

RESEARCH ARTICLE

RECOVERY OF TALL OPEN EUCALYPT FOREST IN SOUTH-WESTERN AUSTRALIA FOLLOWING COMPLETE CROWN SCORCH

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ABSTRACT

We investigated the response of overstorey and mid-storey trees in tall open forest of *Eucalyptus diversicolor* F. Muell., *Eucalyptus jacksonii* Maiden, and *Corymbia calophylla* (Lindl.) K.D. Hill & L.A.S. Johnson over an eight-year period following complete crown scorch by high intensity fire in March 2001. More than 90% of *E. diversicolor* and *E. jacksonii* and 85% of *C. calophylla* remained alive four years after fire, having replaced their crowns by re-sprouting from epicormic buds on the stems and larger branches. Mid-storey trees were more severely affected by fire with almost one third of *Allocasuarina decussata* (Benth.) L.A.S. Johnson stems and all above-ground stems of *Agonis flexuosa* (Willd.) Sweet killed back to ground level. Abundant seedling regeneration of *E. diversicolor* and *E. jacksonii* developed in the year following the fire but seedling density and stocking declined progressively over subsequent years. Survival of *E. diversicolor* seedlings was higher than for *E. jacksonii* seedlings, consistent with findings of earlier research. For both species, initial seedling densities were significantly greater within 25 m of

RESUMEN

Nosotros investigamos la respuesta del dosel superior y medio de árboles en bosques altos y abiertos de *Eucalyptus diversicolor* F. Muell., *Eucalyptus jacksonii* Maiden, y *Corymbia calophylla* (Lindl.) K.D. Hill & L.A.S. Johnson por un período de ocho años, después de la quema total del dosel por un fuego de alta intensidad, ocurrido en marzo de 2001. Más del 90% de *E. diversicolor* y *E. jacksonii*, y el 85% de *C. calophylla* permaneció vivo cuatro años después del fuego, habiéndose reemplazado su dosel mediante el rebrote de brotes epicórmicos del tronco y de ramas largas. Los árboles con doseles en el estrato medio fueron severamente afectados por el fuego, con casi un tercio de los tallos de *Allocasuarina decussata* (Benth.) L.A.S. Johnson y todos los tallos de *Agonis flexuosa* (Willd.) Sweet muertos por el fuego hasta el nivel del suelo. Una abundante regeneración de *E. diversicolor* y *E. jacksonii* se desarrolló al año siguiente del incendio, aunque la densidad y el número de plántulas declinaron progresivamente en los años subsiguientes. La supervivencia de plántulas de *E. diversicolor* fue mayor que la de *E. jacksonii*, consistente con los resultados de investigaciones previas. Para ambas especies, la densidad inicial de plántulas fue significativamente mayor dentro de los 25 m alrede-

potential seed trees, but seedling density was otherwise unrelated to the basal area of surrounding forest. Eight years after the fire, 38% of sample quadrats (4 m²) were stocked with one or more eucalypt saplings, with saplings of *E. diversicolor* and *E. jacksonii* having a mean height of 5 m. Saplings established following the 2001 fire could add a further age class to the stand provided that this cohort persists during subsequent fires. The results of our study provide further evidence to support the view that tall open eucalypt forests in south-west Western Australia rarely experience complete stand replacement even following intense fires, and that multi-aged stands are common.

dor de los potenciales árboles semilleros, aunque contrariamente, la densidad de plántulas no se relacionó con el área basal del bosque circundante. Ocho años después del fuego, el 38% de las parcelas de muestreo (de 4 m²) estaban ocupadas por una o más plántulas de eucalipto, con plántulas de *E. diversicolor* y de *E. jacksonii* cuya altura media era de 5 m. Las plántulas establecidas después del incendio de 2001 pueden añadir una cohorte más al rodal siempre y cuando esta cohorte persista durante fuegos subsecuentes. Los resultados de nuestro estudio proveen de nuevas evidencias que respaldan la idea de que los bosques altos de eucalipto en el sudoeste de Australia rara vez experimentan un completo reemplazo de sus rodales aún después de fuegos intensos, y que lo común en ellos son los rodales multi-etáneos.

Keywords: age structure, crown scorch, epicormic sprouting, eucalyptus forest, regeneration

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INTRODUCTION

Fire has long been recognised as having a dominant role in the regeneration of tall open eucalypt forests in southern Australia (Ashton 1981). Tall open eucalypt forests have a mature height >30 m and canopy cover of 30% to 70%, often with a stratum of mid-storey trees and a dense understorey of shrubs. Fire facilitates regeneration by reducing competition, creating receptive seedbed, stimulating synchronous seedfall, and temporarily eliminating seed predators and seedling pathogens (Jarrett and Petrie 1929, Gilbert 1959, White and Underwood 1974, Ashton 1981, Wardell-Johnson 2000). The effect of past fires is evident in the age class distribution of tall open forests at the landscape scale, and in the structure of stands at the local scale where two or more cohorts of trees

originating from significant regeneration events may be present (Bradshaw and Rayner 1997, Hickey *et al.* 1999, Lindenmayer 2009, Turner *et al.* 2009, Benyon and Lane 2013).

Tall open forests occupy 190 000 ha in south-western Australia, mostly within the Warren region, which is an administrative area that includes 930 000 ha of public land managed primarily for conservation, outdoor recreation, and sustainable timber production (Figure 1). Characteristic overstorey species include karri (*Eucalyptus diversicolor* F. Muell.); marri (*Corymbia calophylla* [Lindl.] K.D. Hill & L.A.S. Johnson); blackbutt (*Eucalyptus patens* Benth.); and the red, yellow, and Ranges tingle (*Eucalyptus jacksonii* Maiden, *E. guilfoylei* Maiden, and *E. brevistylis* Brooker, respectively). Nomenclature for Western Australian plant species follows Florabase (florabase.dpaw.wa.

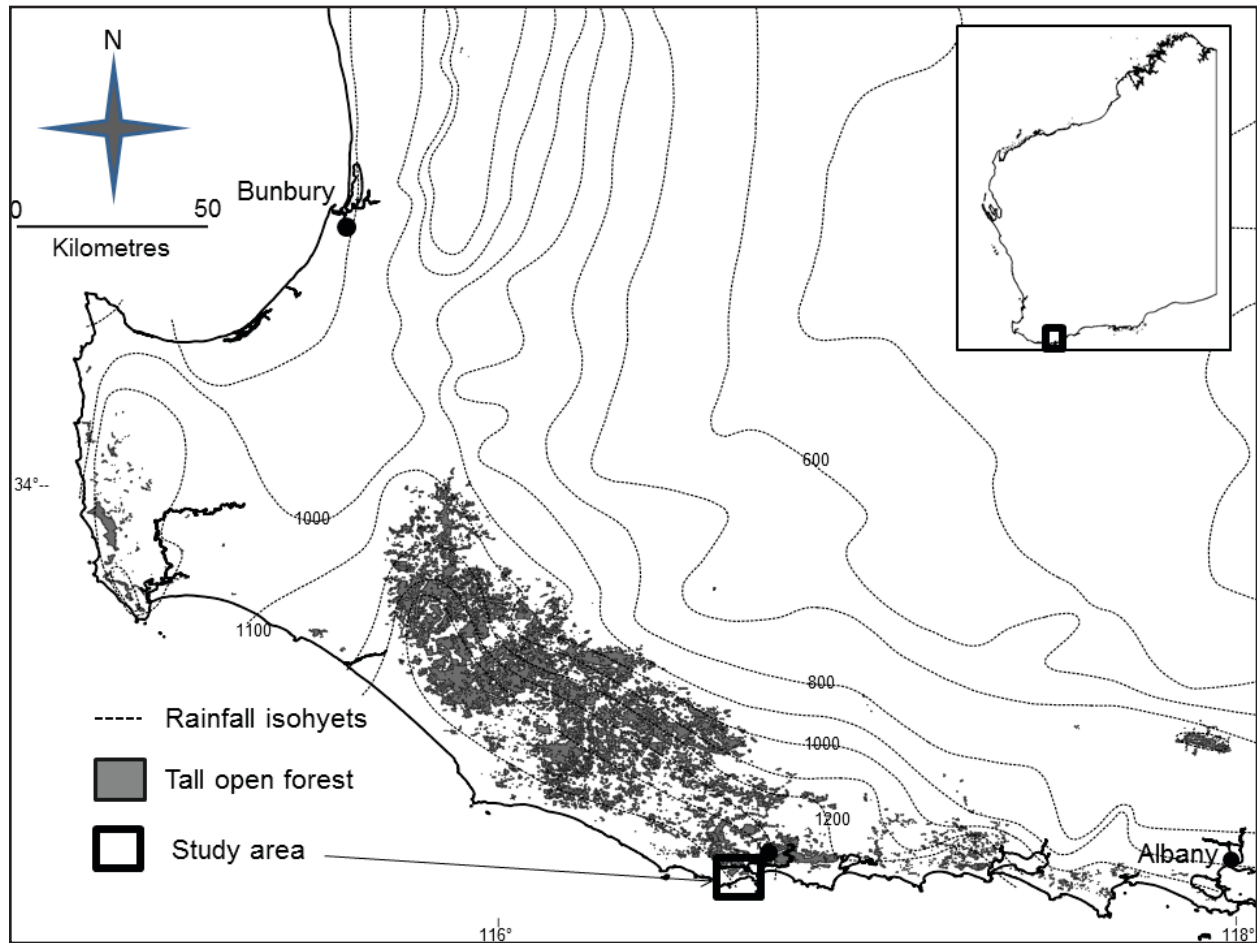


Figure 1. Map showing the distribution of tall open forest in south-western Australia and the location of the study area burnt by the March 2001 bushfire. Inset panel shows the general location of the study area in Western Australia. Rainfall isohyets (mm) are shown.

gov.au; accessed 30 June 2015). Tall open forests occur in areas receiving >1000 mm annual rainfall on a variety of soils (loams, podsols, sandy gravels, and sands) derived from Proterozoic granite and gneiss, and in a mosaic with open forests dominated by jarrah (*Eucalyptus marginata* Sm.) on gravelly soils, and sclerophyll shrublands on highly leached sands (Bradshaw *et al.* 1997, Wardell-Johnson *et al.* 1997). Tall open forests typically have a dense understorey of mid-storey trees and woody shrubs that, if unburnt for several decades, can attain a height >10 m and accumulate a substantial loading of leaf litter, twigs, and small branches that can exceed 70 t ha⁻¹ (Sneeuwjagt 1971, O’Connell 1987, McCaw *et al.* 2002).

South-western Australia has a mediterranean climate with a distinct summer drought and, in most years, litter and understorey fuels in tall open forest are dry enough to ignite and burn in the period from December to March (McCaw and Hanstrum 2003). Unplanned bushfires occur every summer as a result of lightning ignition and accidental or deliberate actions by people (Plucinski *et al.* 2014). Bushfires in tall open forest can be intense and fast moving, particularly in late summer and early autumn when the seasonal drought is at its peak and a high proportion of fine and coarse woody fuels are consumed (Hollis *et al.* 2011). Systematic fire reports available from the late 1930s onwards (McCaw *et al.* 2005) indicate that

large bushfires (>10000 ha) have burnt tall open forest in this region in 1937, 1950, 1952, 1969, 1997, 2002, 2012, and 2015. The fire of February 1937 was the most extensive of these and, while no reliable maps of the fire perimeter exist, newspaper reports indicate that fire activity extended across 150 km in the southern half of the Warren region (McCaw and Hanstrum 2003). The mosaic of vegetation types at the landscape scale means that the perimeters of large fires typically include a mixture of tall open forest, open forest, and shrubland. Systematic fire management in the Warren region began in the 1950s and prescribed fire has been used widely for fuel reduction, and to achieve a range of land management objectives including biodiversity conservation and regeneration following timber harvesting (Burrows and McCaw 2013). Boer *et al.* (2009) identified a statistically significant inverse relationship between the area burnt by prescribed fire and the area burnt by unplanned bushfire over a 52-year study period ending in 2004, with a lag effect persisting for up to six years following prescribed burning.

Eucalypts characteristic of tall open forest in south-western Australia are capable of re-sprouting from epicormic shoots following complete scorching of the canopy (Wardell-Johnson 2000, Burrows and Wardell-Johnson 2003). Their large stature, thick bark, and ability to re-sprout from dormant buds on the stems and branches confer considerable tolerance to fires of moderate to high intensity (fireline intensity 3000 kW m⁻¹ to 7000 kW m⁻¹, following Cheney [1981]). Large old trees are often hollow-butted as a result of stem damage during past fires, and ignition of dead wood in the hollow section of the stem can lead to collapse of the trees. Complete stand replacement is rare even following high intensity fires, and previous studies have concluded that multi-aged stands are common (Bradshaw and Rayner 1997, Wardell-Johnson 2000). The existence of multiple-age cohorts

has been inferred from stand structure and counting of growth rings on a sample of felled trees.

We studied the response of overstorey and mid-storey trees at the stand scale over an eight year period following complete crown scorch by fire in March 2001 in order to quantify (1) changes in stand structure as a result of the fire, and (2) the extent of recruitment of a further cohort of eucalypts from seedlings established following the fire.

METHODS

Study Area

The study was conducted 8 km south-west of Walpole (35° 00' S, 116° 43' E) in the Walpole Nornalup National Park, Australia, in undulating terrain rising to an elevation of 160 m above sea level. Dominant vegetation is tall open forest of *E. diversicolor*, *E. jacksonii* and *C. calophylla* up to 50 m in height with a mid-storey of *Allocasuarina decussata* (Benth.) L.A.S. Johnson, *Agonis flexuosa* (Willd.) Sweet and *Trymalium odoratissimum* subsp. *trifidum* (Rye) Kellermann, Rye & K.R.Thiele. Forest structure maps prepared from air photo interpretation indicate a crown cover of 50% to 80% (Bradshaw *et al.* 1997). Prior to 2001, this area was last burnt by the February 1937 bushfire that defoliated the overstorey across a widespread area of forest around Walpole (Bellanger 1980, Fernie and Fernie 1989).

On 7 March 2001, a lightning strike ignited a fire that burnt for four days under conditions of moderate to high fire danger at the end of seasonal summer drought when the entire litter profile was dry and available for combustion (Table 1). The Soil Dryness Index (Mount 1972, Burrows 1987), which reflects the dryness of soil and coarse woody debris, was at its seasonal peak of 165 mm. Despite temperature and relative humidity being relatively mild, the combination of dry fuels and strong easterly winds on the night of 9

Table 1. Weather and fuel moisture content recorded at Walpole during the March 2001 fire. Fuel moisture contents represent daily minimum values predicted by the Forest Fire Behaviour Tables for Western Australia (Sneeuwjagt and Peet 1985).

Date	Maximum temperature (°C)	Minimum relative humidity (%)	Wind direction and speed at 1500 h (km h ⁻¹)	Fine fuel moisture content (%)	Profile moisture content (%)
7 Mar 2001	33	32	SW 24	11	22
8 Mar 2001	22	63	SSW 14	18	22
9 Mar 2001	21	54	SE 26	18	22
10 Mar 2001	23	47	SE 34	20	22

March caused the head fire to spread 5 km through a mosaic of forest and shrubland with an average rate of spread of 0.35 km hr⁻¹. Fireline intensity in the long-unburnt tall forest was estimated to be in the range 3000 kW m⁻¹ to 7000 kW m⁻¹ with flame heights of up to 10 m. This caused complete crown scorch of tall forest and widespread defoliation of low forest and shrubland.

Forest Measurements

In November 2001, we established an 800 m long belt transect in forest on a westerly facing slope that had been completely crown scorched by the fire (Figure 2). We chose this area because of the relative uniformity of the stand structure, and because it was located in an area where the fire had burnt unimpeded by suppression action. Stand structure was assessed by recording the species, stem diameter (dbh), and crown condition of individual eucalypts, *Allocasuarina decussata* and *Agonis flexuosa* >10 cm dbh, within 25 m either side of the transect. The location of each tree was recorded as the distance along and left or right of the transect. Trees judged to have been dead at the time of the 2001 fire were not included, although we did observe evidence of dead trees that had burnt away partially or completely. Crown condition was described using an ordinal scale based on the location of re-sprouting on the stem and reflecting the relative severity of damage by fire as proposed by Lacey and Johnston

(1990). Ratings were (1) crown recovering from shoots on fine terminal branches, (2) crown recovering from epicormic shoots on intermediate branches without extensive re-sprouting from the stem, (3) crown recovering from epicormic shoots on large branches and the stem, (4) crown dead with epicormic shoots on the stem only, (5) epicormic shoots only arising from the stem below 1.3 m, and (6) tree completely dead. Crown condition was assessed in April 2002 and again in December 2005, respectively 13 months and 52 months after fire.

Seedling regeneration was monitored at 40 permanently marked points located at 20 m intervals along the transect. At each point, the number of eucalypt seedlings was counted within a circular quadrat of 1.13 m radius (4 m²) and the height of the tallest seedling of each species recorded. Counts were undertaken in December 2001; June 2002; and in December 2003, 2005, and 2009. Stem diameter was also recorded for individual plants once they attained a height of 2 m. Seedling densities on individual quadrats, including un-stocked quadrats, were averaged and converted to a per hectare equivalent. The number of stocked quadrats containing one or more live seedlings was used as a measure of site occupancy, consistent with regeneration survey practice common in eucalypt forests (Lutze *et al.* 2004).

The relationship between forest overstorey composition and initial seedling density in the first spring after fire (November 2001) was



Figure 2. (A) Mature forest in the early stages of recovery eight months after being fully crown scorched by the fire of March 2001. Eucalypt seedlings are visible in the foreground. Large trees that have fallen since the fire are evident, including a rough barked *E. jacksonii* (foreground) and a smooth barked *E. diversicolor* (right side, rear of photo). (B) Re-sprouting of epicormic shoots on mature *E. diversicolor* and *E. jacksonii* one year after the fire. Dense seedling regeneration of *E. diversicolor* is visible in the foreground.

investigated for the two dominant species *E. diversicolor* and *E. jacksonii*. We calculated the basal area of each species within a 25 m radius of each seedling quadrat, and the distance to the nearest potential seed tree of each species with a diameter of ≥ 70 cm, up to a distance of 25 m, which was the full width of the sample transect. Trees ≤ 70 cm diameter were excluded because they were immature and yet to develop their full crown size and seed potential (Bradshaw and Rayner 1997). For each species, seedling density was plotted against basal area and the relationship tested by fitting a linear regression. Seedling density was also compared for quadrats located < 25 m

and > 25 m from a potential seed tree of each species using the non-parametric Mann-Whitney test. This distance represents approximately twice the crown radius and half the height of a mature tree (Rotheram 1983).

RESULTS

Overstorey and Mid-Storey Trees

The forest overstorey was dominated by mature eucalypts with a density of 45 stems ha^{-1} and a basal area of 45.7 $\text{m}^2 \text{ha}^{-1}$ (Table 2). Half of the basal area was contributed by *E. diversicolor*, with smaller contributions of *E.*

Table 2. Stand characteristics recorded on a 3.9 ha transect.

Species	Stems ha ⁻¹	Basal area (m ² ha ⁻¹)	Mean dbh (SE) (cm)	dbh of largest tree (cm)
<i>Corymbia calophylla</i>	7	7.9	111 (10)	199
<i>Eucalyptus diversicolor</i>	26	23.6	96 (5)	241
<i>Eucalyptus guilfoylei</i>	1	0.3	62 (11)	89
<i>Eucalyptus jacksonii</i>	10	13.4	112 (11)	345
<i>Eucalyptus marginata</i>	1	0.5	88 (21)	117
<i>Agonis flexuosa</i>	9	0.3	18 (1)	37
<i>Allocasuarina decussata</i>	17	2.5	40 (2)	70

jacksonii and *C. calophylla* and occasional *E. marginata* and *E. guilfoylei*. The modal diameter class of overstorey trees was 125 cm to 149 cm with a secondary peak in the 50 cm to 74 cm diameter class, and occasional very large trees with a stem diameter >2 m, which were mostly *E. jacksonii* (Figure 3). Mid-storey trees were predominantly *Allocasuarina decussata* with a mean stem diameter of 40 cm, and a lesser component of *Agonis flexuosa*.

Most overstorey trees had begun to re-sprout from epicormic buds within one year of the fire (Figure 2). Re-sprouting from epicormic buds on the larger branches and

stems was the most common recovery mechanism observed on *E. diversicolor* and *E. jacksonii*, while *C. calophylla* more commonly re-sprouted from epicormic buds on small and intermediate branches (Table 3). The small number of *E. marginata* and *E. guilfoylei* present also re-sprouted from epicormic buds on the larger branches and stems (data not shown). Mid-storey trees were more severely impacted than the overstorey due to their lower stature, with 7% of *Allocasuarina decussata* dead within the first year and most surviving trees re-sprouting only from the stems and larger branches. Two-thirds of *Agonis flexuosa* stems were killed back to ground level and re-sprouted from basal buds. At 52 months post fire, the proportion of dead trees had increased to 6% of *E. diversicolor*, 9% of *E. jacksonii*, and 15% of *C. calophylla* (Table 3). For surviving trees, the proportion of trees limited to epicormic shoots on the stems had reduced and re-sprouting on fine terminal branches and intermediate branches had increased for all eucalypts. No *E. marginata* or *E. guilfoylei* died following the fire, with all trees re-sprouting from epicormic shoots on terminal and intermediate branches. By 2005, the number of dead *Allocasuarina decussata* had increased four-fold to 29% of trees, with a further 6% re-sprouting only from the base. All *Agonis flexuosa* re-sprouted from basal shoots.

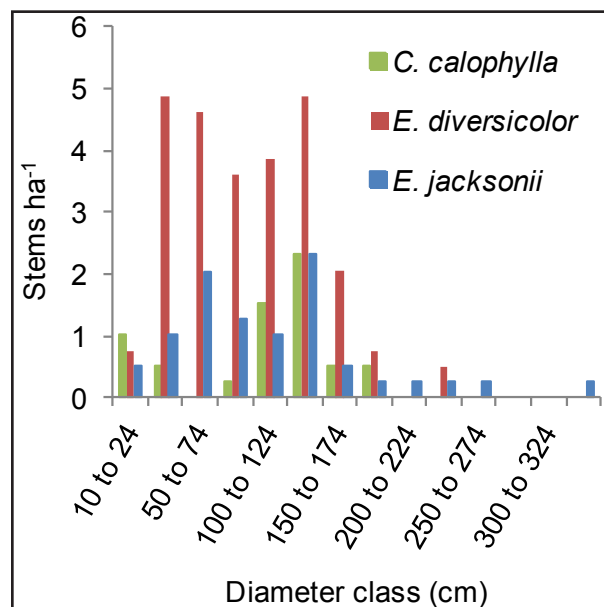


Figure 3. Stem diameter distribution for the three dominant overstorey trees on a 3.9 ha belt transect.

Table 3. Crown condition of fully scorched overstorey and mid-storey trees in 2002 and 2005. Crown condition ratings indicate the predominant location of epicormic shooting on the tree.

Species	Stems (n)	Months since fire	Number (%) of sprouts by location					Base below 1.3 m	Dead n (%)
			Terminal branches	Intermediate branches	Branches and stem	Stems			
<i>C. calophylla</i>	26	13	7 (27)	10 (39)	4 (15)	4 (15)	1 (4)	0 (0)	
		52	19 (73)	2 (8)	0 (0)	0 (0)	1 (4)	4 (15)	
<i>E. diversicolor</i>	101	13	31 (31)	5 (5)	46 (46)	16 (16)	0 (0)	3 (3)	
		52	31 (31)	21 (21)	30 (30)	11 (11)	2 (2)	6 (6)	
<i>E. jacksonii</i>	39	13	4 (10)	4 (10)	25 (64)	5 (13)	0 (0)	1 (3)	
		52	12 (30)	4 (10)	18 (46)	2 (5)	0 (0)	3 (9)	
<i>A. decussata</i>	68	13	18 (26)	16 (24)	19 (28)	10 (15)	0 (0)	5 (7)	
		52	24 (35)	15 (22)	4 (6)	1 (2)	4 (6)	20 (29)	

Seedling Regeneration

Eucalypt seedling densities were highest in November 2001, the first spring after fire (Figure 4). Seedling densities of *E. jacksonii* were initially twice those of *E. diversicolor*, but the percentage of 4 m² quadrats stocked with *E. jacksonii* (53%) was lower than for *E. diversicolor* (73%), indicating a more clumped distribution of *E. jacksonii* seedlings (Figure 5). Few seedlings (<25 ha⁻¹) of other eucalypts

were recorded. The density of *E. diversicolor* seedlings was significantly higher at quadrats located within 25 m radius of a mature tree, but there was no significant relationship ($P > 0.05$) between seedling density and basal area of mature trees in surrounding forest (Table 4, Figure 6). The density of *E. jacksonii* seedlings was also significantly greater on quadrats located within 25 m radius of a mature tree than those located farther away. Seedling density and basal area of mature trees

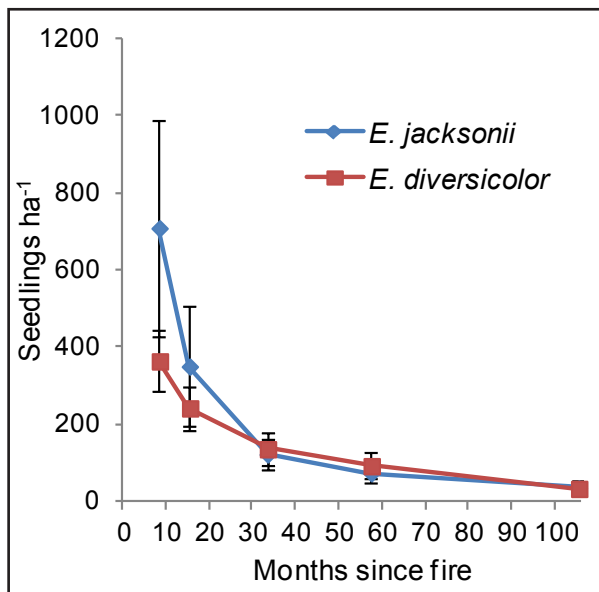


Figure 4. Mean density of seedlings of *E. diversicolor* and *E. jacksonii* recorded at 40 quadrats between November 2001 and December 2009. Bars indicate SE.

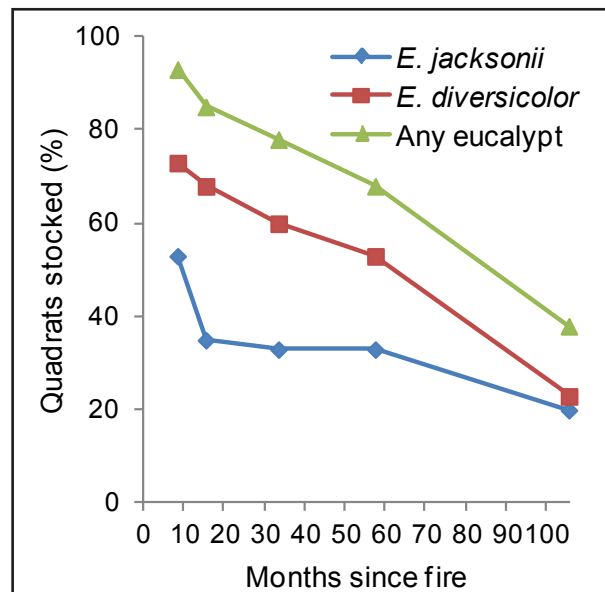


Figure 5. Percentage of quadrats stocked with one or more seedlings of *E. diversicolor*, *E. jacksonii*, or any species of eucalypt between November 2001 and December 2009.

Table 4. Seedling densities of *E. diversicolor* and *E. jacksonii* in November 2001 for quadrats located <25 m and >25 m distant from a potential seed tree of either species. Data are means (SE). Values in each row followed by a different superscript are significantly different ($P < 0.05$; Mann-Whitney test).

Species	Seedling density (m ⁻²)	
	<25 m	>25 m
<i>E. diversicolor</i>	1.8 ^a (0.4)	0.6 ^b (0.4)
<i>E. jacksonii</i>	4.0 ^a (2.2)	0.6 ^b (0.3)

were significantly related ($P < 0.01$) for *E. jacksonii*, with the relationship influenced strongly by very high seedling density at a single quadrat associated with high basal area (62 m² ha⁻¹). By the beginning of winter 2002, 15 months after the fire, seedling densities had reduced by half for *E. jacksonii* and by 35% for *E. diversicolor*. Stocking and density declined progressively over the following seven years and by December 2009, 38% of 4 m² quadrats remained stocked with at least one eucalypt (Figure 5). Densities of surviving *E. diversicolor* and *E. jacksonii* were similar, respectively 33 stems ha⁻¹ and 34 stems ha⁻¹.

Seedlings of *E. diversicolor* and *E. jacksonii* exhibited similar height growth over time and, by 2009, the regeneration cohort consisted of saplings with a mean height of 5 m (Figure 7), and a mean dbhob (dbh outside bark) of 4 cm (SE = 0.6 cm). The largest and most vigorous saplings observed in the general study area were up to 15 m tall and 17 cm dbhob.

DISCUSSION

The existence of multiple-age cohorts in tall open eucalypt forest has generally been inferred from stand structural data including stem diameter size class distribution, tree canopy characteristics, and evidence of fire scarring and charcoal on stems (Bradshaw and Rayner 1997, Hickey *et al.* 1999, Turner *et al.*

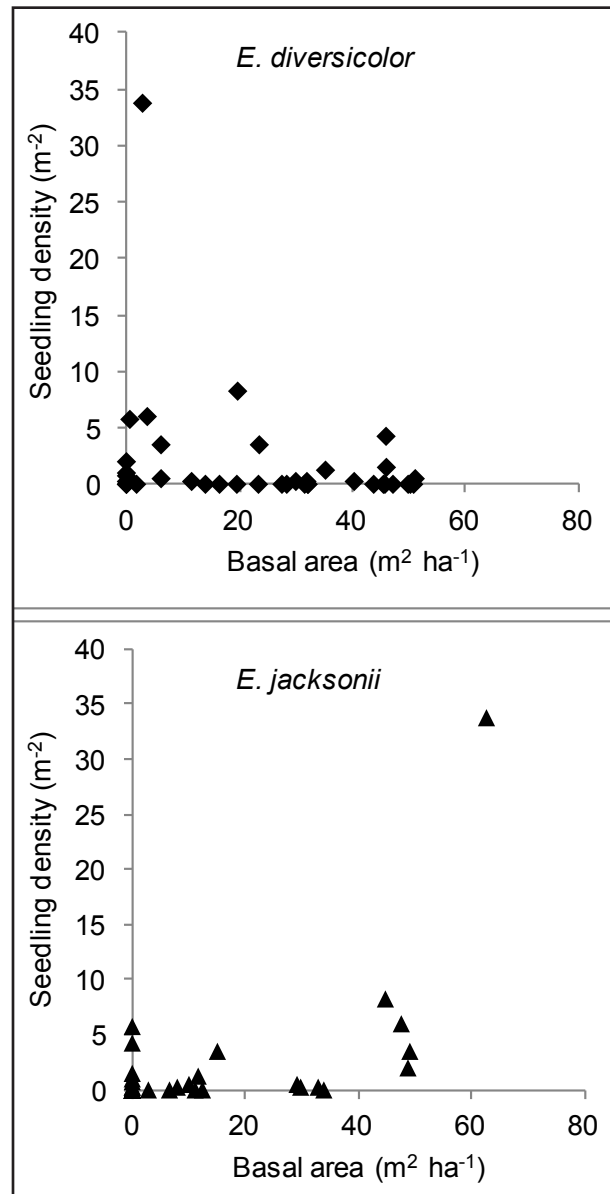


Figure 6. Density of seedlings of *E. diversicolor* and *E. jacksonii* in November 2001 in relation to the basal area of that species within 25 m radius of the quadrat.

2009). Cohort ages have been estimated using tree ring counts for overstorey and fire sensitive mid-storey trees, and from fire records. We employed a different but complementary approach by studying responses at the stand scale over an eight year period following fire. Benyon and Lane (2013) used a similar approach to assess

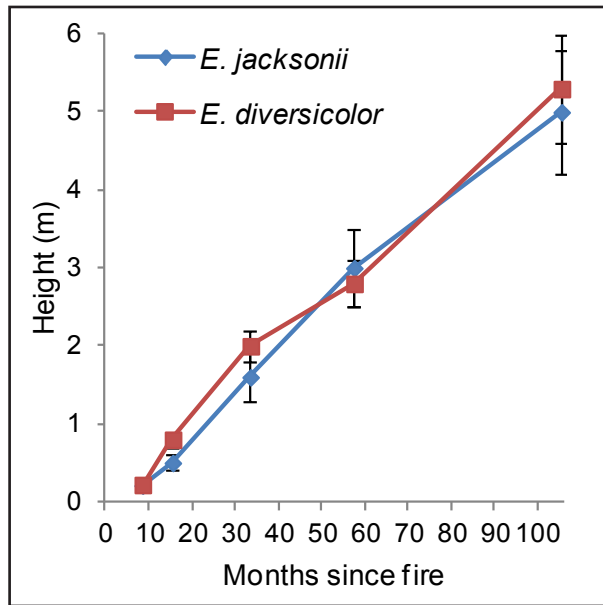


Figure 7. Height of *E. diversicolor* and *E. jacksonii* at intervals between November 2001 and December 2009. Bars indicate SE.

overstorey survival and seedling regeneration at multiple sites following the extensive 2009 bushfires in Victoria, south-eastern Australia, although their observations were limited to the first two years following fire and did not include quantitative assessments of eucalypt seedling density.

Monitoring the fate of particular regeneration cohorts provides scope to better understand the varied factors that may determine the pathway from seedling to mature tree. Seedling densities of *E. jacksonii* were twice those of *E. diversicolor* in the first spring after fire, but this higher density did not persist beyond the third spring after fire. McCaw *et al.* (2000) reported a similar finding from a previous study of seedling recruitment following two low intensity fires in tall open forest near Walpole, with the higher density of *E. jacksonii* seedlings reflecting the relative dominance of overstorey eucalypts in the two stands examined in that study. Overstorey composition does not explain the findings of the present study in which *E. diversicolor* was dominant both in terms of basal area and the

number of stems per hectare. The opportunistic circumstance of the present study meant that no information was available about the size or condition of the seed crop at the time of the fire. McCaw *et al.* (2000) reported little or no persistent recruitment of *E. diversicolor* or *E. jacksonii* following low intensity fires, attributing this to high levels of competition from overstorey and mid-storey trees with intact crowns, and rapid loss of seed bed receptivity due to heavy post-fire litter fall from *Allocasuarina decussata*. In contrast, *E. diversicolor* and *E. jacksonii* saplings established following the 2001 fire have remained competitive with the dense post-fire understorey and have the potential to form an additional cohort within the stand provided they survive subsequent fires. In the absence of a competing overstorey, *E. diversicolor* saplings take at least 15 years to develop to a stage at which they are tolerant of low to moderate intensity fire (McCaw *et al.* 1994), and *E. jacksonii* is likely to require a similar period. Competition from surviving overstorey trees would be expected to suppress the further development of some saplings into more advanced growth stages (Rotheram 1983). The stocking of persistent eucalypt regeneration following the 2001 fire is low in comparison with *E. diversicolor* stands regenerated using seed tree silviculture following timber harvesting (McCaw *et al.* 2002), and much lower than post-fire regeneration density common in some tall open forests in south-eastern Australia (Ashton 1976).

The stand examined in this study included trees of a wide range of size classes with evidence of several distinct cohorts, including a low density of very large trees that have persisted through multiple fire events, including a previous high intensity fire in 1937. Wood *et al.* (2015) reported a similar stand structure from a sample of nine 1 ha plots established in *E. diversicolor* and *E. jacksonii* forest as part of a continental scale

network of plots in tall open eucalypt forest. More than 85% of overstorey trees examined in our study survived complete crown scorch and replaced their crowns from epicormic buds on the stems and larger branches, consistent with the findings of Wardell-Johnson (2000). The capacity of eucalypts from tall open forest in south-west Western Australia to recover from complete crown scorch appears similar to that of the more fire-tolerant eucalypts from tall open forests in south-eastern Australia (Benyon and Lane 2013), including pure stands of *E. nitens* (Deane & Maiden) and mixed species stands of *E. obliqua* L'Hér, *E. baxteri* (Benth.) Maiden & Blakely ex J.M. Black, *E. cypellocarpa* L.A.S. Johnson, and *E. radiata*

Sieber ex DC. Mid-storey trees, particularly *Allocasuarina decussata*, are also capable of surviving fires of moderate to high intensity and can attain considerable age and stature, contributing to structural complexity of the forest that may be important for biodiversity conservation (Lindenmayer 2009).

It is important to recognise that our findings and those of Wardell-Johnson (2000) relate to fires within the lowest decile of potential fire intensity recorded in tall eucalypt forest (Cruz *et al.* 2012). More intense fires, which can potentially include crowning fires, could impact severely on stand structure through increased mortality and accelerated loss of hollow-butted trees.

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