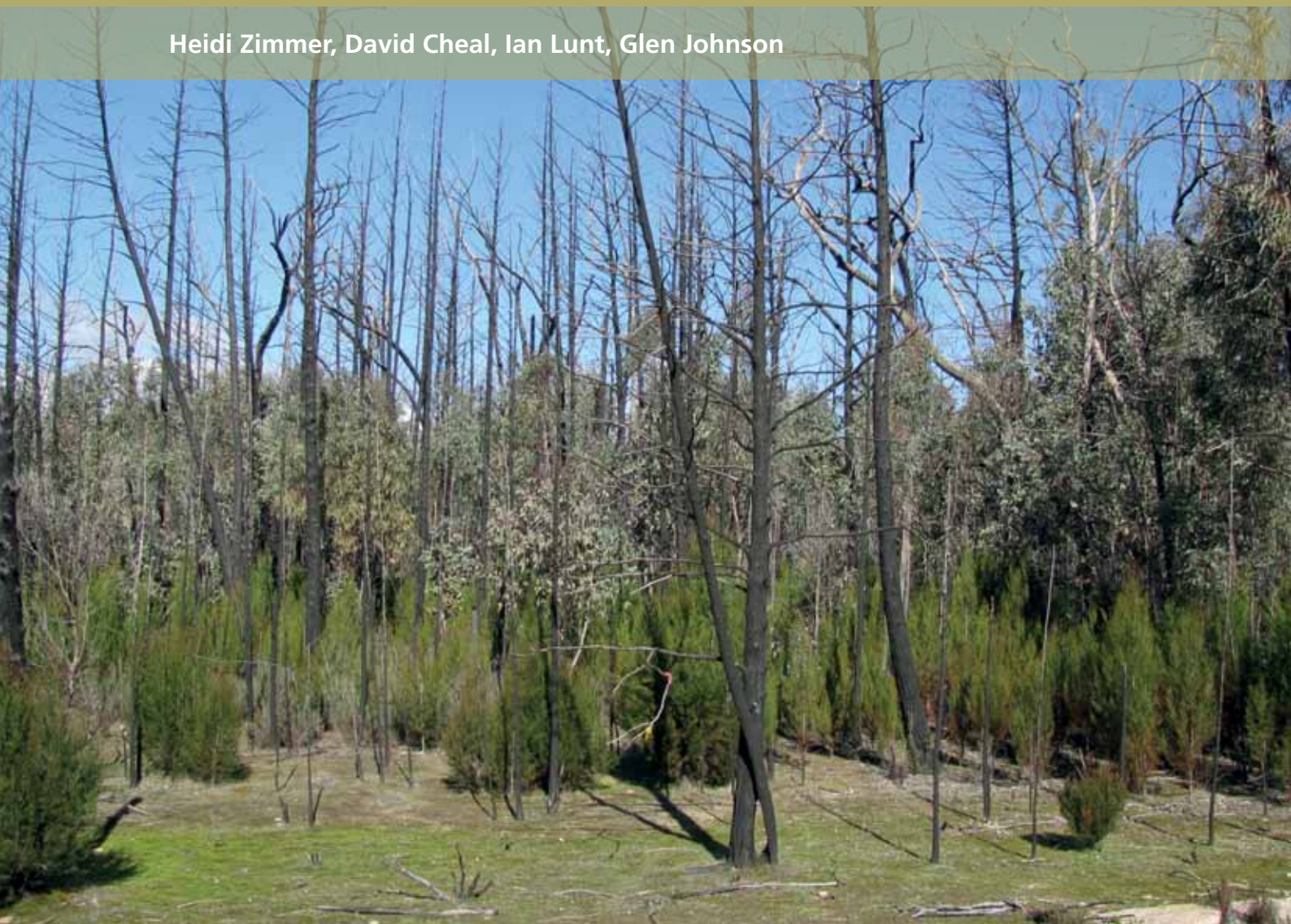# Black Cypress-pine *Callitris endlicheri* fire-sensitive vegetation recovery following high intensity bushfire

Black Saturday Victoria 2009 – Natural values fire recovery program

Heidi Zimmer, David Cheal, Ian Lunt, Glen Johnson

Black Cypress-pine *Callitris endlicheri* fire-sensitive vegetation recovery following high intensity bushfire

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Front Cover photograph: Chiltern–Mt. Pilot National Park, 2010; burnt in 2003. *C. endlicheri* showing strong seedling recruitment (David Cheal).

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Acknowledgements

Summary

This study investigated the response of Black Cypress-pine *Callitris endlicheri* (Parl.) F.M. Bailey to fire at sites in northern Victoria – Flagstaff Range, near Beechworth and the Warby Ranges (2009 fires), and Mt Pilot (2003). *Callitris endlicheri* is fire-sensitive and is usually killed by fire. The study aimed to inform land managers on how to manage to maintain this, and other, *Callitris* species, which are a distinctive component of the Victorian flora.

Grazing exclosures were established in areas burnt in 2009 and additional data was obtained from sites established by Charles Sturt University after a 2003 bushfire. These sites have been revisited and monitoring data collected (almost) annually from 2004–2010. Data was collected on basic demographics including seedling density and growth, size versus age and fecundity.

Comparisons of the responses to fire in the small, mixed stand at Flagstaff Range and the larger, more pure stand of Black Cypress-pine at Mt. Pilot showed similar ecological response.

At Mt. Pilot, there was no significant difference in seedling density between fenced and unfenced areas but seedlings in exclosures were significantly taller.

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 to plots with dense *Eucalyptus* seedlings. 83% of cones were on seedlings taller than 1.5 m and 23% of seedlings >2 m possessed seed cones.

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 six-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 latter stands at greater risk of mortality in future fires and greater risk of browsing in the meantime.

Some *Callitris endlicheri* may begin to produce viable seed by seven years of age but may take up to 15 years or more. It will take longer to establish an adequate seed bank to respond to future fire events. There is a direct and strong relationship between plant size and primary juvenile period. Size is a better indicator of fecundity than tree age.

An extended juvenile period heightens the susceptibility of regenerant seedlings to browsing damage (or removal). Two fires in quick succession will cause local extinctions of *Callitris endlicheri*. Long intervals between fires favour dominance by *Callitris endlicheri*.

After fires, there is competition between *Callitris* seedlings, *Eucalyptus* seedlings and resprouting *Eucalyptus* in mixed stands. Mixed stands are more prone to local extinction of the *Callitris* component than are pure stands of *Callitris* because *Callitris* grow more slowly in mixed stands.

Under all but extreme conditions, fires are more likely to kill small than large *Callitris*. 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. Consequently, over the longer term, protection of *Callitris* populations may reduce forest flammability and potential fire intensity.

Browser exclusion fencing may be of some value, particularly where browser populations are high.

It is concluded that fire response for *Callitris endlicheri* in this study can be extrapolated to a number of other *Callitris species* in parts of Victoria.
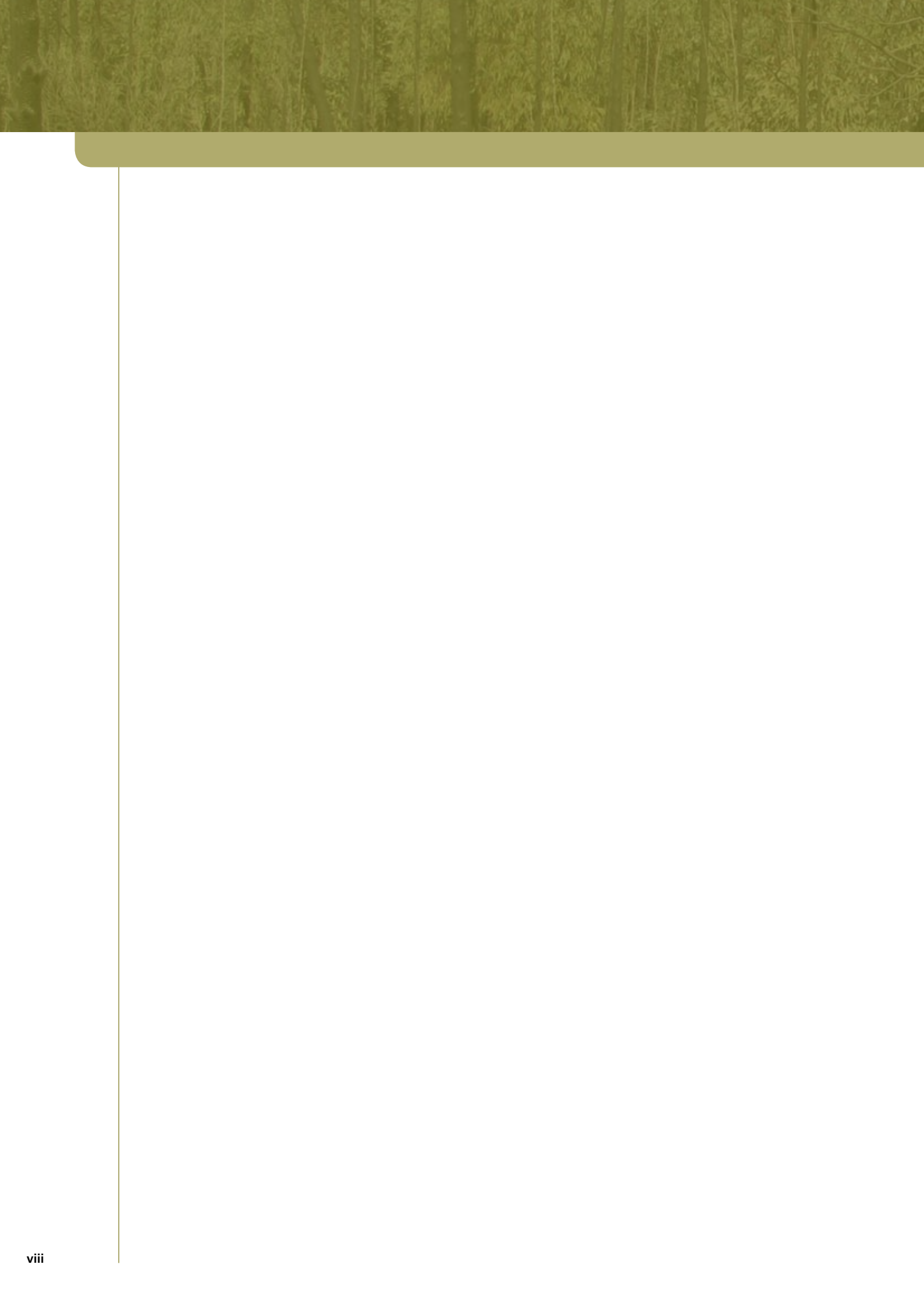
Introduction

Black Cypress-pine *Callitris endlicheri*[1] is an Australian native conifer, moderately common on hilly sites in south-eastern Australia. An open conical tree, growing to a maximum height of around 20 metres, it occurs along Australia's east coast, from south-eastern Queensland to north-eastern Victoria. *Callitris* species are fire sensitive (Bowman and Harris 1995). In general, *Callitris* species are relatively drought tolerant, often occupying warmer and drier niches on relatively shallow stony soils and steep slopes (e.g. *C. columellaris*; Lindsay 1967, Attiwill and Clayton-Green 1984, Clayton-Green and Ashton 1990) and extending well into central Australia. Populations of *C. endlicheri* occur both as co-dominants with various *Eucalyptus* species and as the sole dominant in other sites. Several *C. endlicheri* populations in north-eastern Victoria were affected by bushfire in 2003 in Chiltern-Mt. Pilot National Park and in 2009 in the Flagstaff Range immediately south of Beechworth.

Individuals of *Callitris* species are susceptible to even low intensity fire and many plants are killed by moderate to severe fires. They have little capacity to resprout and often regenerate solely from seed (Walker and Green 1979; Bowman *et al.* 1988a; Bowman and Harris 1995; Keith 1996; Bradstock and Cohn 2002; Harris 2002; Thompson and Eldridge 2005). Historical and current fire regimes are thought to have influenced the distribution and extent of several *Callitris* species (*C. glaucophylla*, Bowman and Latz, 1993; *C. intratropica* R. T. Baker and H. G. Smith, Bowman and Panton 1993, Bowman *et al.* 2001). Due to adult sensitivity to fire and subsequent recruitment from seed, fires at short intervals are perceived to be a significant threat to the long-term persistence of *Callitris* (Keith 1996; Gill and McCarthy 1998; Bowman *et al.* 2001).

Several species of *Callitris* (e.g. *intratropica, glaucophylla, rhomboidea* and *oblonga* A. Rich and Rich) regenerate successfully in inter-fire intervals (cf. *obligate bradyspory*) on sites free from major disturbance. This produces mixed-age stands (Hahs *et al.* 1999, Bowman and Harris 1995). However, disturbance (e.g. grazing), may result in large lags between periods of successful recruitment, resulting in stands with one or two age classes (Sandell *et al.* 2002; Thompson and Eldridge 2005; Murdoch 2006; Briggs *et al.* 2008). Previous studies have shown varying levels of serotiny[2] in *Callitris* species (*C. verrucosa*, strong serotiny, Bradstock and Cohn 2002). The level of serotiny in *C. endlicheri* is unknown.

Seedling emergence in *C. endlicheri* varies according to site, season of burn and moisture. There are interactions among these factors; for example, significant differences in seedling emergence occurred at different sites in different seasons (Knox and Clarke 2006). Seedling emergence was significantly greater in low and moderate intensity burnt sites, compared with unburnt areas (into which seed was sown), indicating the facultative influence of fire (*ibid.*). MacKenzie and Keith (2009) described an adaptive management approach to a population of *C. endlicheri* affected by unplanned fire and threatened by deer browsing. They concluded that low cost measures of seedling protection were effective, although permanent fencing for deer exclusion was likely to be more beneficial in the long-term.

Callitris recruitment is affected by factors other than fire, notably rainfall and browsing. For example, variations in spring and summer rainfall are thought to be prime influences on seedling mortality of *C. endlicheri*; if rainfall is adequate, then mortality is low after the first year (Elsey 1957). Browsing pressure, particularly from rabbits, has been shown to limit recruitment success in *C. glaucophylla* (Austin and Williams 1998; Thompson and Eldridge 2005) and in *Callitris gracilis* (Sandell *et al.* 2002; Murdoch 2006). Previous reports have highlighted the need for grazing exclusion at the seedling stage (Carey *et al.* 2003; MacKenzie and Keith 2009; Cochrane and McDonald 1966; Scott 1992; Sandell 2003; Callister 2004). MacKenzie and Keith (2009) described an adaptive management approach to a population of *C. endlicheri* affected by unplanned fire and threatened by deer browsing. They concluded that low cost measures of seedling protection were effective, although permanent fencing for deer exclusion was likely to be more beneficial in the long-term.

The questions we aim to address are:

- How does the response of *C. endlicheri* to fire vary with fire frequency?

- Is the persistence and recovery of *C. endlicheri* at a site affected by competition with associated eucalypts? Are mixed stands (*Eucalyptus* and *Callitris*) more prone to *Callitris* extinction or decrease after fires compared to pure stands of *Callitris*?

- Are the structure and fire responses of the Flagstaff Range *C. endlicheri* population (a small mixed stand) comparable with the population structure and post-fire responses of the much larger stands north of Beechworth, around Mt. Pilot? How far can we extrapolate results from study of the Mt. Pilot population?

- Does exclusion fencing (or other browsing reduction) increase the likelihood of *Callitris* seedling survival and growth?

- How many years before *C. endlicheri* produce seed? Is tree size a better indicator of fecundity than tree age?

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[1] all vascular plant nomenclature follows Walsh & Entwisle (1994; 1996; 1999)

[2] delayed release from cones of mature seed. In some species, serotiny can delay seed release until the next fire induces the cone scales to open.

This report is presented as three sections:

1. **Section 1 – Flagstaff Range and New Data**. New data collected for the current study utilizing plots established straight after the 2009 fire in the Flagstaff Range, south of Beechworth, and other data collected from a site in the Warby Ranges, north-west of Wangaratta.

2. **Section 2 – Mt. Pilot and new analyses of existing data**. Analyses of data collected by staff and students of Charles Sturt University from sites established after the 2003 fires in the Mt. Pilot area. These sites have been revisited and monitoring data collected (almost) annually up to, and including in, 2010.

3. **Section 3 – Summary of Management Implications**. A summary discussion of the management implications of the whole study, incorporating findings from the data newly collected specifically for this study and from the data collected from the Mt. Pilot longer-term monitoring sites.

1.1 Methods

1.1.1 Study site: Flagstaff Ranges

A small population of *C. endlicheri* exists in the Flagstaff Range State Forest, south of Beechworth, in north-eastern Victoria. Mean annual rainfall at Beechworth is 949 mm (Beechworth [station 82001]; Bureau of Meteorology 2010) and the surface geology of the area is Ordovician sedimentary. The dominant eucalypts at the study site are *Eucalyptus blakelyi* (Blakely's Red Gum) and *Eucalyptus polyanthemos* (Red Box), with *Eucalyptus goniocalyx* (Long-leaf Box) also common in the vicinity.

A one hectare (approximately) patch of *C. endlicheri*, and several large *C. endlicheri* individuals were burnt in the Beechworth-Mudgegonga 'Library Road' fires in February 2009. The 2009 fire perimeter encloses 33,577 ha and was described as a "hot burn" by local land managers. This was evidenced by *E. polyanthemos* re-sprouting only from ground-level (Figures 1, 2). Considerable erosion occurred post-fire; local land managers commented that "the soil was a metre deep across the main road" below the site (Figure 3).

Grazing pressure was identified as a post-fire threat. Three grazing exclosures were established in 2009, in the large burnt *C. endlicheri* patch. One large individual tree, which had fallen, was also fenced. This work was led by local Department of Sustainability and Environment staff Sue Berwick and Glen Johnson. The exclosures were designed to exclude rabbits, goats and macropods, with standard wire mesh to 1.8 m high. Due to the nature of the rocky site conditions, mesh could not be buried in the soil profile but was placed so as to minimize the opportunity for rabbits to burrow under the mesh. After one year, the exclosures showed no sign of entry by any mammalian browsers. The exclosures were approximately rectangular in shape, their long axes aligned with the contour:

- Exclosure 1 : 20 m × 13 m × 22 m × 13 m
- Exclosure 2 : 20 m × 16 m × 20 m × 15 m
- Exclosure 3 : 15 m × 14 m × 10 m × 13 m

Figure 1. Flagstaff Range, *E. polyanthemos* resprouting from lignotubers at or below ground level, *all C. endlicheri* dead; eight months post-fire.

Figure 2. Flagstaff Range, corner of Exclosure 1 showing *C. endlicheri*, cones and intact small branches.

Figure 3. Flagstaff Ranges Exclosure 2, 100% *C. endlicheri* mortality as well as bare soil and runoff issues at the site; eight months post-fire.

1.1.2   Study site: Mt. Pilot

A long-term study of *C. endlicheri* is underway in Chiltern-Mt. Pilot National Park, led by Ian Lunt at Charles Sturt University, Albury. The Eldorado fire of 2003 burnt 10 000 ha of the Chiltern-Mt. Pilot National Park. Since then, data on *C. endlicheri* demography have been collected annually, including measurements of seedling height, 'health' and density, as well as growth of coppicing eucalypts. In May 2010, collection of data on *C. endlicheri* seed cone production began. Demographic data on coincident eucalypts and groundcover have also been collected (Figure 4).

Figure 4. Chiltern-Mt. Pilot National Park, 2010; burnt in 2003. *C. endlicheri* showing strong seedling recruitment (this area was dominated by *C. endlicheri* before the fire).

1.1.3   Study design

Basic demographics

At the Flagstaff Range site, three 10 m × 10 m sample plots were established inside and outside the larger exclosure, creating six plots in total. Plots were permanently marked with metal stakes (star pickets) (Figure 5).

Within each plot the diameter over bark at breast height (dbh) was measured for each tree and the pre-fire stratum (e.g. suppressed, dominant) and post-fire status (e.g. resprouting, consumed) was assessed for each tree. The location of eucalypt coppice (arising from tree base, stem or coppice [arising from tree base, stem or branches]), maximum height and diameter of basal coppice were also measured.

Figure 5. Marking stake for permanent monitoring plot at Flagstaff Range.

Seedling density and growth

Ten 1 m × 1 m quadrats were haphazardly placed within each large quadrat. The number of seedlings and height of each seedling were recorded, along with an assessment of visible browsing impact (Figure 6). Cover of eucalypt coppice, other vegetation cover (grasses, herbs, shrubs and mosses), litter cover and substrate (rocks and bare ground) cover were all estimated.

The differences in seedling height and density inside and outside the exclosure fences were investigated using a t-test (unequal variance, two tails) in *Microsoft Excel 2003*.

To facilitate comparison of results, the experimental design for basic demographics and seedling density and growth was consistent with the methods used at Chiltern-Mt. Pilot National Park. However, there remained some clear differences between these two major sites: the exclosures at the Flagstaff Range cover a substantial part of the old burnt *C. endlicheri* population, while Chiltern-Mt. Pilot encompasses a much larger and more varied population, only part of which has been sampled.

Figure 6. *Callitris endlicheri* seedling affected by browsing.

Finally, 25 seedlings in each 100 m² plot at the Flagstaff Range were individually tagged and numbered so that their fates can be monitored over time (Figure 7). For future survey, seedlings may be easily relocated using a metal detector.

Figure 7. Tagged *C. endlicheri* seedling.

Dendrochronological approach to demographics

Species of *Callitris* have elsewhere been indicated as highly suitable for demographic studies, as it has been assumed or determined that at least some of the species consistently accrue annual tree rings (Pearson and Searson 2002; Baker *et al.* 2008). To determine if *C. endlicheri* accumulates annual tree rings, a small sample of trees of known age was taken from the Warby Ranges in the Warby-Ovens National Park. A plantation of *C. endlicheri* had been established by the Forestry Commission in the mid-1950s, prior to park declaration (to assess the silvicultural prospects for *C. endlicheri* in the Warby Ranges). *Callitris endlicheri* is not indigenous to the Warby Ranges, where *C. glaucophylla* is locally common. These *C. endlicheri* trees were predicted to have c. 60 tree rings, assuming annual tree ring formation. If tree ring accrual proved to be annual, or even tied to a consistent conversion factor, then tree ring counts on *C. endlicheri* elsewhere could be used to determine the ages of other forest stands containing *C. endlicheri.*

Four stem sections were taken from *C. endlicheri* in the Warby Ranges plantation. These sections were prepared using standard dendrochronological procedures (Stokes and Smiley 1968), they were sanded using increasingly fine sandpaper (180 – 600 grit) to remove abrasions from the wood surface and produce a clear view of the wood anatomy. Sections were then scanned at 1800 dpi resolution using a ScanMaker 1000XL scanner (Microtek International Inc.) and visually crossdated using *WinDendro* (Regent Instruments, Canada) image-analysis software.

Fecundity

The timing of this study, 21 months post-fire, did not allow measurement seed production at Flagstaff Range. Data collected at Chiltern-Mt Pilot National Park show seed production is beginning now at seven years post fire (refer to Section 2). Data relevant to cone production collected at Chiltern-Mt. Pilot National Park were tree height, height of cones, location of cones, diameter of cone and whether the cone was intact, damaged, open or closed.

1.2 Results

1.2.1 Demographics

The pre-fire stand o*f C. endlicheri* at Flagstaff Range was dominated by stems in the 10 to 15 cm dbh size class, although trees were as large as > 30 cm dbh (Figure 8). All burnt stems appeared dead.

The basal area of *C. endlicheri* within each plot varied, but was consistently greater than *Eucalyptus* basal area (Figure 9). The unfenced plot 1 (U1) had a considerably lower basal area of *C. endlicheri.* However, two large (approximately 20 cm dbh) *C. endlicheri* occurred immediately outside plot U1. It is likely that these *C. endlicheri* outside the plot, particularly upslope, influenced seed rain.

Figures for basal area should be considered minimum estimates, as it was not uncommon for pre-fire trees to have been completely consumed by the fire (i.e. we observed *Eucalyptus* coppice growing where there was no burnt trunk present) and hence impossible to incorporate into basal area estimates.

The predominant post-fire response of *Eucalyptus* was coppice (basal re-sprouting). Epicormic sprouting (from the trunk or branches) was not seen at the Flagstaff Range site (see Figures 1 and 3). The mean height of basal coppice was 2.1 m (standard deviation 0.8 m). *Eucalyptus* seedlings were scarce; a total of two eucalypt seedlings were recorded for all the plots.

Figure 8. Size structure (dbh) of burnt/ pre-fire *C. endlicheri* at Flagstaff Range.
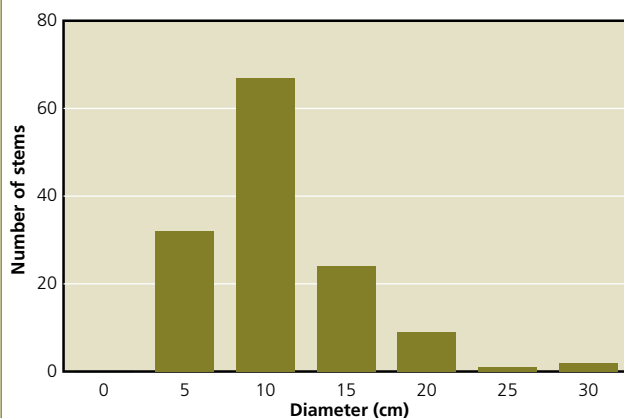
Figure 9. Total basal area of *C. endlicheri* and *Eucalyptus* spp. at Flagstaff Range plots (10 m × 10 m).
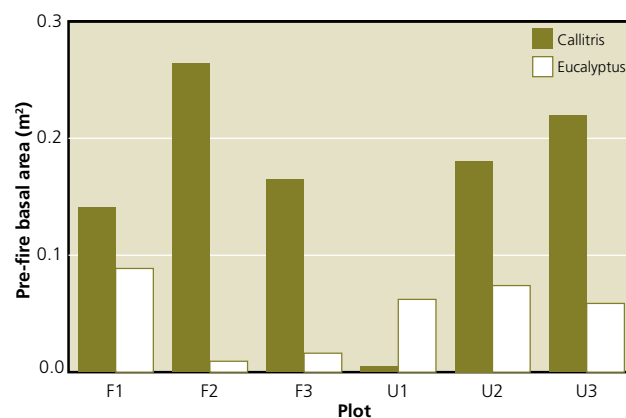
1.2.2   Seedling density and growth

Seedling density (*C. endlicheri*) was apparently greater inside the exclosures compared with outside, but this apparent difference was not statistically significant (t-test; $P = 0.219$) (Figure 11). Whether a larger sample size would show such a difference is undetermined. There was no significant difference in seedling height inside and outside the exclosures (t-test; $P = 0.185$) (Figure 12). Distribution of seedlings within each plot was patchy. There was evidence of considerable runoff and erosion occurring in U2, leaving much of the surface devoid of organic litter and with exposed rocks (Figure 10).

Seedlings appeared to be associated with (micro-)sites with lower bare ground and greater cover of ground plants (Figure 13).

Figure 10. Exposed hill slope, organic litter and finer-grained surface soil removed by heavy storms soon after the 2009 fire, Flagstaff Range.

Figure 11. Mean density of seedlings inside and outside exclosures, Flagstaff Range (mean ± one standard deviation).
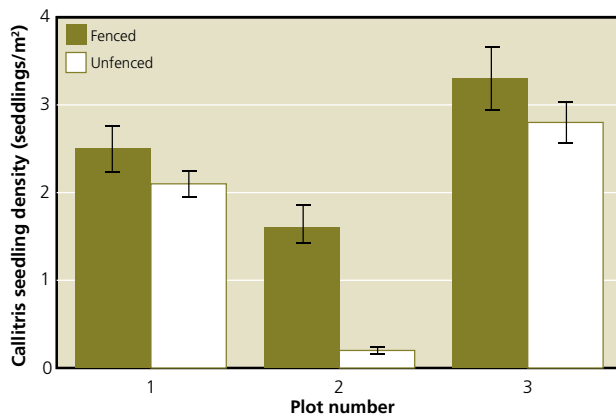
Figure 12. Mean height of seedlings inside and outside exclosures, Flagstaff Range (mean ± one standard deviation).
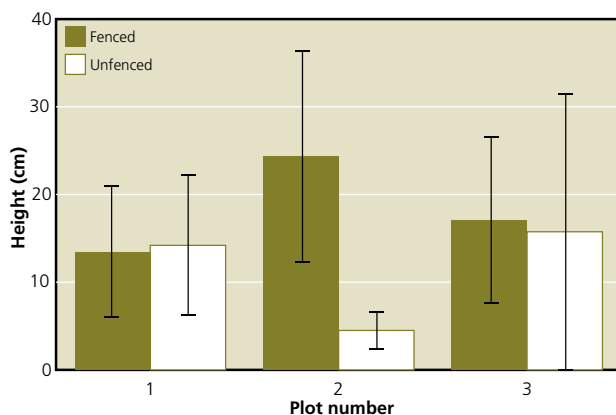
Figure 13. Sub-plot ground cover according to number of seedlings, Flagstaff Range (mean ± one standard deviation).
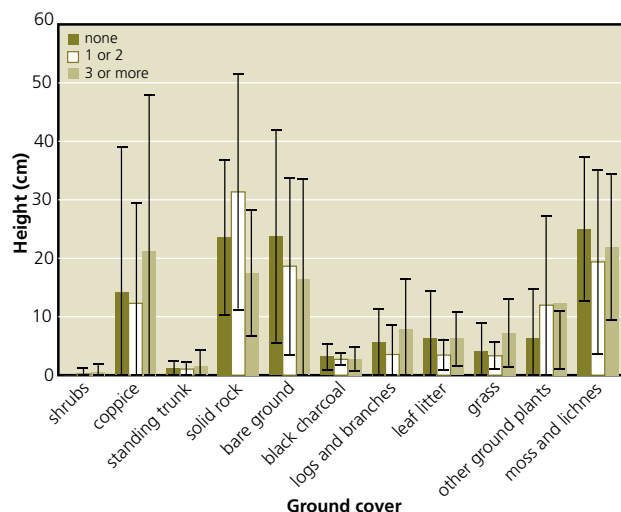
1.2.3 Comparison of Flagstaff Ranges and Chiltern-Mt. Pilot

Callitris endlicheri seedling recruitment at Flagstaff Range after the 2009 fire was compared with the 2004 *C. endlicheri* recruitment at Chiltern Mt. Pilot. The first data collections for these sites occurred at 21 months (Flagstaff Range) and 16 months (Chiltern-Mt. Pilot) post-fire.

Seedling density at Flagstaff Range varied from 0.2 to 3.3 seedlings/m^2 across the six plots sampled (Figure 14). At Chiltern-Mt. Pilot, seedling density ranged from 0 to 7.4 seedlings/m^2 in 2004, with a mean seedling density of 3.0 seedlings/m^2 (fenced) or 3.5 seedlings/m^2 (unfenced) across three sites, each with one fenced and one or two unfenced plots.

Mean seedling height was slightly greater at the Flagstaff Range site, mean height of seedlings 18.2 cm (fenced) and 11.5 cm (unfenced), compared with Chiltern Mt. Pilot in 2004, 12.8 cm (fenced) and 10.5 cm (unfenced) (Figure 15).

Figure 14. Mean density of seedlings inside and outside fences at Chiltern-Mt. Pilot, according to year (mean ± one standard deviation).
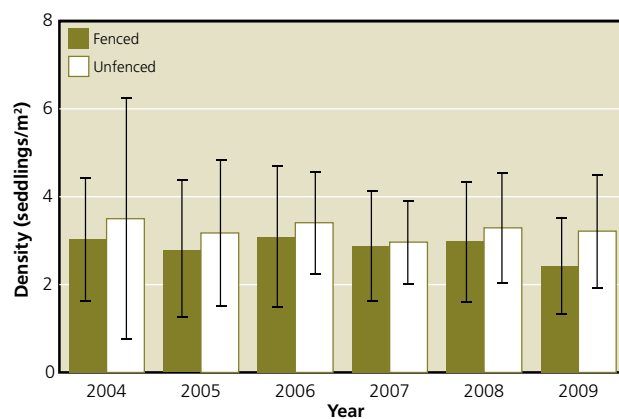
Figure 15. Height of seedlings inside and outside fences at Chiltern-Mt. Pilot, according to year (mean ± one standard deviation).
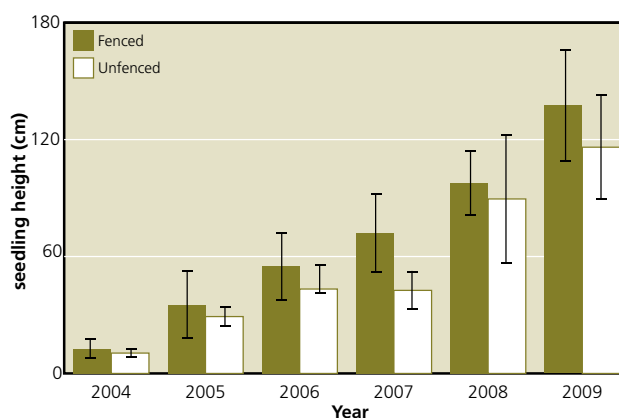
Dendrochronological approach to demographics

Four stem sections were taken from *C. endlicheri* at the Warby Ranges plantation, their attributes are summarised in Table 1.

Tree no.	Diameter at sample height (cm)	Height of sample (cm)	Tree height (m)	Number of tree rings
1	38.4	26	16.2	60
2	39.2	30	15.5	57
3	34.1	20	13.8	47
4	18	38	11.9	57

Although tree ring chronologies measured along different radii within the same tree were successfully visually crossdated ('matched'), there was uncertainty as to what constituted an annual tree ring. The wood anatomy of sampled *C. endlicheri* typically showed around 15 (or 25%) unclear tree rings within each chronology (i.e., faint coloured tree rings and or tree rings lacking clear gradation from large to small diameter tracheids), and 'double rings' were common – these are likely composed of one false ring and one annual ring, but are difficult to differentiate from small rings (Figure 16). However, counts of putative tree rings approximated expected number of tree rings if tree rings were produced annually (i.e., 60). Working with such tree ring chronologies is possible but requires a significant time investment, and ideally would be carried out on stem sections rather than increment cores.

Figure 16. Double rings (left) and poorly differentiated rings (right)

1.2.4 Fecundity

None of the *C. endlicheri* seedlings at Flagstaff Range supported mature or immature cones during the survey in November 2010. However, there were multiple records of

trees with cones at Chiltern-Mt. Pilot in 2010 (seven years post fire), predominantly on seedlings taller than 200 cm (Figure 17). There was considerable variation among cone-bearing seedling heights at Chiltern-Mt. Pilot, ranging from 140 cm to 280 cm.

The cones at Chiltern-Mt. Pilot varied in size and reproductive status. Most cones were intact (undamaged, not forcibly opened) and closed, although many cones were very small (<15 mm diameter) (Table 1, Figure 18).

Table 1. Indicators of cone health/ viability, and number of individuals.

Cone status	Number of cones
Intact, closed	359
Intact, open	4
Damaged, closed	4
Damaged, open	2

Figure 17. Number of cones in each cone size class at Chiltern-Mt. Pilot, 2010.
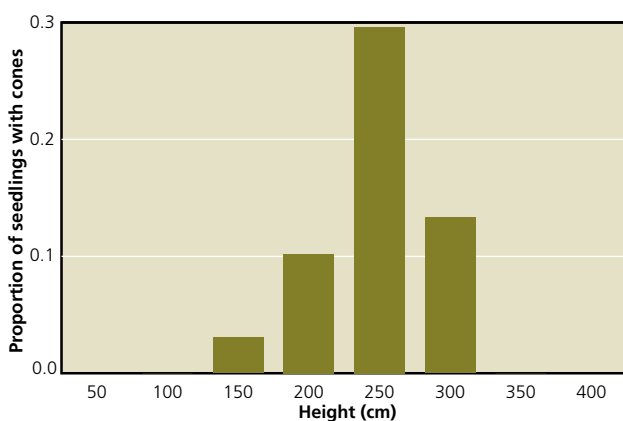
Figure 18. Old fire scar on a veteran *C. endlicheri*, indicating survival from a previous fire, Flagstaff Range.
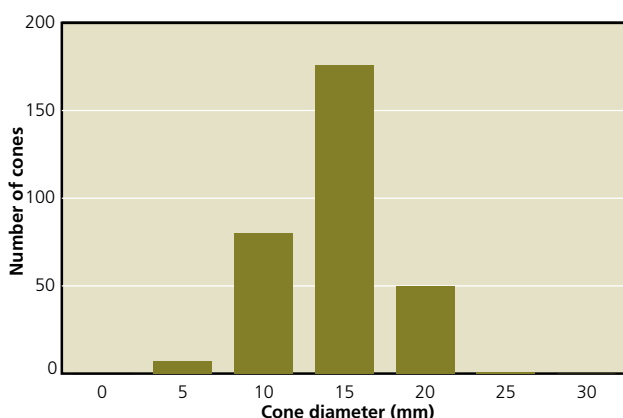
1.3 Discussion

As a general rule, individuals of *Callitris* species are killed by fire and recruit only from seed. Occasional individuals within an otherwise burnt stand may escape the fire due to site-specific factors and very large veterans may develop a zone of reduced fuel in their immediate surrounds, thus heightening their chances of escaping fire. But only a very small proportion of individuals within a fire perimeter escape being killed. Post-fire, seedlings are particularly vulnerable to threats such as grazing, drought and repeat fire. Hence, conditions in the post-fire period are a critical determinant of the obligate-seeding fire-sensitive species persistence at a site.

A population of *Callitris endlicheri* in the Flagstaff Range was burnt in the Black Saturday fires in 2009. Fenced exclosures were established to protect the seedlings from grazing. Detailed monitoring of the fire-affected population was undertaken 21 months post-fire. Seedling heights and densities were measured, and individual seedlings were tagged to monitor long-term survival, inside and outside fences. Monitoring can be repeated in coming years, as the sites are well marked and 'permanently' marked. In this report, these first data from the Flagstaff Range *C. endlicheri* population are compared with data from a nearby population of *C. endlicheri* at Chiltern-Mt. Pilot (burnt in 2003 and monitored from 2004 until present).

Figure 19. Old fire scar on a veteran *C. endlicheri*, indicating survival from a previous fire, Flagstaff Range.

1.3.1 Impacts of browsing

At Flagstaff Range, fencing protection from grazing did not lead to statistically significant differences in *C. endlicheri* seedling height or density, when regenerants within exclosures were compared with regenerants close by, but outside, the exclosures. However, there was evidence of grazing impacts at the site, such as malformed seedling regenerants, which were interpreted as having been browsed (Figure 20). Local land managers suggested the main browsers were rabbits and macropods (Eastern Grey Kangaroo *Macropus giganteus* and Swamp Wallaby *Wallabia bicolor*).

The results from the Flagstaff Range population can be usefully compared with those from the long-term *C. endlicheri* study sites at Chiltern-Mt. Pilot. At the latter site, fencing was associated with significantly taller seedling heights, but this difference became notably more pronounced from the third year post-fire. That the difference in heights was not significant until some years after the fire may reflect the variability of the *C. endlicheri* population at Chiltern-Mt. Pilot, but is more likely attributable to the difference in grazing pressure among sites and seasons. At Beechworth, annual rainfall was slightly above average from 2003–2005 (965–1215 mm/yr), very low in 2006 (413 mm) and ca. 80% of average from 2007–2009 (755–790 mm) (Bureau of Meteorology 2010).

In places accessible to browsers, low values of the parameter 'seedling height' may be attributed to (a) recent germinants, (b) older germinants that are suppressed (by poor growing conditions at a particular site) and (c) germinants that have been browsed. It is not possible to disentangle these factors completely (although see Section 2). Seven years after fire, seedlings at some Chiltern-Mt. Pilot sites are still being maintained below browsing-accessible height (< 50 cm) while at other sites they are taller than two metres.

The influence of browsing on *Callitris* recruitment success has been explored in several previous studies. Browsing by domestic stock and rabbits was documented as suppressing *Callitris gracilis* recruitment in the mallee (Zimmer 1944; Cochrane and McDonald 1966; Sandell *et al.* 2002). In central-western NSW woodlands, Leigh *et al.* (1989) found *Callitris glaucophylla* seedlings appeared only in rabbit exclosures, an observation supported by Scott (1992) in the south of the state and by Thompson and Eldridge (2005) and Briggs *et al.* (2008) from a more regional perspective. Cheal (2004) found that the effect of goat browsing on *Callitris verrucosa* in the Mallee was severe, with all accessible foliage browsed. Browsing can be an important limitation to *Callitris* seedling establishment and growth.

Figure 20. Seedling regenerants, *C. endlicheri,* browsed (outside exclosures) to the left, unbrowsed (inside exclosures) to the right; Flagstaff Range.

Seedling densities inside and outside fences at Chiltern-Mt. Pilot are not significantly different even at seven years post-fire, indicating that while grazing influences height, it has not, as yet, influenced mortality rates. Nevertheless, shorter seedlings, as well as being susceptible to browsing over an extended period, experience greater competition for light and other resources (such as soil moisture), with resprouting eucalypts and other shrubs. In effect, a positive feedback loop is maintained, whereby the smaller (lower height) *Callitris* germinants are suppressed by interspecific competition and kept small. This is in line with the 'tortoise and hare' model of conifer-angiosperm interaction proposed by Bond (1989).

Seedling height is correlated with cone production. Data from Chiltern-Mt. Pilot indicate that the proportion of individuals with cones increases after trees reach around two metres tall. Apart from grazing, growth is influenced by environmental factors, specifically rainfall, temperature, soil nutrients, sunlight and competition for these resources (Oliver and Larson 1996). The minimum time to *C. endlicheri* cone production (or height of two metres), at Chiltern-Mt. Pilot, was seven years. However, some trees may take much longer than this to reach two metres, or even to simply exceed rabbit browse height. Furthermore, cones take additional time to mature; the vast majority of the cones at Chiltern-Mt. Pilot were small and closed.

1.3.2   Impact of environmental conditions

Previous studies suggest that rainfall is an important determinant of seedling survival and growth of some *Callitris* species. In the nearby Warby Ranges; the majority of seedling mortality in *C. glaucophylla*, is thought to occur in the first year (Elsey 1957). Bradstock and Cohn (2002)

noted that post-fire rainfall was important for *Callitris verrucosa* seedling survival and establishment. Moreover, Read (1995) highlighted the need for long periods of above-average rainfall for successful post-fire recruitment in *Callitris glaucophylla* and Harris (2002) reported episodic regeneration in *C. glaucophylla* requiring synchrony between a seed supply and an extended period of above-average rainfall.

The first measurements of the *C. endlicheri* population at Flagstaff Range were from 21 months post-fire. Rainfall was below average for the first 12 months post-fire (755 mm in 2009 cf. average 949 mm), so it is possible that some drought-induced mortality occurred and was not measured. However, rainfall in the second year post-fire is on track to be considerably above average (1247 mm; November 2010). Mortality will be able to be directly measured in this project using permanently tagged seedlings (cf. indirect measurement by changes in seedling density).

Callitris endlicheri seedlings at Flagstaff Range were commonly found in 'clusters' associated with coarse woody debris and litter (Figure 20). Litter is thought to protect seeds from flux in temperature and moisture (Adams 1999; Bonnet *et al.* 2005; Harris *et al.* 2003), and from predators such as ants (Andersen 1988) and rodents (Myster and Pickett 2003). However, at this site, protection from erosion and runoff (surface roughness) that is provided by coarse woody and finer debris may be the most important factor. High intensity fires can increase erosion and runoff by reducing ground cover and altering soil properties (DeBano *et al.* 1998, Wondzell and King 2003). Coarse woody and other lighter debris can slow this runoff, capturing litter and seeds (Ferran and Vallejo 1992; Rice 1993).

Figure 21. *Callitris* seedlings clustered in litter, Flagstaff Range.

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 (RGR) is related to leaf longevity and specific leaf area (Comelissen *et al.* 1996; Reich *et al.* 1999; Wright *et al.* 2004). Gymnosperms characteristically have long-lived leaves of low SLA, which lead to lower RGRs 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* (Cupressaceae), which occurs in tropical, sub-tropical, arid, semi-arid, 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; Clayton-Greene and Ashton 1990; Bowman *et al.* 1988b), 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.* 1988b; 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 (ca. 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.

2.1 Methods

2.1.1 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 approximately 850 mm, based on data from nearby Beechworth (960 mm) and Beechworth Woolshed rainfall gauges (770 mm; Bureau of Meteorology 2010). 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. blakely Maiden i, 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 bushfire (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 sub-dominant *Eucalyptus*. The other six stands were dominated by *Eucalyptus* above smaller *Callitris*, which were presumed to have recruited after 1950.

Permanently marked 100 m^2 (10 m × 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-m^2 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-m^2 plot. For clarity, all post-fire seedling recruits are called 'seedlings' here, 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 (2005-2010) randomly placed 1 m^2 subplots within each 100 m^2 plot. These subplots were re-randomized each year. GOBBH was recorded as 0.1 cm if plants were < 1.3 m tall. Sampling was conducted in autumn 2004 to 2010, but only two sites were sampled in 2009, due to inclement weather. At Beechworth, annual rainfall was slightly above average from 2003–2005 (965–1215 mm/yr), very low in 2006 (413 mm) and ca. 80% of average from 2007–2009 (755–790 mm; Bureau of Meteorology 2010).

2.1.2 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 terms. Analyses were undertaken in GenStat (Ver. 13). 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.

2.2 Results

2.2.1 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/m^2 and 2.8 *Eucalyptus* seedlings/m^2 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. 22a).

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. 22b).

2.2.2 Seedling growth rates

Callitris seedlings were, on average, shorter than *Eucalyptus* seedlings throughout the survey period (Figure 23). 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.

Figure 22. 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.

Figure 23. Predicted mean height of (a) *Callitris* and (b) *Eucalyptus* seedlings in fenced and unfenced plots (back-transformed mean ± standard error).

(a) Callitris

(b) Eucalyptus

(a) Callitris

(b) Eucalyptus
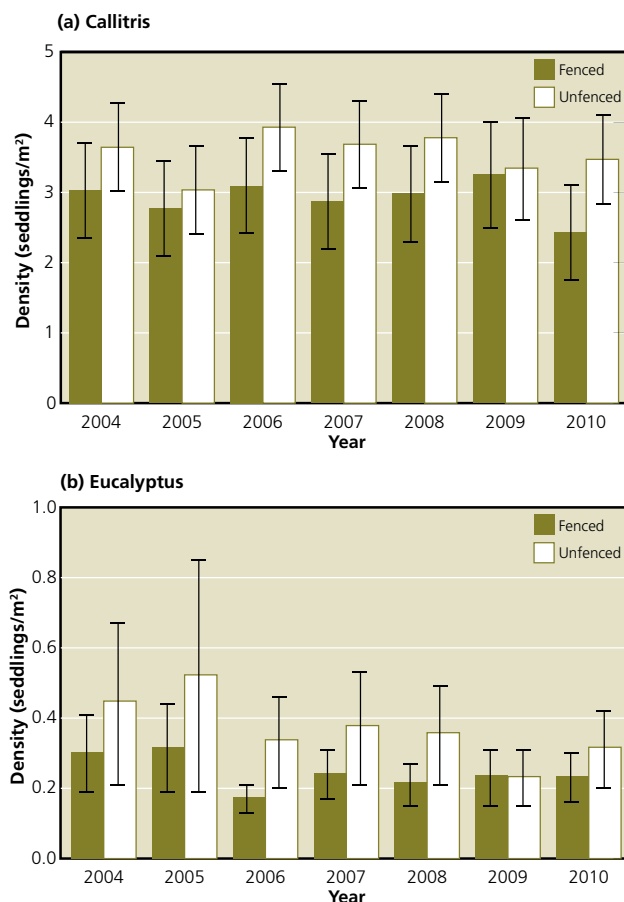
2.2.3   Fencing effects

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 taller in fenced than unfenced plots (Fig. 23a). 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 to 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 ($P = 0.747$) nor year*fencing treatment interaction ($P = 0.558$; Figure 23b). In 2010, the mean height of fenced and unfenced *Eucalyptus* seedlings was 226 cm and 245 cm respectively (t-test, $P = 0.70$).

2.2.4   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 ($P = 0.017$), 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 2). 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 2. Model statistics for linear mixed models 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	0.058
Eucalyptus coppice basal area in 2010	2.58	27	0.108
Fencing treatment	5.67	25	0.017

Table 3. Model statistics for linear mixed models describing the factors associated with *Eucalyptus* seedling heights in 2010. Terms were individually removed from the full fixed model.

Fixed term	F statistic	d.d.f.	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

2.2.5   Seed cone production

In 2010, seven 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 (Figure 24), 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.

Figure 24. The proportion of *Callitris* seedlings in different height classes that possessed seed cones in 2010. Only 19 seedlings were taller than 250 cm.
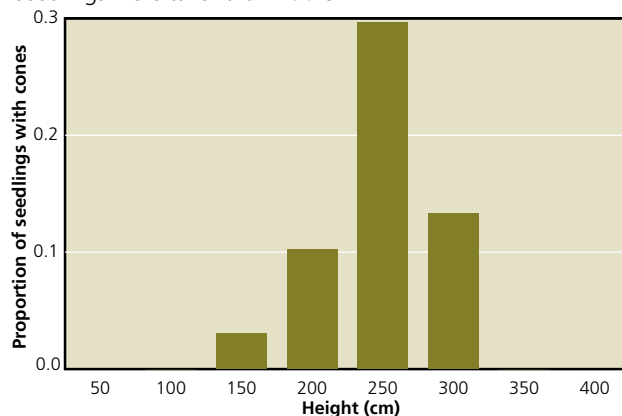
2.3   Discussion

These results illustrate a number of 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 co-existence. We expand on each of these points in the discussion below.

2.3.1   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.* (1988b) 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.

2.3.2   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 remains 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 bushfire (I. Lunt, pers. observ.). In contrast, Mackenzie and Keith (2009) recorded high mortality of *C. endlicheri* seedlings in an area grazed by feral Rusa Deer (*Cervus timorensis*) in coastal NSW. 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, *Callitris glaucophylla*, are known to be sensitive to repeated browsing by rabbits and sheep (Lacey 1972).

2.3.3   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 six years, despite a high sampling intensity. By contrast, the density of *Eucalyptus* seedlings declined by 57% during the six-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 (unbrowsed) *C. endlicheri* seedlings declined by 19% within a 12-month period, from two to three years after fire. Initial seedling densities may have been under-estimated in our study, as sampling began in April 2004, 15 months after the fire. Nevertheless, greater mortality was expected over the following six 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 three years after burning (2003-2005), 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 ca. 80% of average from 2007–2009 (755–790 mm; Bureau of Meteorology 2010).

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 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 (5 000 *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.

2.3.4 Seed cone production

Callitris species are killed when subjected to 100% leaf scorch and do not resprout after fire or form a soil seed bank (Bowman *et al.* 1988b; Hawkins 1966; Stocker 1966; 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 seven 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, p. 7), 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 period 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.* 1988b; 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.

2.4 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*. 1988b; 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.

The inland-draining slopes and ridges stretching from around Beechworth to Pine Mountain, particularly on soils derived from granite or similar igneous rocks, are the principal Victorian occurrence of forests (co-)dominated by Black Cypress-pine *Callitris endlicheri.* These forests are a distinctive landscape feature in a region where eucalypts are otherwise the overwhelmingly dominant canopy trees.

Callitris is a widespread genus—the most widespread native conifer in Australia. There are species in woodland near the tip of Cape York and in rocky gullies in Eastern Tasmania. It occurs in arid, semi-arid, mesic, tropical and temperate environments, to high in the (sub-)alps.

In spite of this ecological and geographical spread, *Callitris* is not commonly the principal tree genus at a site. Part of this ecological restriction may be attributed to its susceptibility to fire. *Callitris* species are markedly susceptible to fire – individuals of all species can be killed by fire of even moderate intensity, and regeneration is thence solely from seed. No *Callitris* species consistently resprouts after being burnt.

Nevertheless, some species occupy (moderately) fire-prone habitats by developing serotinous seed (seed which is held in protective woody cones until fire triggers seed release into the immediate post-fire environment). *Callitris canescens* (in South Australia and west thereof) and *Callitris verrucosa* (in semi-arid southern Australia) occupy such moderately fire-prone environments and utilize serotiny as a survival strategy. Elsewhere, other species are only weakly to moderately serotinous and retain seed in cones in their canopies for a relatively short period, enabling germination and establishment in unburnt vegetation. *Callitris endlicheri* (Black Cypress-pine) is in this latter group.

We have previously discussed the obligately slow growth of *Callitris* seedlings (indeed, obligate slow growth for all conifers) when compared with the high growth rates of eucalypt seedlings. Growth of (post-fire) seedlings is also constrained by competition with coincident eucalypt seedlings and with resprouting eucalypts at the same sites, remembering that resprouting eucalypts are growing on mature, extensively-ramifying root systems.

At the same time, *Callitris* is often interpreted as being more drought (water stress) resistant than associated eucalypts. *Callitris* often grow well in topographically arid sites (such as shallow soil profiles over and amongst rocks on ridges and exposed slopes, as at Mt. Pilot) immersed in a matrix of deeper soils where eucalypts dominate. In addition, exposed rocks may help protect *Callitris* from fires, by breaking fuel continuity, thus providing fire-protected sites. The drought tolerance of *Callitris* may explain the ability of many *Callitris* species to germinate and establish in unburnt vegetation from time to time, whereas associated eucalypts are often unable to establish from seed unless the site has been recently burnt.

Finally, *Callitris* foliage is often not just palatable, but also actively sought by mammalian browsers.

All these ecological features of *Callitris* and associated eucalypts affect the outcome of competitive interactions between these two forest components, and the interactions between *Callitris*, eucalypts and the local environment and disturbance regime. These interactions determine the composition of the tree canopy and whether sites support forests dominated by *Callitris*, by *Eucalyptus* or by an admixture of both. Keeping these considerations in mind, it is timely to address the questions articulated at the beginning of this report, *viz.*:

1. How does the response of *C. endlicheri* to fire vary with fire frequency?

2. Is the persistence and recovery of *C. endlicheri* at a site affected by competition with associated eucalypts? Are mixed stands (*Eucalyptus* and *Callitris*) more prone to *Callitris* extinction or decrease after fires than are pure stands of *Callitris*?

3. Are the structure and fire responses of the Flagstaff Range *C. endlicheri* population (a small mixed stand) comparable with the population structure and post-fire responses of the much larger stands north of Beechworth, around Mt. Pilot? How far can we extrapolate results from study of the Mt. Pilot population?

4. Does exclusion fencing (or other browsing reduction) increase the likelihood of *Callitris* seedling survival and growth?

5. How many years before *C. endlicheri* produce seed? Is tree size a better indicator of fecundity than tree age?

3.1 How does the response of *C. endlicheri* to fire vary with fire frequency?

Black Cypress-pines are usually killed by fire. Wildfires are usually higher severity than prescribed burns and usually kill whole stands. Prescribed fires are usually (but not always) of sufficient severity to kill most trees within a stand. Black Cypress-pines regenerate (almost) solely from seed after being burnt and (due to a low growth rate) have an extended juvenile period, in which there is no local seed reserve for regeneration if the site is burnt again. An extended juvenile period heightens the susceptibility of regenerant seedlings to browsing damage (or removal). Two fires in quick succession will cause local extinctions of Black Cypress-pines. Long intervals between fires favour dominance by Black Cypress-pines.

3.2 Is the persistence and recovery of *C. endlicheri* at a site affected by competition with associated eucalypts? Are mixed stands (*Eucalyptus* and *Callitris*) more prone to *Callitris* extinction or decrease after fires than are pure stands of *Callitris*?

After fires, there is competition between cypress-pine seedlings, eucalypt seedlings and resprouting eucalypts in mixed stands. Cypress-pines are drought tolerant and necessarily slow-growing. Competition with resprouting eucalypts further retards growth in cypress-pines, thus increasing the likelihood that a second fire or browsing will remove regenerating cypress-pines. After fires, mixed stands are more prone to local extinction of the cypress-pine component than are pure stands of cypress-pines.

3.3 Are the structure and fire responses of the Flagstaff Range *C. endlicheri* population (a small mixed stand) comparable with the population structure and post-fire responses of the much larger stands north of Beechworth, around Mt. Pilot? How far can we extrapolate results from study of the Mt. Pilot population?

The Flagstaff Range population exhibited very similar ecological responses to mixed populations around Mt. Pilot. Ecological (and fire) responses were consistent across the species' local range, and consistent with responses from other non-serotinous *Callitris* species elsewhere in Australia. It is clear that ecological behaviour and fire responses of the other non-serotinous cypress-pine species in Victoria can be reliably predicted from this and other studies. These other species are:

- Slender Cypress-pine *Callitris gracilis* in the north-west and far west
- Oyster Bay Cypress-pine *Callitris rhomboidea* in the Grampians, the Gippsland coast and western heathlands
- White Cypress-pine *Callitris glaucophylla* scattered throughout the State.

However, at the same time, the different ecological behaviour deriving from different local populations of browsers must also be taken into account in other sites and with these other species.

Furthermore, we can now reliably predict the long-term implications of changes in fire regimes for Black Cypress-pine *Callitris endlicheri* (and, by extension) other cypress-pines which occur immersed amongst eucalypts, including both bushfires and prescribed fires.

3.4 Does exclusion fencing (or other browsing reduction) increase the likelihood of *Callitris* seedling survival and growth?

Exclusion fencing and other browsing reduction may or may not, increase the survival chances of cypress-pine seedlings, whether in burnt or unburnt stands. In situations with high populations of browsers (such as rabbits, goats or macropods) exclusion fencing and targeted browser reduction will substantially increase cypress-pine seedling survival and enable establishment of new individuals. Where these browsers are less common, cypress-pine survival and establishment is less affected by browsing pressure. In the absence of fire, browsing pressure is the most important determinant of cypress-pine recruitment.

This conclusion is also directly applicable to (all) other cypress-pine species, including the serotinous Scrub Cypress-pine *Callitris verrucosa*.

3.5 How many years before *C. endlicheri* produce seed? Is tree size a better indicator of fecundity than tree age?

The number of years it takes Black Cypress-pines to mature depends on local growth rates. Rapidly growing trees may mature (start producing viable seed) in seven years, but only a very small proportion (~2%) of the population reaches maturity at this early age. Other plants, particularly in other, less favourable situations, will take at least 15 or more years to start producing seed. The time taken to recruit an adequate seed bank for replacement of the parent population is considerably longer (particularly for serotinous species). Minimum tolerable fire intervals vary with local (site) conditions.

There is a direct and strong relationship between plant size and primary juvenile period (time taken to produce viable seed) in Black Cypress-pines (and, by extension, in other cypress-pines as well). Larger plants set viable seed decidedly sooner than smaller plants, even when of the same age. Size is a better indicator of fecundity than tree age. The best indicator of fecundity is the number of mature cones present on trees.

3.6 Concluding remarks

This study has collected data that enable managers (and other ecologists) to predict cypress-pine responses to individual bushfires and to burning regimes that include the application of prescribed fires. Managers may now derive and apply ecologically appropriate fire regimes that can assist local survival of cypress-pines.

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