Dunlop & Webb 1991; Fensham 1992). Gill *et al.* 1990 hypothesized that the rarity of tropical eucalypt seedlings may be due to either regular fires killing cohorts; irregular long-term episodic establishment events; or competitive exclusion of seedlings by other plants.

Field experiments indicate that *E. miniata* recruits more seedlings in unburnt rather than recently burnt savanna (Setterfield 2002). In contrast, seed germination typically occurs as a pulse following most fires in many temperate eucalypts, such as *E. delegatensis* (Bowman & Kirkpatrick 1986; Vivian *et al.* 2008), *E. leucoxylon, E. ovata* (Withers 1978) and *E. regnans* (Ashton 1979). The ability of temperate forest eucalypts to store large quantities of seed in canopy capsules, and to release these seed after fires, overwhelms seed predators and allows dense post fire germination. This mechanism has been reported for *E. regnans* (Ashton 1979) and *E. delegatensis* (O'Dowd & Gill 1984), but is absent in tropical savanna eucalypts.

Very few *E. regnans* seedlings successfully establish in unburnt temperate forests, owing to high levels of disease and herbivory and competition for nutrients and light (Ashton & Chinner 1999). Fire intensity, and subsequent retention of overstorey and leaf litter, can also influence the establishment of temperate forest eucalypts, such as *E. delegatensis* (Vivian *et al.* 2008). In contrast, Setterfield (2002) found for the tropical savanna *E. miniata*, that survival of seedlings in the first few months following emergence may have been reduced in sites burnt prior to germination, owing to poor micro-site conditions, such as higher grass cover and reduced canopy cover in recently burnt than unburnt savanna. More critical to survival in frequently burnt savannas is the low proportion of *E. miniata* seedlings able to survive fire within a year of germination (Fensham 1992; Setterfield 2002).

A feature of tropical savanna eucalypt populations is an abundant bank of stunted, multi-stemmed saplings <2 m tall (Fensham 1994; Bowman & Panton 1995). This reserve of stunted saplings is absent in many temperate forest species, such as *E. regnans*, whose saplings die from pathogen and predator attack in the limited light available in long unburnt forests (Ashton & Chinner 1999).

The prediction of Higgins *et al.* (2000) that regular fires keep saplings stunted in the tropical savanna firetrap by forcing them to re-coppice post-fire from ground level. This has been identified as a critical factor affecting the growth of saplings of several trees of Australian tropical savannas (Bowman *et al.* 1988; Crowley & Garnett 1998). However, tropical eucalypt saplings do not always grow rapidly in the absence of fire, and a proportion may die-back to ground level during the dry season in the absence of fire (Pryor *et al.* 1997). While stunted saplings of *E. tetrodonta* have been documented to grow above 2 m in the absence of fire, *E. miniata* saplings can remain stunted with fire exclusion for two decades (Fensham 1990; Bowman & Panton 1995; Russell-Smith *et al.* 2003).

Regular fire may affect the survival and growth of eucalypt trees. While tropical eucalypts can resprout after full canopy scorch (Gill 1997; Williams et al. 2002), fire intensity can affect the proportion of trees that resprout epicormically from the canopy rather than the trunk base (Williams et al. 1999b). Tree basal area remained stable over 5 years with both fire exclusion and annual early dry season burning in savanna at the Kapalga research station in the Northern Territory, but declined with annual late dry season fires, primarily as a result of stem mortality (Andersen et al. 2005). The basal area of E. miniata trees at the nearby Munmarlary research site increased more in savanna burnt annually in the early dry season for 21 years compared with unburnt and late dry season burnt savanna, while no change in basal area was recorded for E. tetrodonta (Russell-Smith et al. 2003). Vigilante and Bowman (2004) demonstrated an increase in the density of *E. miniata* and *E. tetrodonta* trees (>2 m tall) with increasing intervals between fires in northwestern Australia. In north-eastern Australia, the basal area of C. clarksoniana increased over 5 years irrespective of fire regime (Williams *et al.* 2003). In dry sclerophyll forest of sub-tropical south-eastern Queensland, annual burning in the mid dry season for 44 years produced no effect on the growth rates of *E. acmenoides* and *E. drepanophylla*, but enhanced the growth of *E. tereticornis* in comparison to unburnt forest (Guinto *et al.* 1999).

Tropical eucalypts may be prime examples of savanna trees that counter the irregularity of seedling recruitment events through the persistence of established plants (Bond & Midgley 2001). The life span of a tropical eucalypt may typically be over a century (Mucha 1979). Irregular but recurring drought and the resulting tree death is a major factor in their natural long-term population dynamics (Fensham & Holman 1999).

Most information on eucalypts of tropical savannas comes from studies of trees in the Northern Territory and the Kimberley, especially E. tetradonata and E. miniata. Much less information has been collected on eucalypts of north-eastern Australia and therefore the consistency of demographic patterns of tropical eucalypts has not been tested. Corymbia clarksoniana is a eucalypt that dominates or co-dominates many savannas in coastal and sub-coastal north-eastern Australia. There have been no reported studies of the demographics of this widespread tree, which grows in communities that are frequently burnt. This paper assesses the effect of fire regime on aspects of the population biology of C. clarksoniana by evaluating the effect of fire regime on differing stages in the plant's life cycle. To evaluate the predictions by Higgins et al. (2000) in explaining grass-tree coexistence, particular attention is given to the role of rainfall and fire on seedling emergence and of fire regime on the growth of saplings. The results are used to:

• Test whether the ecology of *C. clarksoniana* is consistent with other tropical eucalypts, especially *E. tetradonta* and *E. miniata*;

Compare the demographics of a tropical eucalypt with eucalypts that dominate temperate forests, to help understand factors governing grass-tree coexistence in tropical savannas.

## **METHODS**

### Study site

Aspects of the population biology of C. clarksoniana were examined in a tropical eucalypt savanna at Cape Cleveland, approximately 25 km east of Townsville, north-eastern Australia (19°16'30"S, 147°02'30"E). The site is dominated by C. clarksoniana, C. tessellaris and E. platyphylla, with a dense layer of grasses, Heteropogon triticeus, H. contortus and Themeda triandra (taxonomy follows Henderson 2002). Townsville experiences summer wet seasons, with 78% of the 1143 mm mean annual rain falling between December and March. Three of the 5 years during this study received above average rainfall (1997, 1998 and 2000) with 1998 experiencing the highest rainfall from August to November recorded in the 61 years of records by the Bureau of Meteorology at the Townsville airport, 25 km from the study site (Table 1).

The study site was burnt in July 1997 and then split into nine parallel blocks of approximately 1 ha in area (80 m width by 130 m length), by slashing 4 m wide fire lines. Three fire treatments were implemented in 1999: unburnt control, or burnt in either the early (May) or late dry season (October) of 1999 (Williams *et al.* 2003). Each fire treatment was imposed on three of the nine 1-ha blocks and the blocks were allocated to treatments using a randomized block design (Williams *et al.* 2003). A 20-m-wide and 700-m-long block, adjacent to and perpendicular with the nine 1-ha blocks was burnt annually to create a fire break for the site.

Year	Annual total	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
(a)													
1997	1496.8	121.6	400.2	453.8	9.0	49.2	9.0	6.2	19.0	16.6	8.4	3.2	400.6
1998	1992.2	973.8	159.8	72.4	52.0	92.0	9.0	8.6	258.2	31.2	108.0	104.8	122.4
1999	1076.4	149.8	317.4	138.4	100.0	9.8	0.4	14.4	6.2	0.2	2.2	186.0	151.6
2000	2399.8	157.4	845.4	176.6	546.2	32.0	31.4	0.4	0.2	0.4	45.4	345.2	219.2
2001	467.2	47.2	236.0	58.4	10.0	0.0	9.4	8.0	0.0	1.2	25.8	71.2	0.0
(b)													
1997	1478.7	132.6	393.2	279.3	2.2	67.6	9.3	10.0	14.0	9.6	43.2	3.0	440.4
1998	1837.1	544.9	303.8	55.0	96.6	89.8	16.6	26.4	52.6	44.4	200.4	140.8	242.0
1999	1111.0	160.6	238.6	102.8	111.0	14.4	0.0	8.0	31.2	4.6	1.6	233.4	204.8
2000	2716.6	79.4	937.6	184.4	442.0	132.6	35.2	0.0	1.2	0.0	46.8	437.2	418.4
2001	441.5	77.2	176.2	64.7	26.2	0.0	22.2	17.0	0.0	2.8	39.4	9.4	6.4

**Table 1.** Monthly rainfall between 1997 and 2001 recorded by the Australian Bureau of Meteorology at (a) the Townsville airport, 25 km west of the study site and (b) Cape Cleveland, 10 km from the study site

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Small experimental fires, such as the 1-ha blocks burnt in this study, may not always provide the full potential fire intensity, nor the patchiness, produced by a larger landscape fire (Russell-Smith et al. 2003). While there were no unburnt patches within burnt treatment blocks in this study, fire intensity may not have been significantly reduced, as recent research indicates fire fronts of 120 m or greater (as present in this trial of 130-m-long blocks) reach their maximum potential rate of spread, and hence potential intensity, almost immediately (Cheney et al. 2001). Small fire block sizes may also lead to concentrated herbivory in recently burnt ground (Whelan 1995). While no cattle were present within the trial area during the study, native herbivores, specifically agile wallabies (Macropus agilis), were present throughout the 5 years. However, the intensity of herbivory after the July 1997 fire was probably minimized by the 10-ha extent of the fire. In August 1999, a wildfire burnt the savanna surrounding the trial site, hence, greatly increasing the area of recently burnt ground soon after the first 1999 fires and prior to any seedling emergence in the early burnt blocks.

## SEED PRODUCTION

The effect of fire season on seed production of *C. clarksoniana* was assessed through surveys of capsule density. Capsules of *C. clarksoniana* were observed to fall when mature, in late September to early November each year (Williams 2003). Seed is shed both prior to and immediately following capsule fall (P. R. Williams *pers. obs.*, 1999). The density of fallen *C. clarksoniana* capsules was counted in December 2000, after the majority of capsules had fallen, to estimate seed production in the year following burning treatments.

Capsules were counted within 50 throws of  $1-m^2$  quadrat in each of the nine 1-ha blocks. The quadrat was thrown in a random direction, at points five paces apart, while walking up and back across each 1-ha block. The number of seeds was counted in each of 30 capsules of *C. clarksoniana*, collected prior to opening, to allow an estimate of seed density from the capsule density data. Seed weight was measured using five replicate batches of 25 seeds.

The effect of fire season on seed production of *C. clarksoniana*, in the year following fire, was based on the density of capsules on the ground, converted to seed density ( $m^{-2}$ ) using the mean number of seeds per capsule estimated from 30 capsules. A non-parametric Kruskal–Wallis ANOVA by ranks was used to assess the statistical significance of differences between fire treatments (unburnt, early and late dry season burnt). The 50 replicates from each 1-ha block were pooled to provide 150 replicates for each fire treatment. A Mann–Whitney *U*-test was used as a *post hoc* compari-

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son, with a Bonferroni adjustment of significance level for multiple comparisons (Sokal & Rohlf 1995).

#### Natural seedling emergence

Annual seedling surveys of the *C. clarksoniana* community were undertaken across each of the nine 1-ha blocks at the start of the wet season (i.e. December) for 5 years, between 1997 and 2001. Seedlings were counted within a  $1-m^2$  quadrat, which was thrown 50 times while traversing up and back through each of the nine 1-ha blocks. The quadrat was thrown in a random direction at each of the 50 points, which were five paces apart.

Mass recruitment of *C. clarksoniana* seedlings occurred across the site in October 1998. This was the only time during the 5-year study where seedling emergence of *C. clarksoniana* occurred, and at that stage the nine 1-ha blocks had remained unburnt for 16 months. In order to document seedling density in more recently burnt savanna, the December 1998 survey also documented the density of *C. clarksoniana* seedlings along the annually burnt fire break block, burnt most recently in September 1998, and along the 4-m-wide-slashed fire line, that separated the fire break block with the nine 1-ha blocks. This was cut 4 months prior to the December 1998 survey.

No replication of the recently burnt treatment was available in December 1998, and therefore results must be interpreted within this design constraint. A non-parametric Kruskal-Wallis ANOVA by ranks was used to examine significance of differences in seedling density between the 450 quadrats within the nine 1-ha blocks, and the 50 quadrats within each of the recently burnt fire break block and the recently slashed block in December 1998. A Mann–Whitney *U*-test was used as a *post hoc* test, with a Bonferroni adjustment for multiple comparisons (Sokal & Rohlf 1995).

#### Seedling emergence from planted seeds

An experiment, testing the effects of fire, grass layer removal and seed burial, was established to examine the micro-site requirements of *C. clarksoniana* for seedling emergence. Seeds were extracted from fallen capsules collected at Cape Cleveland in October 2000, and pooled. Three replicates of 25 seeds were placed on the soil surface, and three replicates of 25 seeds were buried with approximately 5-mm covering of soil, for each of three micro-site disturbance treatments:

- 1. Undisturbed; seeds placed in undisturbed savanna.
- Burnt; seeds placed on recently burnt ground. Each of the replicate fires was implemented across a 2 m × 3 m area on 19 October 2000.

3. Cut; seeds placed in an area that had the herbaceous layer cut and removed across a circular area of 1.5-m radius.

The treatments were established within  $20 \text{ cm} \times 20 \text{ cm}$  plots along the edge of a control block, which had remained unburnt for 3 years at that time. One of the edges of the three unburnt control blocks was randomly selected. Twenty-one possible plot locations were available along the 130-m length of the control block, allowing the separation distance of 6 m required for burnt treatments. Replicates of the three treatments were randomly allocated to the 21 available plot locations. Seeds were placed on the soil surface within plots on 4 December 2000. Seedling emergence was defined by cotyledon emergence and was assessed weekly.

Seed viability was assessed by placing three replicates of 100 seeds onto moist filter paper in a petri dish, sprayed with a 2 g L<sup>-1</sup>-solution of fungicide (Thiram) and incubated in a controlled temperature room at 27.5°C with a 12-h diurnal light regime. After a fortnight, ungerminated seeds were assessed for viability using a tetrazolium test (Moore 1985). A slit was made in seeds, which were then soaked in a 1% tetrazolium solution in the dark for 48 h. Seeds were then dissected under a microscope and assessed for the pink colouration that indicates a viable embryo. The number of viable seeds detected in the tetrazolium test was added to the number of seeds that germinated in the laboratory to produce a total number of viable seeds for each replicate of the control treatment.

The results of the field germination experiment were compared using a two-factor ANOVA to assess microsite disturbance with three levels (undisturbed, burnt and cut) and the factor seed burial (surface sown and buried seed). Data were expressed as percentage of viable seed, as determined from the results of germination in the laboratory and the tetrazolium test.

## Seedling survival

In November 1998, within 1 month of the mass seedling emergence of *C. clarksoniana* at Cape Cleveland, 50 seedlings were tagged in each of the nine 1-ha blocks. Seedlings were easily distinguished from established plants by the presence of broad cotyledons. Seedlings that emerged near the edges of the  $100\text{-m}^2$  plots used in the floristic surveys (Williams *et al.* 2003) were tagged to allow ease of relocation. In each of the nine 1-ha blocks, one of the four edges was randomly selected from each of the four 100-m<sup>2</sup> plots for the examination of seedlings. Additional plot edges were selected where needed to document 50 seedlings per 1-ha block. Seedling locations were tagged by placing fencing wire in the soil, two or

three centimetres from their base. Seedling survival was assessed, and heights measured, 7 months (prior to the May 1999 fires in early burnt 1-ha blocks), 19 months (May 2000) and 36 months (October 2001) after germination.

The statistical significance of differences between seedling survival of C clarksoniana in control, early and late dry season burnt blocks was compared using a one-factor ANOVA. The intention was to perform a repeated measure ANOVA on the percentage seedling survival at 7 months (prior to the May 1999 fires), 19 and 36 months following germination. A Cochran's test (Underwood 1997) indicated variance heterogeneity for the 36-month survival data could not be resolved with data transformations. Therefore, a repeated measure ANOVA was performed on the survival data at seven and 19 months, with a separate non-parametric Kruskal-Wallis ANOVA by ranks used to assess significance of differences between fire treatments at 36 months after germination (Sokal & Rohlf 1995; Zar 1999).

To examine the statistical significance of differences in seedling heights between fire treatments, an independent *t*-test was performed on the heights of seedlings surviving at 36 months in the control and early burnt blocks, as no seedlings remained in the late burnt blocks (Zar 1999).

#### Survival and growth of saplings

Survival and growth of *C. clarksoniana* saplings (defined as individuals <2 m in height) were compared between unburnt, early (May 1999) and late dry season (October 1999) burnt savanna. Heights were recorded for all *C. clarksoniana* saplings within 36,  $100\text{-m}^2$  plots at Cape Cleveland (see Williams *et al.* 2003 for plot design) from March to May 1999, prior to the implementation of the early dry season fires. The saplings were tagged and re-measured at the same time of year in 2000 and 2001.

The influence of fire regime on the growth and survival of *C. clarksoniana* saplings was assessed using a one-factor ANOVA to test the statistical significance of differences in survival and heights of saplings with time since last fire. Differences were assessed for survival and heights of saplings between fire treatments (control, early and late burnt) using a repeated measure ANOVA, with the repeated measure factor 'year' containing three levels (1999–2001). Individuals that were <2 m in height during the initial 1999 survey that grew >2 m by 2001 remained in the analyses to ensure accuracy in assessment of the changes in survival and height. A Spearman;s rank correlation was used to assess the heights of saplings with time since last fire.



**Fig. 1.** Mean (+1 standard error) seed production of *Corymbia clarksoniana* at Cape Cleveland in December 2000, in savanna with different fire histories. Control, last burnt in July 1997; Early burnt, last burnt in May 1999; Late burnt, last burnt October 1999. Columns with different superscripts are significantly different at P < 0.05.

## RESULTS

#### Seed production

The mean number of seeds per capsule of *C. clarksoniana* was 5.0 (n = 30; SE = 0.33). The mean weight per 25 seeds was 0.1924 g (n = 5; SE = 0.01). The late dry season fire of 1999 significantly reduced seed production (as estimated by capsule density on the ground) in the following year, compared with unburnt controls ( $H_{2447} = 11.175$ ; P < 0.004; Fig. 1). Seed production in savanna burnt during the early dry season fire was not significantly different from either unburnt or late burnt sites.

#### Natural seedling emergence

*Corymbia clarksoniana* seedlings were only observed in one of the 5 years of survey, 1998. The additional surveys in 1998 of *C. clarksoniana* seedlings within the fire break block, burnt 3 months prior to the seedling survey, and fire line slashed 4 months prior to the survey, indicated the recently burnt and slashed savanna contained significantly higher densities of *C. clarksoniana* seedlings than in the adjacent nine 1-ha blocks, which had not been burnt for 16 months (Fig. 2).

#### Seedling emergence from planted seeds

Mean seed germination of *C. clarksoniana* in the laboratory was 38% (SE = 7). The tetrazolium test found that a mean of 75% (SE = 5) of seeds were viable. Therefore, 51% of the 75 viable seeds per replicate tested, germinated in the laboratory within a fortnight of sowing.

Of the planted seeds, seedlings only emerged in cut or burnt plots. While no seedlings emerged from seeds planted in the undisturbed plots, differences between



Fig. 2. Mean (+1 standard error) natural seedling density of *Corymbia clarksoniana* in eucalypt savanna in December 1999, at Cape Cleveland. Burnt, burnt 2 months prior to survey; Slashed, grass was cut 4 months prior to survey; Unburnt, savanna that was unburnt for 16 months at the time of survey.



**Fig. 3.** Mean (+1 standard error) percentage seedling emergence of surface sown ( $\Box$ ) and buried ( $\blacksquare$ ) viable seeds of *Corymbia clarksoniana* in eucalypt savanna at Cape Cleveland. Seeds sown on the soil surface and buried to 5 mm in Undisturbed, savanna unburnt for 3 years; Cut, unburnt savanna with the herbaceous layer cut and removed prior to sowing seeds; Burnt, savanna burnt prior to seed sowing.

**Table 2.** Results of two-factor ANOVA of the effect of microsite disturbance and seed burial on seedling emergence of *Corymbia clarksoniana* in eucalypt savanna at Cape Cleveland. *F* statistic, denominator d.f., numerator d.f.

Treatment	F statistic	P value
Micro-site disturbance	$F_{2,12} = 2.822$	0.099
Seed burial	$F_{1,12} = 2.689$	0.127
Disturbance x burial	$F_{2,12} = 0.822$	0.463

treatments were not statistically significant, because of inter-plot variation within treatments (Table 2, Fig. 3).

#### Seedling survival

Only 5% of *C. clarksoniana* seedlings survived to 36 months after germination in undisturbed savanna in control blocks, and no seedlings remained alive in late burnt blocks (Fig. 4). No statistically significant



**Fig. 4.** Mean (+1 standard error) percentage (a) seedling survival and (b) seedling height with age of *Corymbia clarksoniana* in eucalypt savanna at Cape Cleveland. Savanna last burnt July 1997 ( $\Box$ ); savanna burnt in the early dry season (May) 1999 (7 months after germination) and July 1997 ( $\blacksquare$ ); savanna burnt in the late dry season (October) 1999 (11 months after germination) and July 1997 ( $\blacksquare$ ).

**Table 3.** ANOVA results of fire season treatments on the survival of *Corymbia clarksoniana* seedlings that emerged 7 months prior to the early dry season fire

Analysis	F or $H$ Statistic	P value
Repeated measures ANOVA		
at seven and 19 months:		
Fire	$F_{2,6} = 2.184$	0.194
Age of seedling	$F_{1,6} = 55.051$	< 0.001
Fire × Age	$F_{2,6} = 0.459$	0.652
Kruskal–Wallis ANOVA at	$H_{2,6} = 4.300$	0.116
36 months		

 $F_{4,145}$ , F or H value, denominator d.f., numerator d.f.

differences were detected in percentage seedling survival between fire treatments (Table 3). The inability to detect a significant difference, even though no seedlings survived in late burnt savanna after 36 months, was probably a result of the variation in survival in unburnt savanna, where no seedlings survived after 36 months in one of the three replicate blocks. However, a significant age effect was detected in the repeated measures ANOVA for seven and 19 months since germination, indicating a significant decline in seedling survival with time since establishment of cohort (Table 3). Nine per cent of *C. clarksoniana* seedlings that were alive in early burnt blocks immediately prior to the May 1999 fires, were alive 1 year following those burns.

Growth of *C. clarksoniana* seedlings levelled off after 19 months, with no additional height recorded by 36 months. The mean height of *C. clarksoniana* 



**Fig. 5.** Mean (+1 standard error) annual growth of *Corymbia clarksoniana* saplings (<2 m tall in 1999) with years since fire.

seedlings after 36 months was not significantly different between control and early burnt blocks ( $t_9 = 0.995$ , P > 0.05; Fig. 5b).

#### Survival and growth of saplings

All *C. clarksoniana* saplings that were <1.5 m at the time of fire re-grew from sub-soil buds at the base of the stem. Saplings greater than 1.5 m tended to sprout epicormically from buds on the stem. Most saplings re-grew to their pre-fire heights in the first year after fire, resulting in annual growth being significantly greater in the first year after fire than subsequent years (F = 54.19, P < 0.001; Fig. 5). Annual growth of >0.3 m in the second to fourth year after fire occurred only four times, the greatest being 0.7 m in one sapling in savanna unburnt for 3 years. Three saplings grew above 2 m in height between 1999 and 2001 in savanna burnt in the early dry season of 1999.

No significant fire by year interaction, which would indicate an effect of the 1999 fires, was detected for the density or height of *C. clarksoniana* saplings (Table 4). However, a significant block effect was found for both density and height, with fewer saplings in the third block of control, early and late burnt sites. A significant year effect for height indicated growth of *C. clarksoniana* saplings between 1999 and 2001 consistent across all treatments (Fig. 6; Table 4). A significant positive correlation was detected between the height of saplings and years since last fire, indicating an overall increase between 1 and 4 years after fire (n = 1080, Spearman's R = 0.090, P < 0.003; Fig. 7).

#### DISCUSSION

#### Seed production

Late dry season fires reduced seed production by C. *clarksoniana* in the year after burning. This probably

Species	Fire	Block	Year	Fire × Year	
Density Height	$F_{2,6} = 0.146 \ F_{2,6} = 0.310$	$F_{6,27}=4.989^{\star\star\star} \ F_{6,27}=4.137^{\star\star}$	$F_{2,12} = 0.191$ $F_{2,12} = 17.181^{***}$	$F_{4,12} = 2.989$ $F_{4,12} = 0.850$	

Table 4. Repeated measures ANOVA results of *Corymbia clarksoniana* sapling density and height between 1999 and 2001 in control, early and late burnt blocks

 $F_{2,6}$ , F value, denominator d.f., numerator d.f.; F values without an asterisk (\*) are not significantly different at P > 0.05; \*P < 0.05; \*P < 0.01; \*\*P < 0.001.



**Fig. 6.** Mean (+1 standard error) (a) density and (b) height of *Corymbia clarksoniana* saplings between 1999 and 2001 in control ( $\Box$ ), early ( $\blacksquare$ ), and late dry season burnt ( $\equiv$ ) savanna at Cape Cleveland. Note the 1999 figures were recorded prior to the early and late dry season fires of that year.



**Fig. 7.** Mean (±1 standard error) height of *Corymbia clarksoniana* saplings (<2 m tall in 1999) with years since fire in eucalypt savanna at Cape Cleveland.

resulted from mortality of flower buds caused by the canopy scorching of late fires. This is similar to other tropical eucalypts, *E. miniata* and *E. tetrodonta*, which Setterfield (1997) demonstrated to have reduced seed production after both early and late dry season annual fires. Seed production in temperate forest eucalypts can vary strongly between years in the absence of fire (Ashton & Attiwill 1994; Pook *et al.* 1997). It is completely extinguished by canopy burning of fire-killed forest eucalypts, but the effect of fire on subsequent seed production of resprouting forest eucalypts of southern Australia requires evaluation.

The ability of many temperate forest eucalypts to store serotinous seed banks provides a mechanism to overcome annual fluctuations in seed production, by storing three or more years of seed, and by ensuring

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abundant seed falls into the immediate post-fire environment. The absence of a serotinous seed bank in tropical savanna eucalypts removes the direct fire-cued seed fall mechanism, which may be less important in savannas where frequent fire provides an ash bed every few years. The timing of seed fall by tropical savanna eucalypts is consistently in the late dry season and wet season (Burrows & Burrows 1992; Brennan 1996; Setterfield & Williams 1996; Williams 2003). This indicates the importance of timing seed fall with the onset of wet season rainfall. By having seed fall occur in the late dry season rather than wet season, *C. clarksoniana* hedges its bets by linking seed fall soon after any mid to late dry season fires, but requires unusually early wet season rain.

#### Natural seedling emergence

Seedling emergence of C. clarksoniana was observed exclusively in 1998, indicating irregular recruitment events. That year had the highest recorded rainfall from August to November (the period prior to and during seed drop and germination for C. clarksoniana), more than four times the average rainfall for those pre-wet season months. If seedling recruitment events for this tree are linked to high rainfall at the time of seed drop, then recruitment events may by quite rare, as rainfall of more than twice the average from August to November has only been recorded eight times in the last 61 years. Two of those years occurred during this study (1998 and 2000), with no natural seedling recruitment of C. clarksoniana in 2000, suggesting very high rainfall at the period of seed drop may be necessary. Seed germination after above average rainfall has also been observed for E. tereticornis (Fensham & Fairfax 2006). This pattern of episodic seedling emergence resembles that of some tropical rainforest trees. For instance Connell and Green (2000) documented only six episodes of dense seedling emergence over 32 years, by a tropical rainforest tree in northeastern Australia.

Seedling surveys of *C. clarksoniana* in 1998 indicated that while this species does germinate in savanna that has remained unburnt for 16 months, seedlings emerged in recently burnt and slashed savanna at 14–17 times the density of unburnt savanna. These

results should be considered in the light of the fact that the data were collected from only a single slashed and recently burnt block, and differences may have resulted from a separate factor linked within the recently burnt and slashed areas. However, given the proximity of these areas to the unburnt blocks, the results suggest seedling emergence of *C. clarksoniana* can be enhanced in burnt savanna, and sites with low herbaceous cover.

#### Seedling emergence from planted seeds

Due to low and variable germination, experimental manipulation of micro-site did not provide conclusive proof that seedling emergence of C. clarksoniana is increased in recently burnt savanna or where the ground cover is removed. No seedlings emerged from seed sown in undisturbed savanna, while slightly higher recruitment occurred from buried rather than surface sown seeds in burnt or cut savanna. However, the increased seedling emergence documented in the seedling surveys in recently burnt and slashed savanna, coupled with the absence of recruitment from seeds experimentally sown onto undisturbed plots, combine to provide some evidence that C. clarksoniana seedling emergence is enhanced where the herbaceous cover is thin, and particularly when seeds fall onto recently burnt ground.

The irregularity of *C. clarksoniana* seedling emergence, occurring only once in this 5-year study and not triggered by every fire, is consistent with that of other tropical savanna eucalypts (Lacey 1974; Gill *et al.* 1990; Fensham 1992; Setterfield 2002). The restriction of natural *C. clarksoniana* seedling emergence following the highest recorded rainfall event during the period of seed drop, supports model of Higgins *et al.* (2000) that rainfall governs tropical savanna tree recruitment.

When C. clarksoniana germination did occur after high rainfall, the greater density of seedlings in recently burnt savanna was consistent with the post-fire germination of many temperate forest eucalypts (Ashton 1979), where greatest seedling density can occur in areas of higher fire intensity (Vivian et al. 2008). This contrasts with the tropical E. miniata, which recruits seedlings at greater density in unburnt savanna (Setterfield 2002). These differences between the two tropical eucalypts may reflect different micro-site environments in the savanna investigated by Setterfield (2002), which experiences an annual dry season senescence of much of the herbaceous layer, in contrast to that at Cape Cleveland, which is dominated by a perennial herbaceous layer. Competition with a dense grass layer has been demonstrated to reduce recruitment of temperate forest eucalypts, such as E. strzeleckii (Moxham & Dorrough 2008).

#### Seedling survival

Five per cent of *C. clarksoniana* seedlings survived in unburnt savanna after 3 years, while only 1% survived in savanna burnt in the early dry season, 6 months after germination. A small number of *C. clarksoniana* seedlings resprouted after late dry season fires that occurred 1 year after germination; however, no seedlings remained alive in late burnt savanna 3 years after germination. Young seedlings of coexisting grasses and herbs have greater percentage survival after fire (Williams 2004). These data indicate that when the occasional recruitment of *C. clarksoniana* occurs, the absence of fire for several years will allow a greater density of seedlings to establish.

The fire-sensitivity of young *C. clarksoniana* seedlings corresponds with that of *E. miniata* (Setterfield 2002) and seedlings of South American savanna trees (Hoffmann 1998). Low levels of seedling survival in the absence of fire may be common among all eucalypts. Fensham (1992) found very low (<5%) seedling survival of *E. miniata* and *E. tetradonata* seedlings in unburnt tropical savanna. Seedling survival of temperate forest eucalypts is also typically low (i.e. <10%) after two or 3 years (e.g. Withers 1978; O'Dowd & Gill 1984; Bowman & Kirkpatrick 1986), although *E. regnans* can have up to 70% seedling survival after 3 years (van der Meer *et al.* 1999).

Even though only 5% of C. clarksoniana seedlings survived in the absence of fire for 3 years, this equates to 250 seedlings per ha where seed fell onto, and germinated within, unburnt savanna. Had the greater density of seedlings that germinated after the 1998 fire remained unburnt for 3 years, it is possible that 5000 seedlings per ha may have been present in 2001. This represents a substantial addition to the population of approximately 1000 saplings and 150 trees per ha. Given several germination events over the >100 year life span of each mature tree, the seedling density germinating in unburnt savanna may be sufficient to replace lost mature trees over time. However, the absence of fire for several years after germination is critical to allow sufficient seedling survival. Constant annual or biennial burning may inhibit the establishment of seedlings into the sapling bank, which could potentially lead to reduced tree density and a more open savanna structure in the long term, especially if intense fires cause top kill of existing trees.

#### Survival and growth of saplings

The density of *C. clarksoniana* saplings remained stable between 1999 and 2001, irrespective of fire regime. *Corymbia clarksoniana* saplings were not killed by fire, but rapidly re-grew after both early and late dry season fires, to return to their pre-fire heights within a year of burning. The rapid post-fire re-growth of *C. clarksoni*ana saplings, allowing a return to pre-burn height is consistent with coppicing saplings of other savanna trees in northern Australia (Fensham 1994) and South America (Hoffmann & Solbrig 2003), although fire can also cause considerable mortality of South American saplings (Hoffmann 1998).

While no significant interaction between fire treatment and year could be detected for sapling height, a significant block effect indicated there was existing variation in sapling heights between plots at the commencement of this study, which may be due to species interactions, patchiness of previous fires or edaphic factors. A significant year effect in sapling heights reflects the growth of C. clarksoniana saplings between 1999 and 2001, which was consistent across all fire regimes. While the interaction between fire and year was not significant in the repeated measures ANOVA, a significant correlation between sapling height and time since fire was detected, with a steady increase in height with time since fire. This apparent inconsistency in statistical results can be explained by the fact that the comparisons between burnt and unburnt plots in the repeated measures analyses did not compare sapling heights at the extreme range in time since fire, namely one and 4 years post-fire, as the 2000 comparison assessed 1 and 3 years after fire, and the 2001 data compared 2 and 4 years post-fire.

The data indicate that C. clarksoniana saplings slowly increase in height in the absence of fire. As a result of the rapid return to pre-fire heights, burning may only inhibit the incremental growth in C. clarksoniana sapling height by a single year. However, sapling growth in the second and subsequent years after fire is slow, averaging about 7 cm a year. Combined with seedling growth data, these data suggest that a new C. clarksoniana seedling may grow to 2 m in height after about 30 years without fire, or about 40 years if subjected to fires every 3 years. This assumes that seedlings increase their growth rate to an average of 7 cm a year in their fourth year. This sapling aspect of the study has only evaluated fires in a single year and a sequence of fires may stunt sapling growth. It is also likely though that other factors stunt sapling growth, including insect attack (Fensham 1994) and competition with other species, other saplings and canopy trees (Fensham & Bowman 1992; Pryor et al. 1997).

The escape of stunted juvenile savanna trees from the flame zone has been repeatedly documented in tropical savannas experiencing infrequent fires (Higgins *et al.* 2000). This includes many noneucalypt trees of northern Australia, with intervals greater than 2 or 3 years allowing the release of stunted saplings (Bowman *et al.* 1988; Crowley & Garnett 1998; Russell-Smith *et al.* 2003). The growth of tropical eucalypt saplings beyond the flame zone may require longer fire intervals than many noneucalypt species, for example, *E. miniata* remained stunted after the absence of fire for 21 years (Russell-Smith *et al.* 2003). While this study suggests *C. clarksoniana* saplings have the potential to grow steadily to reach 2 m in height, only about 1% of all saplings did so over 3 years.

In contrast to the slow growth of tropical eucalypt saplings, the growth rates of temperate forest eucalypt seedlings can be rapid, with *E. regnans* seedlings reaching 2–5 m in height within 3 years of germination (van der Meer *et al.* 1999).

## CONCLUSION

Natural seedling emergence of C. clarksoniana only occurred in the year of above average rainfall during the period of seed fall. Fire was demonstrated to affect C. clarksoniana seed production; may have been a secondary factor (after rainfall) promoting seedling emergence; reduced seedling survival and inhibited juvenile sapling growth into the canopy. The demographics of C. clarksoniana are consistent with other tropical savanna eucalypts, with the exception of a clear rainfall link to seedling recruitment and apparent enhanced seedling density in recently burnt ground. The rainfallpromoted seedling emergence and reduction of seedling survival and sapling growth by fire, are consistent with the predictions of Higgins et al. (2000) that grass-tree coexistence in savannas is governed by rainfall limiting tree seedling recruitment and regular fires limiting the growth of juvenile trees to the canopy.

There are several key demographic characteristics that distinguish tropical savanna eucalypts from temperate forest eucalypts, allowing them to survive in frequently burnt, grassy communities, rather than less frequently but more intensely burnt temperate forests. In contrast to temperate forest eucalypts, tropical savanna eucalypts lack canopy-stored seed; time seed fall to coincide with the onset of predictable wet season rain; have very rare seedling emergence events, including a lack of mass germination after each fire; possess an abundant sapling bank that can remain stunted for many years; and every tropical eucalypt species has the ability to epicormically resprout after all but the most intense fires, to maintain canopy structure.

These differences between tropical savanna and temperate forest eucalypts suggest that in frequently burnt, grassy communities with predictable moderatelevel disturbance and consistent wet–dry seasons, the persistence of established saplings and mature plants is more effective for population persistence than mass or regular seedling recruitment events. Some temperate forest eucalypts, such as *E. regnans* and *E. delegatensis*, which experience occasional fires of very high intensity that kill mature trees, may have long-lived individuals but also rely on fire-triggered mass germination and rapid or at least continuous sapling growth rates to the canopy. The combination of poor seedling recruitment strategies, coupled with characteristics allowing longterm persistence of established plants, indicate tropical savanna eucalypts function through the persistence niche rather than the regeneration niche (Bond & Midgley 2001; Keith *et al.* 2007).

#### **ACKNOWLEDGEMENTS**

I am grateful to the Townsville staff of Queensland Parks and Wildlife Service for implementing the trial fires; Eleanor Collins who assisted with field work and Drs Bob Congdon, Tony Grice and Peter Clarke who provided advice throughout the study.

Drs Mike Steele and Bob Mayer provided expert statistical advice. I gratefully acknowledge funding support for this project from James Cook University. This paper was improved by suggestions from Professor Mike Bull and two anonymous referees.

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