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Interactions between dense *Callitris* regeneration and *Eucalyptus* and *Callitris* canopy trees in semi-arid woodlands

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Running head: Canopy-regeneration interactions in semi-arid woodlands

Introduction

Woody plant encroachment is a major issue in semi-arid regions throughout the world (Scholes & Archer 1997; Asner *et al.* 2004). Mechanisms responsible for its occurrence are still poorly understood, but encroachment has variously been attributed to increased CO₂, and changes in climate, soils, grazing and fire regimes (Bond & Midgley 2000; Sankaran *et al.* 2005; Fensham *et al.* 2005, Eldridge *et al.* 2011). The most commonly cited mechanism is a decline in fire frequency and intensity, resulting from reductions in grass fuels by introduced grazers (Noble 1997; Scholes & Archer 1997; Asner *et al.* 2004, Eldridge *et al.* 2011). In particular, this has contributed to the encroachment of fire-sensitive woody plants (Belsky & Blumenthal 1997; Burrows 2002). Understanding the long-term dynamics of encroaching fire-sensitive woody plants and canopy dominants in the absence of fire is the aim of this research.

The effects of existing tree canopies on woody plant encroachment are not easily predicted from the ecological literature. Patterns vary from establishment beneath canopies or in gaps or continuous filling from gap to canopy (Harrington *et al.* 1981; Haase *et al.* 1996; Belsky & Blumenthal 1997; Barnes & Archer 1999). The success of woody species establishment under canopies is partly dependent on requirements for water, nutrients and light and how these resources are modified by canopy tree species along rainfall gradients (Veblen 1992; Bertness & Callaway 1994). Most evidence for positive effects of canopies on woody establishment is in lower rainfall areas, where canopies improve micro-climatic conditions (e.g. temperature and water), thereby facilitating establishment (Holmgren *et al.* 1997).

The influence of woody encroachment on canopy plants is generally negative (Callaway & Walker 1997; Belsky & Blumenthal 1997; Barnes & Archer 1999). The increased competition can accelerate mortality of canopy plants by reducing their vigour and increasing their vulnerability to insect attack and pathogens, especially during periods of water deficit (Belsky & Blumenthal 1997; Barnes & Archer 1999). Increased competition can also reduce opportunities for establishment of canopy plants by reducing their seed production or making conditions unsuitable for their establishment by pre-empting resources (McPherson *et al.* 1988; Barnes & Archer 1999) or changing fire regimes (Covington & Moore 1994). So, strong inter-specific competition has the potential to lead to major changes in species composition (Belsky & Blumenthal 1997, Barnes & Archer 1999).

Climate, especially rainfall, influences the demography of woody plants in semi-arid systems (Schwinning *et al.* 2004; Fensham *et al.* 2005; Holmgren *et al.* 2006a; Shinneman & Baker 2009). Woody plants establish during periods of above average rainfall (Schwinning & Sala 2004; Fensham *et al.* 2005; Kraaij & Ward 2006) and have increased rates of mortality during droughts (Holmgren *et al.* 2006a; Fensham *et al.* 2009; Shinneman & Baker 2009). As droughts are predicted to increase in severity in many semi-arid systems (IPCC 2007), there may be fewer opportunities for establishment of woody species (Garcia *et al.* 1999; Castro *et al.* 2005) and accelerated rates of thinning (Fensham *et al.* 2009). Given that droughts preferentially thin at higher levels of competition (Belsky & Blumenthal 1997; Guarin & Taylor 2005; Fensham *et al.* 2009), dense woody regeneration and ageing canopy trees that overtop them are likely to suffer higher levels of mortality than those at lower levels of competition (Belsky & Blumenthal 1997).

Understanding how climate influences competitive interactions between canopy trees and regeneration is vital for predicting future changes in semi-arid systems, especially under climate change. Within this system, competitive interactions may vary along a rainfall gradient. For example, canopies more commonly facilitate seedling establishment at lower than higher rainfall (Holmgren *et al.* 1997). Canopy tree densities are likely to decline with declining rainfall (Specht & Specht 1999) or may be influenced by disturbances, like logging (Lunt *et al.* 2006; Ross *et al.* 2012). Drought may also have a greater negative effect on plant survival at lower than higher rainfall (Lacey 1972). So, the combined effects of competition and drought may variably drive plant dynamics along a rainfall gradient.

Semi-arid SE Australia underwent dense encroachment by a range of woody species, including *Callitris glaucophylla* after European settlement in the 1800s (Hodgkinson & Harrington 1985; Noble 1997). This encroachment coincided with widespread changes in fire and grazing regimes and canopy tree removal (Noble 1997). In many places woodland dominants, *C. glaucophylla* and a range of *Eucalyptus* species, were both removed or ringbarked at different rates, shifting dominance from *Eucalyptus* species to *C. glaucophylla* (Lunt *et al.* 2006; Ross *et al.* 2012). Although the dynamics of monospecific stands of *C. glaucophylla* have been well researched at the stand scale (Lacey 1972, 1973; FCNSW 1988), there is comparatively little research on dynamics within mixed stands of *Eucalyptus* species and *C. glaucophylla* and this is restricted to temperate climates (Clayton-Greene 1981; Clayton-Greene & Ashton 1990; Lunt *et al.* 2011).

Eucalyptus species are fast growing, resprouting angiosperms with large open canopies, whilst *C. glaucophylla* is a slow growing, obligate-seeding gymnosperm with a relatively small dense canopy (Lacey 1973; FCNSW 1988; Bowman & Harris 1995; Williams & Woinarski 1997). Both genera are considered drought tolerant, and achieve low water usage by different means (Zeppel & Eamus 2008). *Callitris glaucophylla* reduce canopy conductance, whereas *Eucalyptus* species reduce leaf area by shedding leaves before recovery by resprouting (Pook *et al.* 1966; Attiwill & Clayton-Greene 1984; Clayton-Greene & Ashton 1990). During drought, mortality of a range of *Eucalyptus* species and *C. glaucophylla* has been greatest at higher levels of competition and in drier areas (Lacey 1972, 1973; Allen 1998; Fensham & Holman 1999; Fensham *et al.* 2009), although these patterns have rarely been quantified (e.g. Fensham & Holman 1999; Fensham *et al.* 2005; Fensham *et al.* 2009).

There is a need to better understand the long-term dynamics of encroaching fire-sensitive woody plants and canopy dominants in the absence of fire. To contribute to this objective, we examined how canopy trees of *Eucalyptus* species and *C. glaucophylla* influenced the survival, growth and reproduction of *C. glaucophylla* saplings, and how these in turn influenced the survival of the canopy trees along a rainfall gradient during drought conditions. The following hypotheses were proposed: (1) densities of saplings will be greater in gaps than under canopies, and as rainfall increases, densities will increase in gaps and decrease under canopies; (2) growth rates and the probability of reproducing will be greater for saplings without canopy or sapling competition and will increase in areas of higher rainfall; (3) sapling densities, growth rates and the probability of reproducing will be greater under *Eucalyptus* than *Callitris* canopies; (4) denser saplings will experience greater mortality during a

drought; (5) recent drought mortality of *Eucalyptus* and *Callitris* canopy trees will be greater when dense sapling regeneration is present in low rainfall areas.

Materials and Methods

Study area

The study was undertaken in woodlands co-dominated by *Callitris glaucophylla* Joy Thomps. & L.A.S. Johnson and a range of *Eucalyptus* species (*E. microcarpa* Maiden (Grey Box), *E. populnea* L. Johnsonn & K. Hill (Bimble Box), *E. melliodora* A. Cunn. Ex Schauer (Yellow Box), *E. blakelyi* Maiden (Blakely's Red-gum) and *E. sideroxylon* A. Cunn. ex Wools (Red Ironbark) in central New South Wales, south-eastern Australia. Six State Forests were sampled along a gradient of mean annual rainfall, from 363 mm in the west (32.74°S, 145.57°E) to 621 mm in the east (33.34°S, 148.21°E). Selected forests were dominated by mature *Callitris* and *Eucalyptus* canopy trees that established in the late 1800s, and contained abundant *Callitris* saplings that regenerated in the 1950s (Lacey 1972; Allen 1998). These saplings were typically 3-6 m tall and less than 3 cm diameter at breast height (DBH). *Eucalyptus* saplings were very uncommon in each forest and were not sampled. The region experienced drought conditions for eight years prior to sampling in October to December 2008. Mean annual rainfall at each site from 2001 to 2008 was lower than the long-term mean annual rainfall i.e. from west to east, sites experienced 0.88, 0.76, 0.78, 0.88, 0.72 and 0.79 of their long-term mean annual rainfall (Fig. 1; Bureau of Meteorology 2010).

Effects of tree canopies on saplings

To assess the effects of tree canopies on the density, growth and survival of *Callitris* saplings, we counted the number of live and recently dead saplings in paired quadrats: one placed directly beneath the canopy, and another immediately adjacent. Four to six canopy trees of each genus (*Callitris* and *Eucalyptus*) with intact green crowns and surrounded by dense *Callitris* saplings were randomly selected at each site. The species, height, DBH and canopy area of each canopy tree was recorded. We compared the effects of tree canopy cover on *Callitris* sapling densities by counting live and recently dead *Callitris* saplings in paired quadrats with: one quadrat beneath the canopy and another immediately adjacent to the canopy on the same side of the tree. There was no consistent placement of the paired quadrats on one side of the tree, since sapling location varied. Each quadrat was 8 m² with the dimension varying with the dimension of the canopy and the distribution of saplings in the adjoining quadrat. Recently dead *Callitris* saplings were identified by their brown foliage or the presence of fine twigs.

To investigate the competitive effects of overtopping canopy trees and surrounding *Callitris* saplings on *Callitris* saplings, we measured the height, diameter at breast height (DBH) and presence of fruiting cones on: (1) the *Callitris* sapling closest to the trunk of the canopy tree in the quadrat beneath the canopy; (2) a random *Callitris* sapling in the adjoining quadrat beyond the canopy; (3) the tallest *Callitris* sapling in the adjoining quadrat beyond the canopy; and (4) the closest *Callitris* sapling that was ≥ 1 m away from all saplings and canopy trees. These four sapling classes are

hereafter referred to as ‘canopy’, ‘random’, ‘dominant’, and ‘isolated’ *Callitris* saplings.

Effects of saplings on canopy trees

To assess relationships between sapling competition and mortality of dominant canopy trees, recent mortality of *Eucalyptus* and *Callitris* canopy trees was recorded along a pair of transects at each site, one with and one without dense *Callitris* regeneration. Both transects were placed in similar micro-topographic positions, and we assumed that differences in *Callitris* sapling densities between transects resulted from chance or past disturbances, and were not related to abiotic factors. Recently dead canopy trees possessed brown leaves or fine twigs and no resprouting buds. The first 20 *Callitris* and 20 *Eucalyptus* canopy trees were sampled along each transect, the length of which varied with tree density. To provide an index of water stress on dominant *Eucalyptus* trees, the degree of leaf loss (Pook *et al.* 1966; Attiwill & Clayton-Greene 1984; Clayton-Greene & Ashton 1990) on each tree was estimated using four categories: 0-5, 6-20, 21-50 and >50%. We also recorded the position of the lowest resprouts on each *Eucalyptus* tree using four categories (base, trunk, branch, none), with lower resprouting positions indicating higher stress levels (Bellingham & Sparrow 2000; Vesik and Westoby 2003). Stress levels could not easily be assessed on *Callitris*, and only canopy death was recorded. *Callitris* trees were considered dead if there were no green leaves or reprints.

The underlying assumption of the study design is that differences in sapling performance between canopy positions (e.g. saplings beneath *versus* between tree canopies) reflect competitive neighbourhood effects of dominant trees and surrounding saplings at each site rather than underlying abiotic patterns. Similarly, we assume that differences in tree mortality between areas with and without dense saplings reflect competitive effects of saplings on trees, rather than other independent site effects, since paired sites had similar tree sizes, tree species and tree densities and were placed in similar topographic positions in close proximity.

Statistical analyses

We examined how a range of variables influenced the density of live saplings, sapling height, and sapling DBH. Firstly, we used a split plot analysis of variance (ANOVA) design since measurements of saplings under each canopy and in an adjacent gap were not independent. The whole plot stratum consisted of the factorial combination of Sites (1-6) and canopy Genus (*Eucalyptus*, *Callitris*); the sub-plot stratum was formed by the main effect of canopy Position (gap, canopy) or sapling Class (under canopy, random in gap, dominant in gap, isolated in gap) for sapling height and DBH, together with its interactions with Sites and Genus.

Since Sites were located along a rainfall gradient, we then orthogonally partitioned the Sites factor effect into a Rainfall regression variate effect to seek the possibility of a linear response of live sapling density (or height and DBH) of saplings to mean annual Rainfall (363, 421, 453, 494, 580, 621 mm from west to east; Steel and Torrie 1960; Quinn and Keough 2002). Site interactions with other factors were also partitioned into linear effects and deviations from linear effects.

An ANOVA of the density of recently dead saplings examined the same effects as the density of live saplings (see above). Since we wanted to investigate the effects of the recent drought from 2001 to 2008 on sapling death, the Site factor was replaced with Total Rainfall at each site during this drought period (2540, 2554, 2822, 3344, 3804, 3927 mm from west to east). In addition the variate Total Density of saplings (live and dead) was included, with the possibility that the slope may vary with canopy Genus, canopy Position and their interaction.

Fisher's protected LSD multiple comparison test was used for *post hoc* paired comparisons in all the analyses. Diagnostic checks of these and subsequent models included examination of the residuals for outliers and goodness of fit and where necessary data were transformed using natural logarithms. Analyses were undertaken using GenStat (GenStat 2009).

Generalised linear models, with a binomial error structure and logit link function, were used to analyse differences in the frequency of dead *Callitris* canopy trees, the frequency of *Eucalyptus* canopy trees with >5% leaf loss and the frequency of *Eucalyptus* canopy trees resprouting from the trunk. There were no analyses of the frequency of *Eucalyptus* mortality, because only two deaths were recorded. Explanatory variables included the presence of dense *Callitris* sapling regeneration, mean annual Rainfall at each site, Total Rainfall at each site from 2001 to 2008, *Callitris* canopy tree density and *Eucalyptus* canopy tree density. Pearson's correlation tests were used to examine associations between the continuous explanatory variables to determine those which could be included in each model.

Results

Effects of tree canopies on saplings

Callitris sapling density was significantly lower beneath tree canopies than in the gaps between tree canopies (1.31 and 2.08 mean number of saplings m⁻², respectively, Table 1). As mean annual Rainfall declined, there was a subtle but significant decline in sapling density in the gap, and an increase in density under the canopy (Table 1, Fig. 2). Sapling density was not significantly different between canopy Genus (Table 1).

When pooled across sites, sapling height and DBH ($\log_e(\text{DBH}+1)$), differed significantly amongst most sapling Classes: sapling height under canopies (*Eucalyptus* and *Callitris* combined) was similar to random saplings in gaps, both being shorter than dominant saplings in gaps, which were shorter than isolated saplings in gaps (canopy = random < dominant < isolated); sapling DBH was lowest on random saplings in gaps, followed in order by canopy, dominant and isolated saplings (random < canopy < dominant < isolated; Table 1, Figs 3a & 3b). Saplings growing under the canopies of *Eucalyptus* trees were significantly taller but did not have significantly bigger DBHs than those under the canopies of *Callitris* trees (Figs 3a & 3b). There was no significant association between either sapling height or DBH and mean annual Rainfall (Table 1). However, as mean annual Rainfall increased, there was a significant decline in DBH of saplings under *Eucalyptus* canopies and an

increase under *Callitris* canopies (Table 1; - 0.000569 Rainfall, + 0.001092 Rainfall, respectively).

Although data on the proportional occurrence of fruiting cones on saplings were not analysed as few plants set fruits, isolated saplings were more likely to have cones than saplings in any other sapling Class (Fig. 3c).

The density of recently dead saplings was significantly greater in the gaps between the tree canopies than under the tree canopies (1.5 (mean) ± 0.11 (se), 1.1 ± 0.15 , respectively) and greater under *Callitris* than *Eucalyptus* canopies (1.43 ± 0.09 , 1.12 ± 0.18 , respectively; Table 1). Consistent with this, the density of recently dead saplings increased significantly as the Total Density of saplings increased (Fig. 4). There was no significant association between recently dead saplings and mean annual Rainfall (Table 1) and despite a suggestion that canopy Genus significantly influence the density of recently dead saplings along the Rainfall gradient, the associated significant deviation tells us that this does not fully summarise the situation.

Effects of saplings on canopy trees

The strong correlations between a number of continuous explanatory variables (mean annual rainfall was positively correlated with total rainfall and negatively correlated with *Callitris* canopy tree densities; total rainfall was negatively correlated with *Callitris* canopy tree densities; *Callitris* and *Eucalyptus* canopy tree densities were positively correlated; Table 2), limited analyses of *Callitris* and *Eucalyptus* canopy tree mortality and stress, respectively to those containing a single explanatory variable, or two separate regression equations based on the presence or absence of dense *Callitris* sapling regeneration (Table 3).

Recent mortality of *Callitris* canopy trees was positively associated with the presence of *Callitris* sapling regeneration but no other variables (Table 3; probability of mortality with regeneration = 0.14 (mean) ± 0.04 (se); probability without regeneration = 0.03 ± 0.02). Although few *Eucalyptus* canopy trees died (2 of 237 trees) during the 2001-2008 drought, individuals nevertheless showed signs of stress by leaf loss and resprouting from the trunk. A higher frequency of *Eucalyptus* canopy trees with >5% leaf loss was associated with denser *Eucalyptus* stands (Table 3, Fig. 5). A higher frequency of *Eucalyptus* canopy trees resprouting from the trunk was associated with lower mean annual Rainfall and Total Rainfall at each site from 2001 to 2008, and with higher densities of *Callitris* and *Eucalyptus* canopy trees (Table 3, Fig. 6). The frequency of *Eucalyptus* canopy trees resprouting from the trunk was not significantly associated with the presence of dense *Callitris* regeneration (Table 3). These results suggest that *Callitris* canopy trees suffer greater competition than *Eucalyptus* canopy trees from dense *Callitris* sapling regeneration.

Discussion

The results indicate competitive relationships amongst *Callitris* saplings and *Eucalyptus* and *Callitris* canopy tree dynamics along the rainfall gradient. Saplings were less dense, smaller and less likely to be mature under canopies than in gaps along the rainfall gradient, with no evidence of canopies facilitating sapling success. Drought preferentially thinned saplings at higher density and those under *Callitris* canopies. In turn, the effects of drought in combination with sapling regeneration or

stand density reduced the resilience of canopy trees: *Callitris* canopy trees surrounded by dense sapling regeneration suffered greater mortality than similarly placed *Eucalyptus* canopy trees, which suffered greater levels of stress at higher stand densities at the lower end of the rainfall gradient. These trends suggest that interactions among climate, canopies and regeneration influence stand dynamics in this semi-arid system.

Canopy effects on Callitris sapling density, growth and reproduction

Callitris saplings were less abundant under the canopies of mature trees than in the gaps between them. Despite this difference, saplings still occurred at relatively high densities (mean = 1.31 saplings m⁻²) under canopies. Thus, rather than exclude *Callitris* regeneration, canopy trees appeared to restrict their regeneration. A number of studies in semi-arid regions have similarly found lower densities of woody plants under tree canopies than in the gaps (Harrington *et al.* 1981; Holmgren *et al.* 1997). Conversely, other studies have found that canopies facilitate shrub survival, resulting in a higher density under the canopy than in the gap (Harrington *et al.* 1981; Haase *et al.* 1996; Holmgren *et al.* 1997; Barnes & Archer 1999). We found no evidence that canopy trees facilitated *Callitris* establishment, directly or indirectly, along the rainfall gradient.

Saplings under canopies were short and without cones, as were the majority of saplings surrounded by dense sapling regeneration in gaps. Slow growth rates and negligible seed production have previously been recorded in dense stands of similarly aged *Callitris* saplings (Lacey 1972; Hawkins 1966; FCNSW 1988). Silvicultural thinning of these dense stands has resulted in enhanced growth rates (Knott 1995; Ross *et al.* 2008) and reproductive rates of remaining plants (Hawkins 1966; Lacey 1972; FCNSW 1988), since larger plants have the capacity to develop more cones (Lunt *et al.* 2011). Similarly, we found that growth rates and the occurrence of fruiting cones were greater for the less frequent isolated saplings in gaps. Soil water is a critical resource regulating competitive interactions in dry climates (Schwinning & Sala 2004; Castro *et al.* 2005; Holmgren *et al.* 2006), and is likely to be the major regulator of sapling density, growth and reproductive rates beneath tree canopies and in dense sapling stands.

Density and growth of Callitris saplings under Callitris and Eucalyptus canopies

While *Callitris* sapling densities were similar under the canopies of both tree genera, saplings under *Eucalyptus* trees were, on average, 0.89 m taller than those under *Callitris* trees. The difference probably reflects faster growth rates beneath *Eucalyptus* than *Callitris* trees. Given that these canopy dominants have similar rates of water usage (Zeppel & Eamus 2008) and similar distributions of root biomass in the soil (Burrows *et al.* 2001; Eberbach 2003), faster growth under *Eucalyptus* may be related to their higher nutrient litter and greater light infiltration through their more open canopies (Clayton-Greene 1981; Bowman & Wilson 1988). Both these factors have been found to influence plant performance in other semi-arid systems (Holmgren *et al.* 1997; Armas & Pugnaire 2005).

Mortality of Callitris saplings during drought

As hypothesised, the mortality of *Callitris* saplings during the drought was greater at higher densities of saplings, resulting in 28% mortality compared with 0.4% at the lowest density. Density dependent mortality of woody species, including *Callitris* has previously been observed during droughts (Lacey 1973; FCNSW 1988; Belsky & Blumenthal 1997). This thinning is especially important for species with slow rates of self-thinning under less severe climatic conditions, like *Callitris* (Lacey 1972, 1973; FCNSW 1988; Lunt *et al.* 2011), especially in the absence of other density regulating disturbances, like fire (Lacey 1973; Bowman *et al.* 1988; Fule & Covington 1998).

Callitris saplings under *Callitris* canopies were smaller and had greater mortality during the drought than those under *Eucalyptus* canopies. Higher levels of mortality may result from shorter plants having smaller root systems perhaps. This suggests that in the longer term, as droughts are predicted to increase in frequency and severity (Nicholls 2004; CSIRO & BOM 2007; Hennessey *et al.* 2008), *Callitris* saplings under *Eucalyptus* canopies are more likely to succeed than those under *Callitris* canopies.

Mortality of Callitris and Eucalyptus canopy trees during drought

During the drought, *Callitris* canopy trees surrounded by dense *Callitris* saplings suffered greater mortality than those growing in open areas (14.2% *c.f.* 3.3%). This confirms anecdotal forestry records of greater mortality of mature trees in stands containing dense saplings (Lacey 1973; FCNSW 1988; Allen 1998). We assume that tree mortality was influenced by competition from dense saplings rather than abiotic site factors, as both patch types occurred in similar topographic positions. By comparison, few *Eucalyptus* canopy trees died during the drought (0.8%). This differs from a study by Fensham and Holman (1999), in which 29% of eucalypts died after a severe drought in northern Queensland in the 1990s. The lower mortality in our study may be because our sites were located on gently undulating, high productivity soils. Despite low mortality, *Eucalyptus* canopy trees showed signs of stress during the drought. Unlike *Callitris* trees, which reduce canopy conductance during periods of water stress, *Eucalyptus* trees reduce leaf area by shedding leaves before resprouting (Pook *et al.* 1966; Attiwill and Clayton-Greene 1984; Clayton-Greene and Ashton 1990; Zeppel and Eamus 2008). We found that *Eucalyptus* canopy trees with higher levels of leaf loss (>5%) were more frequent at higher stand densities of *Eucalyptus*. In contrast during the 1990s drought, Fensham and Holman (1999) found no correlation between dieback and basal area within *Eucalyptus* stands.

Predictions of future drought and fire regimes are likely to accentuate *Callitris* dominance in this semi-arid system. If droughts increase in frequency and intensity (Nicholls 2004; CSIRO & BOM 2007; Hennessey *et al.* 2008), leading to low herbaceous fuels and consequent infrequent fires (Bradstock 2010), *Eucalyptus* seedlings may remain rare, as their recruitment is dependent on the occurrence of fire (Gill 1997). Instead, the ubiquitous *Callitris* saplings are likely to replace dying *Callitris* and *Eucalyptus* canopy trees, thus increasing *Callitris* dominance.

Conclusion

These results indicate significant relationships between spatial patterns of *Callitris* saplings and mature trees. These patterns are consistent with competitive interactions among species, cohorts and individuals, with soil moisture likely to be a key limiting resource. Thus, mature trees appear to moderate rather than exclude *Callitris* regeneration beneath their canopies, and dense regeneration in turn appears to influence canopy tree dynamics, by enhancing conspecific canopy stress and mortality during drought periods. Dense *Callitris* regeneration is likely to influence future stand dynamics, with outcomes being strongly influenced by the frequency of future droughts and disturbances such as fire.

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Table 1. Results from analyses of variance used to examine the effects of a range of explanatory variables on (a) the density of live *Callitris* saplings, (b) sapling height, (c) sapling diameter at breast height $\log_e(\text{DBH}+1)$ and (d) density of recently dead saplings $\log_e(10*\text{Dead}+1)$. Significance levels are: ns = $P>0.05$; * = $P<0.05$; ** = $P<0.01$; * = $P<0.001$.**

(a) Density of live saplings			(b) Sapling height			(c) DBH	(d) Density of dead saplings		
Source of Variation	d.f.	P	Source of Variation	d.f.	P	P	Source of Variation	d.f.	P
Tree stratum			Tree stratum						
Site	5	*	Site	5	***	***	Site	5	***
Genus (<i>Eucalyptus</i> , <i>Callitris</i>)	1	ns	Genus	1	*	ns	Genus	1	***
Site.Genus	5	ns	Site.Genus	5	ns	ns	Position	1	***
Residual	52		Residual	52			Site.Genus	5	*
							Position.Site	5	*
Tree.Position stratum			Tree.Class stratum						
Position (gap, canopy)	1	***	Class (c,r,d,i) ^B	3	***	***	Position.Genus	1	ns
Position.Site	5	*	Class.Site	15	***	***	Position.Site.Genus	5	ns
Position.Genus	1	ns	Class.Genus	3	*	***	Total Density	1	***
Position.Site.Genus	5	ns	Class.Site.Genus	15	ns	ns	Total Density.Genus	1	ns
							Total Density.Position	1	ns
Residual ^A	52		Residual	149			Tot. Density.Position.Genus	1	ns
Total	127		Total	248			Residual	100	
							Total	127	

^A Listed degrees of freedom indicate non-full factorial nature of trials due to variable (4-6) number of canopy trees per Genus being measured.

^B Sapling Class: c = closest to trunk under canopy; r = random in gap; d = dominant in gap; i = isolated in gap.

Table 2. Correlations between continuous explanatory variables used in Generalised Linear Models (GLM) to examine their associations with the frequency of *Callitris* canopy tree mortality, *Eucalyptus* canopy trees with >5% leaf loss and *Eucalyptus* canopy trees resprouting from the trunk ($n = 12$).

Significance levels are: * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

	Mean annual rainfall	Total rainfall (2001-08)	<i>Callitris</i> canopy tree density
Total rainfall (2001-08)	0.97**		
<i>Callitris</i> canopy tree density	-0.67*	-0.78**	
<i>Eucalyptus</i> canopy tree density	-0.40	-0.57	0.64*

Table 3. Levels of significance of the explanatory variable terms used to examine associations with the frequency of (a) *Callitris* canopy tree mortality, (b) *Eucalyptus* canopy trees with >5% leaf loss and (c) *Eucalyptus* canopy trees resprouting from the trunk using Generalised Linear Models (GLM).

Significance levels are: ns = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

Explanatory variables	(a)	(b)	(c)
	<i>Callitris</i> mortality <i>P</i>	<i>Eucalyptus</i> >5% leaf loss <i>P</i>	<i>Eucalyptus</i> trunk resprouting <i>P</i>
Dense sapling regeneration	*	ns	ns
Mean annual Rainfall	ns	ns	*
Sapling regeneration x Mean annual Rainfall	ns	ns	ns
Total Rainfall (2001-08)	ns	ns	**
Sapling regeneration x Total Rainfall (2001-08)	ns	ns	ns
<i>Callitris</i> canopy tree density	ns	ns	**
Sapling regeneration x <i>Callitris</i> canopy density	ns	ns	ns
<i>Eucalyptus</i> canopy tree density	ns	*	**
Sapling regeneration x <i>Eucalyptus</i> canopy density	ns	ns	ns

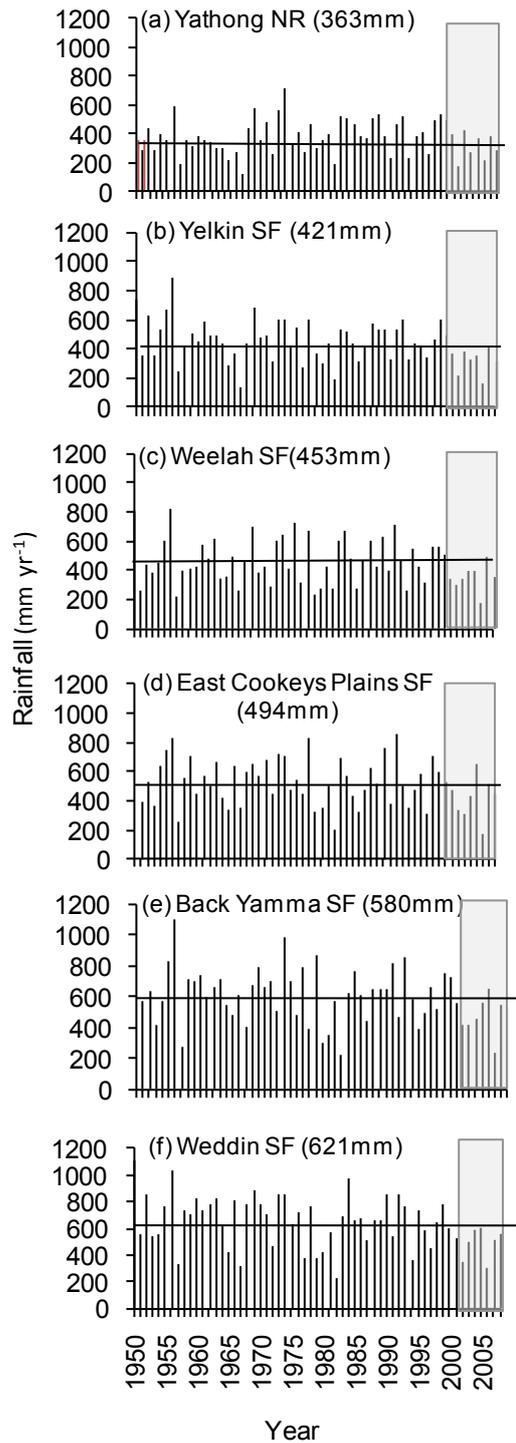


Fig. 1. Annual rainfall at the six sites from west to east (top to bottom) along the rainfall gradient from 1950 to 2008 (Bureau of Meteorology 2010). The period of recent drought from 2001 to 2008 is shaded grey. Long-term mean annual rainfall (since records began in the 1880s) at each site is bracketed and represented by a horizontal line.

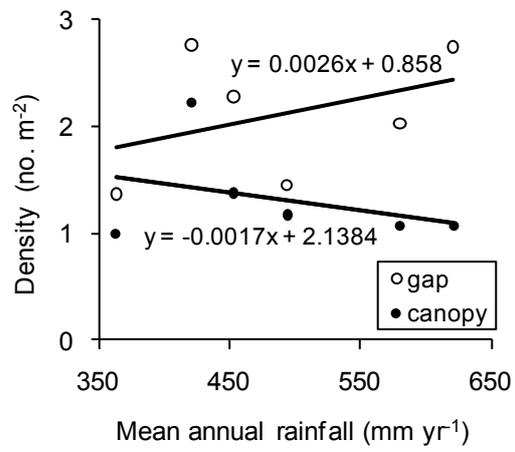


Fig. 2. Linear regressions of the density of live *Callitris* saplings in gaps and under canopies with mean annual rainfall.

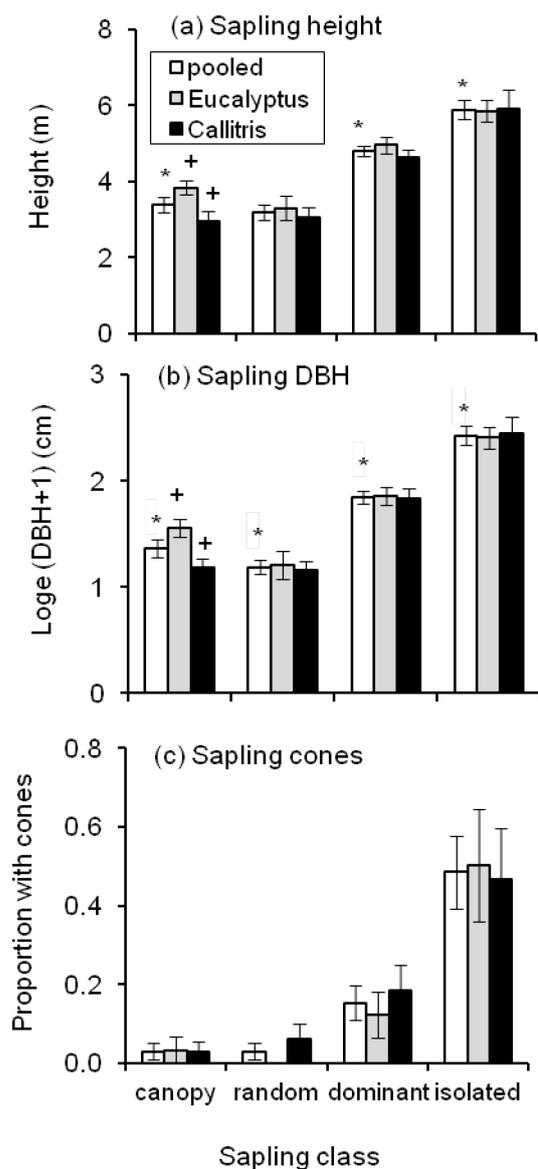


Fig. 3. (a) Height, (b) diameter at breast height (DBH) and (c) fruiting cones of *Callitris* saplings in different Classes and in relation to canopy Genus (pooled, *Eucalyptus*, *Callitris*). Data are mean and standard error, while asterisks and pluses indicate significant differences between Class means and between Genus means for the same Class, respectively. Data on fruiting cones were not analysed, as few plants had cones.

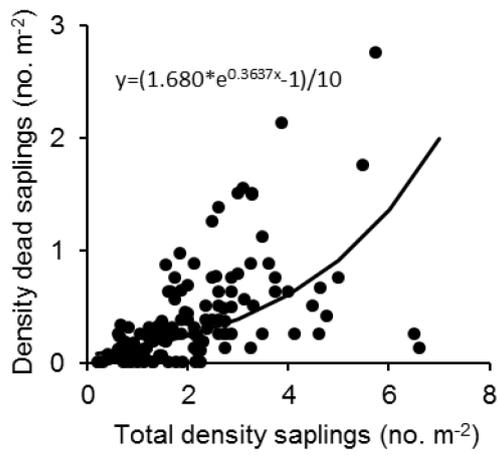


Fig. 4. The relationship between the density of recently dead *Callitris* saplings with total *Callitris* sapling density (alive and dead). The equation for the fitted relationship is also given.

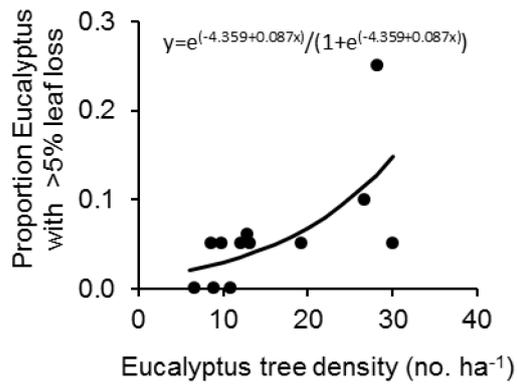


Fig. 5. The proportional occurrence of *Eucalyptus* canopy trees with >5% leaf loss in relation to the density of *Eucalyptus* canopy trees.. The equation for the fitted relationship is also given.

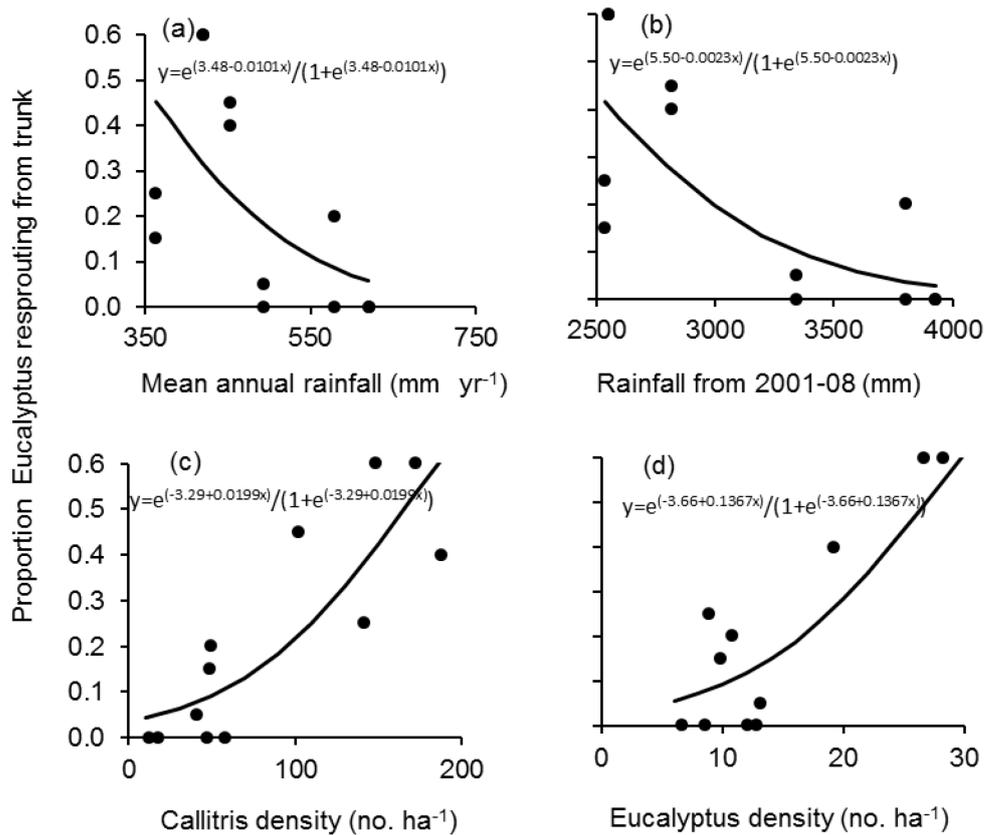


Fig. 6. The proportional occurrence of *Eucalyptus* canopy trees resprouting from the trunk with: (a) mean annual Rainfall; (b) Total Rainfall from 2001 to 2008; (c) density of *Callitris* canopy trees; and (d) density *Eucalyptus* canopy trees. The equation for each fitted relationship is also given.