The tortoise and the hare? Post-fire regeneration in mixed *Eucalyptus–Callitris* forest

Ian D. Lunt[A,D], *Heidi C. Zimmer*[B,C] *and David C. Cheal*[B]

[A]Institute for Land, Water and Society, Charles Sturt University, PO Box 789, Albury, NSW 2640, Australia.
[B]Arthur Rylah Institute, Department of Sustainability and Environment, 123 Brown Street, Heidelberg,
Vic. 3081, Australia.
[C]Present address: School of Biological Sciences, Faculty of Science, Monash University, Clayton,
Vic. 3800, Australia.
[D]Corresponding author. Email: ilunt@csu.edu.au

Abstract. Seedling regeneration after a high intensity wildfire was assessed in a mixed forest dominated by *Eucalyptus* species and *Callitris endlicheri* (Parl.) F.M. Bailey. Patterns were compared against the 'slow seedling' or 'tortoise-and-hare' theory of competitive interactions between gymnosperms and angiosperms. Browsing effects were documented using fenced plots, and seedling density, mortality and height were assessed over 6 years, from 2004–10. Consistent with expectations, *Eucalyptus* seedlings grew faster than *Callitris* seedlings in most situations. *Callitris* seedlings grew faster and produced seed cones sooner in plots with fewer *Eucalyptus* seedlings compared with plots with dense *Eucalyptus* seedlings. The local growth rates of *Callitris* seedlings were not associated with long-term site suitability for *Callitris*, as many plots with diminutive *Callitris* seedlings and dense *Eucalyptus* seedlings were dominated by *Callitris* trees before the 2003 fire. Contrary to expectations, few *Callitris* seedlings died during the 6-year period, so competition during the regeneration phase did not regulate co-existence. Strong drought tolerance and the ability to persist in dense, unthinned stands may enable *Callitris* to persist beneath dense *Eucalyptus* regeneration. Nevertheless, *Callitris* seedlings growing with dense *Eucalyptus* seedlings have a longer primary juvenile period than seedlings in sites with fewer seedling or adult eucalypts, which places these stands at greater risk of mortality in future fires and greater risk of browsing in the meantime.

Introduction

A principal goal of vegetation ecology is to understand the factors that influence vegetation patterns and dynamics. In 1989, William Bond developed a general model to interpret competitive interactions among two groups of seed plants: the gymnosperms and angiosperms. Bond's (1989) 'slow seedling' or 'tortoise-and-hare' hypothesis stated that, because gymnosperm seedlings had lower growth rates than angiosperm seedlings due to architectural constraints, gymnosperms were largely restricted to low productivity ecosystems where they escaped competition from vigorous, fast-growing angiosperms. By contrast, in productive ecosystems, competition from angiosperms would suppress gymnosperm growth rates, leaving gymnosperm seedlings vulnerable to processes that cause size-dependent mortality, such as drought, herbivory and fire. In some instances, gymnosperm decline would be hastened if angiosperms promoted adverse disturbances, for example, where grasses fuelled fires that killed gymnosperm seedlings (Bond and Scott 2010). Cast in the language of Grime's (2001) plant strategy scheme, gymnosperms were viewed by Bond (1989) as 'stress tolerators', poorly equipped to regenerate and persist in productive environments dominated by more 'competitive' angiosperms.

Our understanding of the physiological mechanisms underlying low growth rates of gymnosperm seedlings has

since been refined (Becker *et al*. 1999; Becker 2000; Lusk *et al*. 2003; Brodribb *et al*. 2005), and Bond's 'slow seedling' model may be viewed within a broader plant leaf economics spectrum, in which relative growth rate is related to leaf longevity and specific leaf area (Cornelissen *et al*. 1996; Reich *et al*. 1999; Wright *et al*. 2004). Gymnosperms characteristically have long-lived leaves of low specific leaf area, which lead to lower relative growth rate than many, but not all, angiosperms (Reich *et al*. 1999; Lusk *et al*. 2003).

The most widespread and abundant genus of gymnosperms in Australia is *Callitris* (Family Cupressaceae), which occurs in tropical, subtropical, arid, semiarid, Mediterranean and temperate regions (Bowman and Harris 1995). *Callitris* dynamics have received considerable attention from fire ecologists as *Callitris* are often killed by fire and usually do not resprout after being subjected to 100% leaf scorch (Lacey 1973; Bradstock and Cohn 2002; Russell-Smith 2006). Consequently, population dynamics are highly sensitive to changes in fire regimes (Bowman and Panton 1993; Bradstock *et al*. 2006; Prior *et al*. 2010). Surprisingly, Bond's (1989) model has never been referred to in studies on *Callitris* ecology. This may be because few studies have documented interactions between *Callitris* and other woody species (e.g. Clayton-Greene 1981; Bowman *et al*. 1988; Clayton-Greene and Ashton 1990), even though *Callitris* occur in heathlands, woodlands and forests dominated by *Eucalyptus* and

other woody plants (Bowman and Harris 1995). In savannah and arid woodlands, fire regimes and *Callitris* dynamics are regulated by dominant grasses rather than woody plants (Bowman *et al.* 1988; Bradstock and Cohn 2002). Indeed, we know of only one study (an unpublished seedling pot trial) that has documented competitive interactions between *Callitris* seedlings and other woody taxa (Clayton-Greene 1981).

This paucity of information raises the question, to what extent do interactions with woody angiosperms influence *Callitris* dynamics in productive forest ecosystems? Under Bond's (1989) model, inter-specific interactions could influence the ability of non-resprouting *Callitris* to persist in ecosystems dominated by flammable, resprouting angiosperms. In this study, we attempt to address this issue by asking: to what extent are post-fire recruitment patterns in a mixed *Callitris–Eucalyptus* forest in a relatively high rainfall region (~850-mm mean annual rainfall) consistent with Bond's slow seedling hypothesis? We discuss the implications of these patterns for species co-existence and fire management. Our study is observational rather than manipulative, which means that while we can assess whether patterns are consistent with Bond's hypothesis, we cannot be definitive about the mechanisms that underlie observed patterns.

Materials and methods

Study area

The study was conducted in Chiltern-Mt Pilot National Park in north-eastern Victoria, Australia. Mean annual rainfall in the study area is ~850 mm, based on data from nearby Beechworth (960 mm) and Beechworth Woolshed rainfall gauges (770 mm; Bureau of Meteorology 2011). The underlying geology is Devonian granite and the topography is moderately to steeply undulating (Parks Victoria 2008). The area supports dry sclerophyll forests dominated by *Eucalyptus macrorhyncha* F.Muell. ex Benth., *E. goniocalyx* F.Muell., *E. polyanthemos* Schauer and *E. blakelyi* Maiden, with patches dominated by *Callitris endlicheri*. Most *Callitris*-dominated stands are small (<1 ha) and in close proximity to rocky outcrops (Watson 2004).

In January 2003, 7300 ha of the reserve burnt in a high intensity wildfire (Watson 2004). In July 2003, two, 10 × 10-m fenced plots were erected in each of three burnt *Callitris* stands near Mt Pilot to assess browsing impacts on *Callitris* seedlings. Post-fire vegetation monitoring began in autumn 2004. Twelve stands of *Callitris* were selected within a 2.2-km radius of the Mt Pilot summit (36°15′06′S, 146°40′13′E). All 12 sites were burnt at high intensity, as evidenced by complete mortality of pre-fire *Callitris* and resprouting of surviving *Eucalyptus* from basal coppice rather than from epicormic buds on trunks or branches. Six stands, including the three stands containing fenced plots, were dominated by mature *C. endlicheri*, presumed to have recruited in the late 1800s, with subdominant *Eucalyptus*. The other six stands were dominated by *Eucalyptus* above smaller *Callitris*, which were presumed to have recruited after 1950.

Permanently marked 100-m² (10 × 10 m) plots were established at each site. Paired unfenced plots were established at the three fenced sites, giving four plots in total at these sites (plus an extra unfenced plot in one large stand), and two unfenced plots were established in the nine stands without fences. Pre-fire

stand structure was estimated in autumn 2004 by measuring all dead and resprouting trees in each 100-m² plot. Small saplings that were totally incinerated would not have been detected.

The height, number of stems, and girth over bark at breast height (GOBBH) of the largest stem was recorded annually for all coppicing *Eucalyptus* in each 100-m² plot. For clarity, all post-fire seedling recruits are called 'seedlings' in this paper, even though many had grown tall (i.e. to 'sapling' size) by the end of the monitoring period. The species identity, height and GOBBH of all post-fire seedlings were assessed annually in 10 (in 2004) and 20 (2005–10) randomly placed 1-m² subplots within each 100-m² plot. These subplots were re-randomised each year. GOBBH was recorded as 0.1 cm if plants were <1.3 m tall. Sampling was conducted in autumn 2004–10, but only two sites were sampled in 2009, due to inclement weather. At Beechworth, annual rainfall was slightly above average from 2003 to 2005 (965–1215 mm/year), very low in 2006 (413 mm) and ~80% of average from 2007 to 2009 (755–790 mm; Bureau of Meteorology 2011).

Data analysis

Linear mixed models were used to examine:

(1) The relationship between initial seedling density (including live and dead seedlings in 2004) and the pre-fire basal area of each genus;
(2) The effects of fencing and time on the density and height of live seedlings of each genus; and
(3) Associations between seedling height in 2010 and (a) the pre-fire basal area of each genus, (b) the density of competing seedlings in 2010, and (c) the basal area of resprouting *Eucalyptus* in 2010.

The influence of fencing on seedling heights and densities was assessed using data from the three sites with fenced and unfenced plots only. In each case, year, fencing treatment, basal area (at the plot scale), and seedling density in subplots were included as fixed effects, and nested sites, plots and subplots were incorporated as random effects. Where necessary, density, height and basal area data were log-transformed to meet the assumption of constant variance. *F*-tests were used to investigate the significance of individual model term. Analyses were undertaken in GENSTAT version 13 (VSN International 2010). In addition *t*-tests were used to compare: (1) the height of *Eucalyptus* and *Callitris* seedlings in 2010, (2) the proportion of seedlings in fenced and unfenced plots with evidence of browsing in 2010, and (3) the mean height of seedlings in fenced and unfenced plots in 2010. Few *Callitris* seedlings produced seed cones by 2010. Consequently, associations between the density of *Callitris* and *Eucalyptus* seedlings versus the number of *Callitris* seedlings bearing seed cones and the number of cones produced were analysed at the plot scale, using Spearman's rank correlation coefficients.

Results

Seedling density and mortality

Callitris and *Eucalyptus* seedlings both regenerated at high density after the 2003 fire. On average, there were 5.8 *Callitris* seedlings/m² and 2.8 *Eucalyptus* seedlings/m² in 2004, 16 months after the fire. The initial, post-fire density of *Callitris* seedlings was significantly and positively associated

with the pre-fire basal area of *Callitris* ($P = 0.031$). After accounting for the association of *Callitris* seedling density with *Callitris* pre-fire basal area, the association with *Eucalyptus* pre-fire basal area was not significant. By contrast, the initial density of *Eucalyptus* seedlings was not significantly associated with the pre-fire basal area of either genus ($P = 0.333$ and 0.717 for *Eucalyptus* and *Callitris*, respectively).

Mortality rates after the first monitoring event were extremely low for both genera. The mean density of live *Callitris* seedlings apparently declined from 5.2 to 3.7 seedlings/m^2 from 2004 to 2010; however, this change was not statistically significant (at $P < 0.05$). The mean density of *Callitris* seedlings did not change significantly over time ($P = 0.783$) nor did it differ significantly across fencing treatments, when all plots (including all unfenced plots) were compared ($P = 0.348$). Similarly, when data from only the three sites with fenced plots were analysed, the density of *Callitris* seedlings was not significantly associated with year ($P = 0.723$), fencing ($P = 0.392$) nor the year*fencing interaction ($P = 0.945$; Fig. 1*a*).

By contrast, there was a significant decline in the density of live *Eucalyptus* seedlings over the same period. Across all sites, mean (back-transformed) density declined from 2.8 to 1.2 seedlings/m^2. When data from all plots were analysed, the density of *Eucalyptus* seedlings differed significantly among years ($P < 0.001$) but not among fencing treatments ($P = 0.122$) or with the year*fencing interaction (0.348). When data from only the three sites with fenced plots were analysed, the density of *Eucalyptus* seedlings was not significantly affected by year ($P = 0.224$), fencing ($P = 0.428$) nor year*fencing interaction ($P = 0.947$; Fig. 1*b*).

Seedling growth rates

Callitris seedlings were, on average, shorter than *Eucalyptus* seedlings throughout the survey period (Fig. 2). In 2010, the mean height of *Eucalyptus* seedlings was over twice that of *Callitris* seedlings (184 cf. 84 cm; *t*-test, $P < 0.001$), and the tallest *Eucalyptus* seedling was over twice as tall as the tallest *Callitris* seedling (max. height, 800 cf. 350 cm). In 2010, 30% of *Callitris* seedlings were <0.5 m tall.

Fencing effects

In 2010, it appeared that more *Callitris* seedlings showed evidence of browsing in unfenced than fenced plots (25% cf. 2% at the plot scale) although this difference was not significant at the $P = 0.05$ level (paired *t*-test, $P = 0.09$). *Callitris* seedlings grew
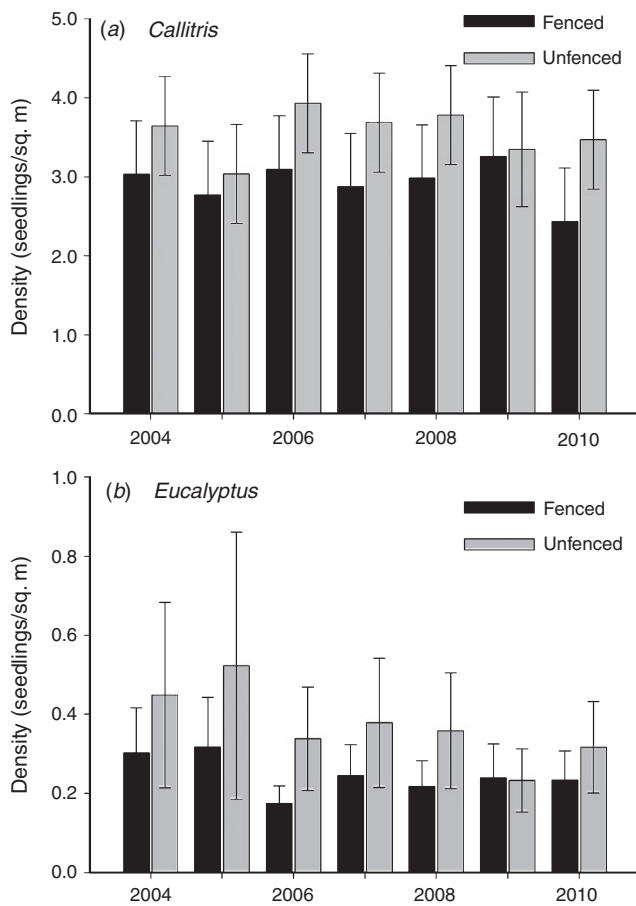

Fig. 1. Predicted density of live (*a*) *Callitris* (mean ± standard error) and (*b*) *Eucalyptus* seedlings in fenced and unfenced plots (back-transformed mean ± standard error) after the 2003 fire at Mt Pilot.
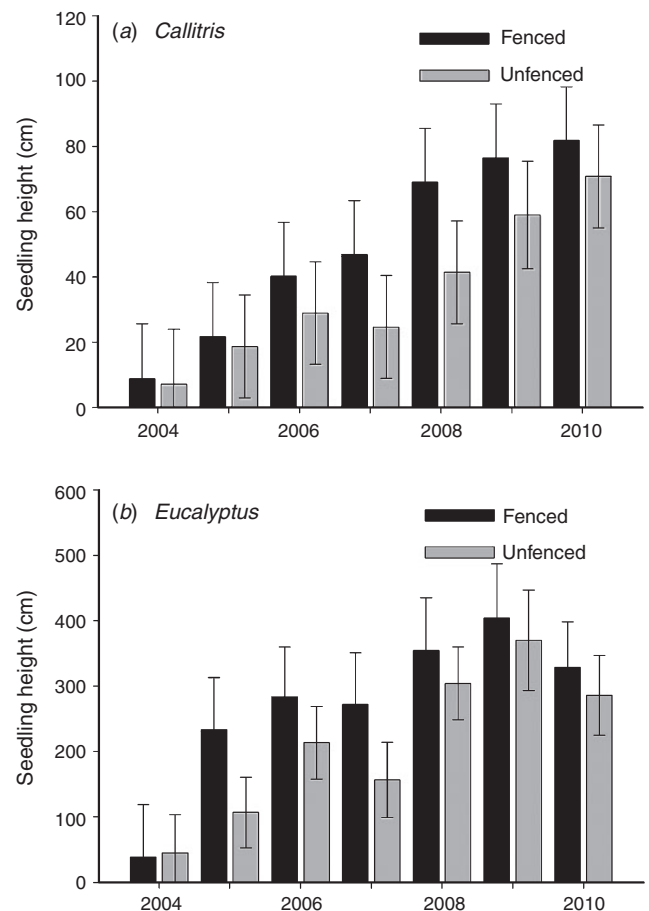

Fig. 2. Predicted mean height of (*a*) *Callitris* and (*b*) *Eucalyptus* seedlings in fenced and unfenced plots (back-transformed mean ± standard error).

taller in fenced than unfenced plots (Fig. 2*a*). The mean (back-transformed) height of *Callitris* seedlings varied significantly with year (*P* < 0.001) and fencing treatment (*P* = 0.007) with no significant year*fencing interaction (*P* = 0.198). In 2010, the mean height of *Callitris* seedlings in fenced plots was 145 cm compared with 116 cm in unfenced plots (*t*-test, *P* < 0.001). By contrast, only 5% of all *Eucalyptus* seedlings surveyed in 2010 (in all fenced and unfenced plots) displayed evidence of browsing. No *Eucalyptus* seedlings were browsed within the three fenced plots in 2010. Consequently, the height of *Eucalyptus* seedlings varied significantly with year (*P* = 0.002) but there was no significant fencing effect (*P* = 0.747) or year*fencing treatment interaction (*P* = 0.558; Fig. 2*b*). In 2010, the mean height of fenced and unfenced *Eucalyptus* seedlings was 226 and 245 cm, respectively (*t*-test, *P* = 0.70).

Factors associated with seedling height

The linear mixed model showed that the height of *Callitris* seedlings in 2010 was significantly and positively associated with fencing (*P* = 0.025), and negatively associated with the density of *Eucalyptus* seedlings (*P* = 0.006). After accounting for these terms, there was no significant association with (a) the density of *Callitris* seedlings, (b) the basal area of coppicing *Eucalyptus*, nor (c) the pre-fire basal area of *Callitris* or *Eucalyptus* (Table 1). The lack of association between *Callitris* seedling heights and the pre-fire basal area of either genus suggests that *Callitris* seedlings neither grew better nor worse in plots dominated by either genus before the fire.

In contrast, the height of *Eucalyptus* seedlings in 2010 was significantly negatively associated with *Eucalyptus* seedling density (*P* < 0.001) and positively associated with *Callitris* seedling density (*P* = 0.002) and the pre-fire basal area of *Callitris* (*P* = 0.053; Table 2), which indicates that *Eucalyptus* seedlings grew faster where *Callitris* dominated before the fire.

Table 1. Model statistics for linear mixed model describing the factors associated with *Callitris* seedling heights in 2010

Terms were individually removed from the full fixed model, d.d.f. = denominator degrees of freedom, numerator degrees of freedom = 1

Fixed term	*F*-statistic	d.d.f.	Probability (F pr)
Eucalyptus density in 2010	7.6	419.5	0.006
Callitris density in 2010	3.59	329.3	0.059
Eucalyptus coppice basal area in 2010	2.58	27	0.120
Fencing treatment	5.67	25	0.025

Table 2. Model statistics for linear mixed model describing the factors associated with *Eucalyptus* seedling heights in 2010

Terms were individually removed from the full fixed model, d.d.f. = denominator degrees of freedom, numerator degrees of freedom = 1

Fixed term	*F*-statistic	d.d.f.	Probability (F pr)
Fencing treatment	0.73	29.5	0.401
Log *Callitris* basal area in 2004	4.18	22.0	0.053
Log *Callitris* density in 2010	9.70	257.5	0.002
Log *Eucalyptus* density in 2010	11.25	251.5	<0.001

Seed cone production

In 2010, 7 years after the fire, 2% of *Callitris* seedlings possessed seed cones. Seed cones were almost entirely restricted to the tallest seedlings. Thus, 83% of cones were on seedlings taller than 150 cm (Fig. 3), and 23% of seedlings >2 m possessed seed cones (*n* = 100). The shortest seedling with seed cones was 140 cm tall. Cone production varied from <5% to almost 30% of *Callitris* seedlings at each plot.

In 2010, there was no significant correlation between the number of *Callitris* seedlings in each plot and either the number of *Callitris* seedlings bearing seed cones (Spearman's rank correlation coefficient, rho = −0.030, d.f. = 29, *P* = 0.874) or the number of seed cones produced (rho = −0.039, *P* = 0.833). However, there was a significant negative correlation between the number of *Eucalyptus* seedlings in each plot and the number of *Callitris* seedlings bearing seed cones (rho = −0.454, *P* = 0.010) and the number of seed cones produced (rho = −0.448, *P* = 0.012). The total number of *Eucalyptus* and *Callitris* seedlings in each plot was positively correlated (rho = 0.380, *P* = 0.0352). Thus, *Callitris* seedlings produced more seed cones in plots with fewer *Eucalyptus* seedlings.

Discussion

These results illustrate several patterns that are consistent with Bond's (1989) slow seedling hypothesis: (1) *Eucalyptus* seedlings grew faster than *Callitris* seedlings; (2) *Callitris* seedlings grew faster, and produced seed cones sooner, in plots with fewer *Eucalyptus* seedlings; and (3) small *Callitris* seedlings growing beneath dense *Eucalyptus* seedlings remained vulnerable to browsing and burning for longer than tall *Callitris* seedlings in areas with fewer *Eucalyptus* seedlings. Spatial variations in the growth rate of *Callitris* seedlings were not related to the suitability of sites to support *Callitris*, as many patches with small *Callitris* and dense *Eucalyptus* seedlings were dominated by mature *Callitris* before the 2003 fire. However, contrary to Bond's (1989) theory, few *Callitris* seedlings died, so competition during the regeneration phase did not regulate
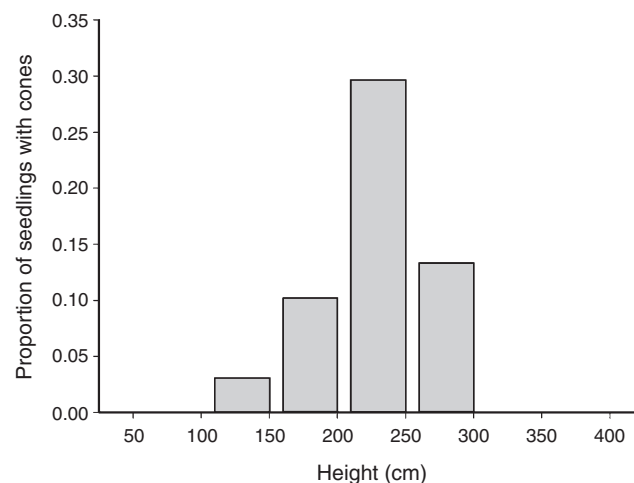

Fig. 3. The proportion of *Callitris* seedlings in different height classes that possessed seed cones in 2010. Only 19 seedlings were taller than 250 cm.

co-existence. We expand on each of these points in the discussion below.

Seedling growth rates

The lower growth rate of *Callitris* compared with *Eucalyptus* seedlings is consistent with the global trend for lower growth rates in gymnosperms than in sympatric angiosperms (Bond 1989; Reich *et al*. 1999; Lusk *et al*. 2003), and with pot and field trials in which planted *Eucalyptus* seedlings grew faster than *Callitris* seedlings (Clayton-Greene 1981; Allcock and Hik 2004). Apart from fencing, the factor most strongly associated with the growth rate of *Callitris* seedlings was the density of *Eucalyptus* seedlings. *Callitris* seedlings grew slowest where *Eucalyptus* seedlings were most abundant, and fastest where *Eucalyptus* seedlings were most sparse. Removal experiments are required to disentangle the effects of abiotic site factors and competition on *Callitris* growth rates. Nevertheless, the negative association suggests that competition from dense, tall *Eucalyptus* seedlings may have slowed the growth of smaller *Callitris* seedlings. The lack of a significant association between the growth rate of *Callitris* seedlings and the pre-fire basal area of *Callitris* indicates that sites with dense *Eucalyptus* seedlings and small *Callitris* seedlings were not unsuitable for *Callitris* growth and persistence; *Callitris* dominated some of these sites before the fire. In contrast to savanna ecosystems, grasses had very low cover and biomass at Mt Pilot, and grass competition is unlikely to have had a substantial impact on growth rates or survival of *Callitris* or *Eucalyptus* seedlings, except perhaps in the first year or two after fire.

Silvicultural trials have demonstrated that the growth rate of retained *Callitris* is enhanced when dense *Callitris* stands are thinned (Knott 1995; Ross *et al*. 2008). However, few studies have documented competitive interactions between *Callitris* and *Eucalyptus*. Clayton-Greene (1981) reported that *Eucalyptus melliodora* seedlings suppressed the growth of *Callitris glaucophylla* seedlings in a pot competition experiment. In a small thinning trial, Bowman *et al*. (1988) found that *Callitris* grew fastest in treatments with the lowest representation of co-occurring *Eucalyptus* and *Callitris*, but unfortunately their results do not clearly differentiate the competitive effects that were exerted by the two genera.

Browsing damage

Results from the fencing trial indicate that slow-growing *Callitris* seedlings were vulnerable to browsing, and that browsing magnified the height difference between the two genera. However, this set-back was temporary rather than persistent. As time progressed, the height difference between fenced and unfenced *Callitris* seedlings diminished, perhaps because taller, older plants were less accessible to browsing animals. Nevertheless, a high proportion of *Callitris* seedlings at Mt Pilot remain vulnerable to future damage by browsing animals and other disturbances.

The low level of mortality in grazed plots is likely to reflect low herbivore densities, as few large herbivores were observed in the first few years after the 2003 wildfire (I. Lunt, pers. obs.). In contrast, Mackenzie and Keith (2009) recorded high mortality of *C. endlicheri* seedlings in an area grazed by feral *Cervus*

timorensis (Rusa Deer) in coastal New South Wales. Over 12 months, 98% of unprotected seedlings were browsed at least once, leading to a 59% decline in seedling density (Mackenzie and Keith 2009). Seedlings of the related species, *C. glaucophylla*, are known to be sensitive to repeated browsing by rabbits and sheep (Lacey 1972).

Seedling mortality

In contrast with Bond's (1989) theory, *Callitris* populations did not decline markedly during the establishment period due to direct competition with angiosperms nor any other cause. We recorded no significant decline in the density of *Callitris* seedlings over 6 years, despite a high sampling intensity. By contrast, the density of *Eucalyptus* seedlings declined by 57% during the 6-year period, consistent with many studies that have documented self-thinning in *Eucalyptus* stands after fire (Florence 1996).

The stability in *Callitris* numbers was surprising, as small seedlings are usually highly susceptible to mortality arising from insufficient resources and disturbances, and the survey period included years with marked rainfall deficiencies. By contrast, Mackenzie and Keith (2009) found that the density of protected (ungrazed) *C. endlicheri* seedlings declined by 19% within a 12-month period, from 2 to 3 years after fire. Initial seedling densities may have been underestimated in our study, as sampling began in April 2004, 15 months after the fire. Nevertheless, greater mortality was expected over the following 6 years, especially given that *Callitris* seedlings were so much smaller than associated *Eucalyptus* seedlings. Post-fire rainfall at the nearby Beechworth weather station was slightly higher than the long-term average for the first 3 years after burning (2003–05), which would have assisted initial seedling establishment. However, rainfall in subsequent years was relatively low, with just 43% of mean annual rainfall in 2006 (413 mm) and ~80% of average from 2007 to 2009 (755–790 mm; Bureau of Meteorology 2011).

Callitris species are extremely drought tolerant (Attiwill and Clayton-Greene 1984; Zeppel and Eamus 2008; Brodribb *et al*. 2010), and saplings self-thin extremely slowly, forming dense 'locked stands' containing suppressed, slow-growing trees (Lacey 1973; Thompson and Eldridge 2005; Ross *et al*. 2008). Lacey (1973) reported that 'in excess of . . . 125 000 [trees]/ha are commonly encountered over widespread areas' in 20-year-old stands of *C. glaucophylla*. At the 100-m^2 plot scale, the maximum density of *C. endlicheri* seedlings at Mt Pilot in 2010 was 13 050 seedlings/ha. In unburnt areas at Mt Pilot, stands suspected to be over 100 years old contain up to 50 live *Callitris*/100 m^2 (5000 *Callitris*/ha) and exceed 60 m^2/ha basal area (I. Lunt, unpubl. data). Thus, *C. endlicheri* can persist in dense stands for many decades, similar to *C. glaucophylla*. This ability to tolerate low resource levels, especially low levels of soil moisture (Brodribb *et al*. 2010), for lengthy periods, may allow *C. endlicheri* to persist in mixed forests containing dense *Eucalyptus* regrowth, provided that plants are not killed by fire or other disturbances.

Seed cone production

Callitris species are usually killed when subjected to 100% leaf scorch and do not resprout after fire or form a soil seed bank (Hawkins 1966; Stocker 1966; Bowman *et al*. 1988; Cohn *et al*.

2011). Consequently, populations are prone to extinction if high intensity fires occur before regenerating plants set seed (Keith 1996). *Callitris* populations at Mt Pilot will remain susceptible to fires for many years as only 2% of plants had formed seed cones within 7 years of the 2003 fire. A fire-free period of at least 15 years is considered necessary to maintain populations of *Callitris* species elsewhere (Price and Bowman 1994; Russell-Smith *et al.* 1998; Bradstock and Cohn 2002).

Our results show that the length of the primary juvenile period (or duration of 'immaturity risk') is size dependent, as fast-growing, tall seedlings produced seed cones earlier than smaller, slow-growing seedlings. Moreover, rates of plant growth and seed production were both negatively associated with the density of *Eucalyptus* seedlings. *Callitris* seedlings grew faster and produced seed cones earlier in plots with fewer *Eucalyptus* seedlings, regardless of the density of *Callitris* seedlings.

Thinning trails have shown that competition constrains plant growth and levels of seed production in *Callitris* (Lacey 1972; Knott 1995; Thompson and Eldridge 2005). However, little information is available on the effects of stocking levels on the primary juvenile period, other than the general observation that, 'suppressed trees exhibit little flowering and therefore have poor seed production' (Lacey 1972), and similar observations (Prober and Thiele 2004). However, competition has been shown to extend the primary juvenile period in other conifers, including *Pinus* species (Cremer 1992; Verkaik and Espelta 2006). Thus, while removal experiments are required before spatial variations in primary juvenile periods can unequivocally be attributed to competition from *Eucalyptus* seedlings, this interpretation is consistent with prior information (Lacey 1972, 1973; Clayton-Greene 1981; FCNSW 1988), and it appears highly likely that competition contributes at least partly to the observed pattern.

These patterns have implications for future fire management. Under all but extreme conditions, fires are more likely to kill small than large *Callitris* (Bowman *et al.* 1988; Prober and Thiele 2004; Cohn *et al.* 2011; Zimmer *et al.* 2011). Consequently, if managers aim to maintain *Callitris* populations, then fires of moderate to high intensity should be excluded from areas containing young *Callitris* and moderate to dense *Eucalyptus* regeneration for longer than areas containing young *Callitris* amid sparse *Eucalyptus* regeneration. High basal area of *Callitris* reduces fire intensity in mixed *Eucalyptus*–*Callitris* stands (Bowman and Wilson 1988; Cohn *et al.* 2011). Consequently, over the longer term, protection of *Callitris* populations may reduce forest flammability and potential fire intensity.

Conclusion

These results indicate that Bond's (1989) model provides a useful framework for interpreting *Callitris* dynamics in mixed forests co-dominated by *Eucalyptus*. Australian ecologists have commonly interpreted *Callitris* dynamics in fire-prone ecosystems in relation to immaturity risk, or the risk of repeated fires occurring before regenerating plants set adequate seed (Bowman *et al.* 1988; Russell-Smith *et al.* 1998; Bradstock and Cohn 2002; Thompson and Eldridge 2005). This attribute is clearly important at Mt Pilot, as elsewhere. However, Bond's (1989) model highlights that immaturity risk may be strongly influenced by competition from co-occurring species. By inhibiting plant growth and lengthening the primary juvenile period, competitors may extend the period of immaturity risk, and potentially reduce the habitability of productive environments for *Callitris* and other non-resprouters. The mechanism of this extended immaturity risk may include an extended opportunity for browsing to eliminate *Callitris* seedlings and for fires to burn (and hence kill) plants before adequate seed is set. Regardless of the physiological or anatomical mechanisms that control growth rates, the spatial pattern of slower *Callitris* growth in areas with dense *Eucalyptus* regeneration has implications for future fire management. To maintain *Callitris* populations, fire-free intervals should be longer in areas stocked with *Callitris*, particularly areas in which *Callitris* is a minor component of the flora and where dense *Eucalyptus* regeneration dominates the regrowing vegetation.

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