How do slow-growing, fire-sensitive conifers survive in flammable eucalypt woodlands?

J.S. Cohn, I.D. Lunt, K.A. Ross & R.A. Bradstock

Abstract

Question: To what extent do low flammability fuel traits enhance the survival and persistence of fire-sensitive (slow-growing, non-serotinous, non-resprouting) dominant trees in highly flammable landscapes, under varying fire-weather conditions?

Location: Mixed forests co-dominated by flammable Eucalyptus species and fire-sensitive Callitris glaucophylla in Pilliga State Forest, southeast Australia.

Methods: The influence of vegetation composition (relative abundance of Callitris and flammable Eucalyptus) on fire intensity and survival of fire-sensitive Callitris was assessed across gradients of Callitris abundance in mixed Eucalyptus–Callitris forests that burned under low-moderate and extreme fire-weather conditions.

Results: In areas that burned under low-moderate fire-weather conditions, as Callitris abundance increased, fire intensity declined and Callitris survival increased (46%). By comparison, in extreme fire-weather conditions, lower fire intensity at higher levels of Callitris abundance, was not sufficient to increase Callitris survival (4%). Callitris survival was also positively related to trunk diameter. Ground fuel type, but not biomass, varied with vegetation composition.

Conclusions: These results demonstrate that flammable feedbacks, mediated by low flammability fuel traits of dominant trees, can provide an important mechanism for enhancing the survival and persistence of slow-growing, non-serotinous, non-resprouting, fire-killed trees in highly flammable landscapes. By modifying vegetation and fuel structure, patches of fire-sensitive Callitris reduce fire intensity, and thereby reduce Callitris mortality, enhancing population persistence. However, this feedback loop is insufficient to ensure Callitris survival under extreme fire-weather conditions, when fire intensity is greater. After burning, stands remain vulnerable to future fires, until trees grow large enough to modify fuel levels and reduce stand flammability.

Introduction

In many plant communities, disturbance prevents competitive exclusion and promotes species co-existence, as described by non-equilibrium theories of diversity (Bond & van Wilgen 1996; Huston 2003). Fire is a major disturbance regime in many ecosystems, and fire regimes dramatically affect ecosystem processes, structure and composition across large areas of the world (Bond & Keeley 2005; Pausas & Keeley 2009).

Plant species possess a range of traits to enable populations to persist in flammable landscapes, including the ability to resprout from aerial or buried tissues, persistent aerial (serotinous) or buried seed banks, and thick bark to protect tissues from heat (Whelan 1995; Keeley & Zedler 1998). Additionally, rapid growth rates and short juvenile periods enable populations to persist under short interfire intervals (Noble & Slatyer 1980). Nevertheless, species without these attributes survive in frequently burned ecosystems. Among the most notable examples are long-lived, slow-growing, non-resprouting woody plants without a persistent seed bank (Schwilk & Ackerly 2001; Rodrigo et al. 2007), hereafter termed ‘fire-sensitive species’. Their persistence has posed a conundrum for fire
ecologists: how do such species survive in flammable landscapes?

Spatial and temporal variability in fire intensity is likely to be the principal mechanism by which fire-sensitive species persist in flammable landscapes (Cowling 1987; Williams et al. 1994; Whelan 1995). This variability can result from environmental features that create fire refuges, such as rock outcrops and other forms of topographic protection (Clarke 2002; Alexander et. al. 2006; Knapp & Keeley 2006); temporal and spatial variations in fuels, which are influenced by fire-weather, disturbance history, plant species composition and other factors (Catchpole 2002; Knapp & Keeley 2006; Boer et al. 2008); and stochastic factors such as short-term variations in fire-weather (Bessie & Johnson 1995). Relationships among these factors create highly variable fire patterns, even in large intense wildfires (Turner et al. 2003), thereby enabling fire-sensitive species to persist.

In addition to these factors, fire-sensitive species may also possess ‘fuel’ traits that directly reduce fire intensity and thereby promote their own survival (Cowling 1987; van Wilgen et al. 1990; Bowman 1998). Traits associated with low flammability (i.e. the potential for a stand to ignite and burn at high fire intensity) include foliage with high water content and a low C:N ratio, which enables rapid leaf litter decomposition; tightly packed and poorly aerated leaf litter; shedding of lower branches; and the ability to suppress understorey plants (Schwilk & Ackerly 2001; Scarf & Westoby 2006). These traits may have evolved under selective forces other than fire.

In forests, dominant tree species strongly influence stand flammability by contributing to surface litter and above-ground fuel levels, which in turn control the potential for fires to ignite, spread laterally and propagate into tree crowns (Williams et al. 1994; Catchpole 2002). Consequently, where co-occurring dominant species possess different flammable traits, spatial variations in their relative abundance may create patterns in fire intensity across the landscape (Williamson & Black 1981; Bond & van Wilgen 1996).

However, the degree to which plant traits can influence stand flammability depends on the relative influence of fuels and fire-weather on fire intensity. In some ecosystems, fuel characteristics influence fire intensity under all weather conditions (Hely et al. 2001). In these circumstances, plant traits that reduce fire intensity may enhance survival of fire-sensitive species in all fire events. By contrast, in other systems, fuel characteristics do not influence fire intensity under extreme fire-weather conditions (Bessie & Johnson 1995; Turner et al. 2003). In these circumstances, traits of fire-sensitive species may have a weaker influence on stand flammability, or consequent plant survival, under extreme fire-weather conditions.

Many studies have documented the effects of vegetation composition and structure on fire intensity (Papió & Trabaud 1990; Fonda et al. 1998; Schwilk 2003), and others have documented the effects of fire intensity on plant survival (Williamson & Black 1981; Bowman & Wilson 1988; Rebertus et al. 1989; Bowman & Panton 1993). However, a systematic exploration of the way that stand flammability varies in response to variations in composition (i.e. mixtures of species with contrasting flammable traits) and weather conditions is lacking. Such a study would yield insight into the way that ‘flammable feedback’ as a function of species composition could influence the potential for fire-sensitive species to survive fire and persist in frequently burned, flammable landscapes.

In Australia, fire-sensitive conifers of the genus Callitris often occur, at varying densities and spatial configurations, in highly flammable forests and woodlands dominated by Eucalyptus trees. The flammable traits (i.e. fuel characteristics) of these alternative dominants contrast strongly in the manner outlined above (Bowman & Wilson 1988; Scarf & Westoby 2006). Callitris spatial patterns commonly appear to reflect disturbance history rather than underlying abiotic features (Austin & Williams 1988; Bowman et al. 1988; Harris & Lamb 2001). In this study, we use a mixed forest dominated by these two genera as a model system to examine how patches of fire-sensitive species influence fire intensity and consequent plant survival under contrasting fire-weather conditions. Our results illuminate an important mechanism by which fire-sensitive species persist in flammable landscapes.

Methods

Study area

The study was undertaken in the Pilliga Conservation Reserve and State Forest (270,000 ha) in north-eastern New South Wales, southeast Australia. The area experiences a quasi-Mediterranean climate of warm, dry summers and mild, moist winters (Gill & Moore 1990). Topography is flat to gently undulating. The dominant trees include Callitris glaucophylla J. Thoms. & L. Johnson and C. endlicheri (Parl.) Bailey, and Eucalyptus crebra F. Muell., E. fibrosa F. Muell., E. nubila Maiden & Blakely and E. trachycarpa (F. Muell.) K.D. Hill & L.A.S. Johnson (Binns & Beckers 2001). Dense patches of C. glaucophylla and C. endlicheri, typically 0.01–0.25 km² in size (hereafter ‘Callitris patches’) are scattered throughout a more open matrix dominated by Eucalyptus with scattered Callitris (hereafter ‘Eucalyptus matrix’). Within this matrix, Callitris patches do not occupy distinctive soil types or topographic positions.

Callitris glaucophylla and C. endlicheri are slow-growing, fire-sensitive, long-lived (ca. 200 years) trees (Bowman &
Harris 1995). Trees are killed by 100% crown scorch, although larger trees may survive low-intensity fires (Lacey 1973). Seeds are shed on maturity (Lacey 1973) and seedling establishment is dependent on above-average rainfall (Austin & Williams 1988). By comparison, *Eucalyptus* species in the study area resprout and regenerate from seedlings after fires (Lindsay 1967; Gill & Bradstock 1992).

Fire history records indicate two domains of fire behaviour in the ‘Pilliga’ (Brookhouse et al. 1999). In the western half where *Callitris* and *Eucalyptus* are dominants, fires are less frequent and cover smaller areas than in the eastern half where *Eucalyptus* are dominant (Brookhouse et al. 1999). The last fire in the study area was in 1951.

On 29.11.2006, during a lengthy drought (Australian Bureau of Meteorology unpubl. data), lightning ignited a number of fires in the Pilliga, one of which is the focus of this study. Approximately 70 000 ha burned in the first 24 h in extreme fire-weather conditions, and over the following 2 weeks, a further 27 000 ha burned in low-moderate fire-weather conditions (DECC NSW unpubl. data). Fire-weather conditions were defined by the Forest Fire Danger Index (FFDI), which is based on a drought factor and ambient air temperature, wind speed and relative humidity (Noble et al. 1980). During extreme conditions, the maximum temperature and wind speed reached 37 °C and 57 km h\(^{-1}\), respectively, and the minimum humidity was 12%. Under low-moderate fire-weather conditions, maximum temperatures and wind speeds reached 27–34 °C and 31–61 km h\(^{-1}\) respectively, relative humidity was 20–46% and 18.6 mm of rainfall was received (Australian Bureau of Meteorology unpubl. data).

Sampling was undertaken within the burned area (approximately 35 × 30 km in extent) and data on fuel characteristics were collected within 2 km in an adjacent unburned area. Within the burned area, extreme and low-moderate fire-weather zones had been delineated by fire severity mapping, which used a combination of satellite imagery, weather data and field verification (DECC NSW unpubl. data). Sampling locations were determined from 1:50000 scale aerial photos taken in 2003. *Callitris* patches were at least 1 ha and dominated by *C. glaucophylla* and/or *C. endlicheri*, which have comparable architecture and leaf characteristics, and we assume similar flammability (Harden 2000; Scarff & Westoby 2006). Sampling occurred 10–12 months after the fire, in September–November 2007, and was restricted to areas of < 5° slope.

**Fire intensity and *Callitris* survival**

The survey was designed to measure and model changes in fire intensity and *Callitris* survival in relation to vegetation composition (relative abundance of *Eucalyptus* and *Callitris*) in two fire-weather zones. In each fire-weather zone, paired quadrats were placed in the direction of the fire, so that the ‘incoming’ quadrat burned before the ‘outgoing’ quadrat (Fig. 1). Fire intensity and *Callitris* survival in the outgoing quadrat were thereby influenced by, and analysed in terms of, fire intensity in the incoming quadrat (i.e. the local antecedent fire intensity) and vegetation composition in the outgoing quadrat. This design optimized the potential to determine how small-scale changes in vegetation composition affected fire intensity, by isolating compositional impacts from background variations in local fire intensity.

To maximize vegetation composition comparisons, each quadrat was replicated two times in each fire-weather zone, giving 40 pairs in the extreme fire-weather zone and 40 pairs in the low-moderate fire-weather zone. All replicates of quadrat pairs placed in

![Fig. 1. Diagrammatic representation of the sampling design within the burned area. Data were collected in paired quadrats located across four vegetation transitions: in the *Eucalyptus* matrix (E–E), across the *Eucalyptus* matrix–*Callitris* patch boundary (E–C), in *Callitris* patches (C–C) and across the *Callitris* patch–*Eucalyptus* matrix boundary (C–E). Paired quadrats were placed in the direction of the fire, so that the incoming quadrat burned before the outgoing quadrat.](image_url)
either the *Eucalyptus* matrix or *Callitris* patch were placed in different patches, which were sometimes shared by quadrat pairs placed across the *Eucalyptus* matrix–*Callitris* patch boundary or in reverse order. Each quadrat pair across the *Eucalyptus* matrix–*Callitris* patch boundary (or reverse order) sampled a unique combination of patches. To promote independence between samples, all quadrat pairs were separated by at least 100 m.

Fire direction was determined from: (1) reports on prevailing wind direction, (2) lower char heights on the windward side of trees than the more protected leeward side (Wyant et al. 1986), and (3) shrubs bent and remaining fixed in the direction of the fire during strong winds.

Vegetation composition was assessed in terms of the basal area and density of *Callitris* and *Eucalyptus* in each quadrat, by counting the number of trees in each DBH size class (0–5, 5.1–10, 10.1–20, 20.1–30, etc., to 60.1–70 cm). Sparsely distributed larger trees (> 20-cm DBH) were measured in a larger quadrat (15 m × 15 m) centred on the main inner quadrat (10 m × 10 m) and not overlapping the adjacent paired quadrat.

Fire intensity was estimated using char height and post-fire stem tip diameter. Char height provides a relative measure of fire intensity (Cain 1984) and stem tip diameter is correlated with maximum surface temperatures during a fire (Moreno & Oechel 1989). Stem tip diameter indicates the minimum diameter of branches remaining after the fire, with more intense fires leaving larger diameter branches.

To provide a consistent index of fire intensity and survival, char height, percentage canopy scorch and survival were measured on standardized size classes of trees. Two trees from each of the number of trees in each DBH size class were assessed in the centre of each 10 m × 10 m quadrat: small *Callitris* (3–15-cm DBH) and large *Callitris* and *Eucalyptus* (> 15-cm DBH). The ‘small’ *Callitris* size class established after 1952 and ‘large’ *Callitris* from 1890 to 1911 (Austin & Williams 1988; Norris et al. 1991). Canopy scorch was measured as the percentage of the canopy with brown leaves. *Callitris* trees were considered alive if they had green leaves. Minimum stem tip diameters were measured on *Callitris* saplings (1–4-cm DBH), on branches of at least 1-cm length and approximately 1.3 m from the ground. Five branches were sampled on each of five *Callitris* in each quadrat.

Fuel characteristics

Ground fuel characteristics were sampled in an unburned area adjacent to the burned area, with four unpaired replicate quadrats in each vegetation type (*Eucalyptus* matrix and *Callitris* patches). Sampling occurred in November 2007 (12 months after the fire), to approximate seasonal grass and herb conditions at the time of the fire.

*Callitris* and *Eucalyptus* basal area and density were assessed in 10 m × 10 m quadrats, using the same methods as in burned areas (see above), to enable vegetation composition to be compared between the burned and unburned area. The following fuel characteristics were measured in four 1 m × 1 m quadrats, positioned 2 m inside each corner of a 10 m × 10 m quadrat: percentage cover of bare ground; leaf litter of *Callitris* and *Eucalyptus*, grass, herbs and shrubs; the number of all shrubs and shrubs > 1-m tall; and the average height of shrubs, grasses and herbs. Litter depths were measured in each quadrat and at six other fixed locations within each 10 m × 10 m quadrat. Ground fuel was collected in a 0.25 m × 0.25 m plot in the centre of each 1 m × 1 m quadrat. Fuel was sorted into total fine fuel (litter, twigs < 6-mm diameter, bark), grasses, herbs, and twigs 6–20-mm diameter. Samples were dried for 24 h at 70 °C and weighed.

Statistical analyses

We analysed the data (Fig. 1) in two ways to highlight different phenomena. First, we treated vegetation composition as a categorical variable, to compare attributes between the two vegetation types (*Eucalyptus* matrix and *Callitris* patches) in the two fire-weather zones. This analysis used data from quadrat pairs within the matrix and patches, and quadrat pairs that straddled matrix—patch boundaries were excluded (Fig. 1). Second, we used data from all quadrat pairs to assess how vegetation composition, as a continuous variable, affected fire intensity. We analysed fire intensity in outgoing quadrats as a function of fire intensity in incoming quadrats and vegetation composition in outgoing quadrats, in both fire-weather zones. This design allowed us to minimize the effects of local variations in fire intensity caused by other factors.

Two factor analyses of variance (ANOVA) were used to examine whether *Callitris* and *Eucalyptus* basal areas, fire intensity indicators and *Callitris* survival varied with vegetation type (*Eucalyptus* matrix and *Callitris* patches), fire-weather zone (low-moderate, extreme) and their interactions. Data from the incoming and outgoing quadrats were pooled. Basal area data were transformed (square root) to correct for skewing and heterogeneity of variance. Tukey tests were used for post-hoc pair-wise comparisons (Quinn & Keough 2002).

Linear regressions were used to examine the relationships between fire intensity indicators in the outgoing quadrat (‘Intensity Indicator Out’) and fire intensity indicators in the incoming quadrat (‘Intensity Indicator In’).
In’) and the abundance of *Callitris* and *Eucalyptus* in the outgoing quadrat, within each fire-weather zone (low-moderate, extreme):

Intensity Indicator Out \~ Intensity Indicator In  
+ *Callitris* Abundance Out  
+ *Eucalyptus* Abundance Out

Pearson’s correlation coefficient was used to check for collinearity between predictor variables. Akaike information criterion (AIC) was used to compare models, the best of which had the smallest AIC (Quinn & Keough 2002).

Logistic regressions (logit-link) were used to examine the survival of *Callitris* in relation to intensity (char height) on *Callitris* and *Callitris* size (DBH and height) in the low-moderate fire-weather zone only, since most *Callitris* died in the extreme fire-weather zone:

*Callitris* Survival \~ Char Height on *Callitris*  
\times *Callitris* Size

Correlation tests were used to determine significant collinearity between predictor variables, which precluded them from testing within the same model. A pseudo-$R^2$ was calculated for each model ($R^2 = 1 - (\text{residual deviance/null deviance})$) and AIC was used to compare models (Veall & Zimmermann 1996).

To assess whether the basal areas of *Callitris* and *Eucalyptus* in each vegetation type in the unburned area were representative of the burned area, Kruskal-Wallis tests were used. Kruskal-Wallis tests were also used to examine the effects of vegetation type (*Eucalyptus* matrix and *Callitris* patches) on ground fuel characteristics, including shrub cover, shrub density, *Eucalyptus* and *Callitris* leaf litter cover, litter depth, bare ground cover, shrub height, fine fuel weight and total fuel weight (fine fuel weight, grass, herbs, twigs 6–20-mm diameter). Given their sparseness, data on grass and herb cover were not analysed.

**Results**

**Patch and matrix contrasts**

As expected, vegetation composition did not differ between the two fire-weather zones but varied significantly between vegetation types (Fig. 2a). Whilst *Callitris* basal area was greater in the *Callitris* patches than the *Eucalyptus* matrix ($F_{1,33} = 58.26, P < 0.001$), *Eucalyptus* basal area was marginally significantly higher in the *Eucalyptus* matrix than in the *Callitris* patches ($F_{1,33} = 3.42, P = 0.07$).

Fire intensity, as indicated by char height and stem tip diameter was significantly greater in extreme than in low-moderate fire-weather zones ($F_{1,33} = 51.26, P < 0.001$; $F_{1,27} = 69.12, P < 0.001$; Fig. 2b and c). Stem tip diameter

![Fig. 2. Differences in (a) vegetation composition (basal area), fire intensity expressed as (b) char height and (c) stem tip diameter, and (d) *Callitris* survival within the *Eucalyptus* matrix and *Callitris* patches, under extreme and low-moderate fire-weather conditions. Data are means with standard errors. Asterisks indicate significant differences between the matrix and patches.](image-url)
indicated that fire intensity was greater in the *Eucalyptus* matrix than in *Callitris* patches in both fire-weather zones ($F_{1,33} = 10.87, P = 0.003$); there was no significant interaction between stem tip diameter and fire-weather ($F_{1,27} = 0.45, P = 0.51$). By contrast, an interaction between char height and fire-weather indicated higher fire intensity in the *Eucalyptus* matrix compared with the *Callitris* patches only in the low-moderate fire-weather zone ($F_{1,27} = 8.43, P = 0.007$). Char height was limited by tree height in the extreme fire-weather zone.

*Callitris* survival was significantly greater in *Callitris* patches in the low-moderate fire-weather zone than in *Callitris* patches in the extreme fire-weather zone or the *Eucalyptus* matrix in both fire-weather zones ($F_{1,30} = 9.90, P = 0.004$; Fig. 2d).

**Fire intensity**

In the extreme fire-weather zone, stem tip diameter in the outgoing quadrat was linearly and positively related to stem tip diameter in the incoming quadrat (Table 1; Fig. 3), but was not significantly influenced by *Callitris* or *Eucalyptus* basal area or density in the outgoing quadrat. Similar trends were found for char height, although this fire intensity measure was often limited by tree height (57/70 cases). Thus, modelling indicated that vegetation composition had little influence on fire intensity at the paired quadrat scale under extreme fire-weather conditions. This is in contrast to the results from the ‘patch and matrix contrasts’.

By comparison, vegetation composition influenced fire intensity in the low-moderate fire-weather zone. In this zone, char height in the outgoing quadrat was positively related to incoming fire intensity (char height) and negatively related to *Callitris* basal area or density in the outgoing quadrat (Table 1). Thus, fire intensity declined with increased basal area or density of *Callitris*. For example, char height declined from 5 m to 3 m when *Callitris* basal area was greatest (20 m$^2$ ha$^{-1}$; Fig. 4).

<table>
<thead>
<tr>
<th>Intensity Indicator</th>
<th>Abundance Measure</th>
<th>Coefficients</th>
<th>$F_{	ext{adj}}$</th>
<th>P</th>
<th>AIC</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a) Extreme fire-weather zone</td>
<td>Stem tip diam.</td>
<td>0.76 0.78 ns</td>
<td>21_{1,21}</td>
<td>&lt; 0.001</td>
<td>48</td>
<td>0.47</td>
</tr>
<tr>
<td>Char height</td>
<td>3.41 0.68 ns</td>
<td>20_{1,33}</td>
<td>0.001</td>
<td>163</td>
<td>0.35</td>
<td></td>
</tr>
<tr>
<td>(b) Low-moderate fire-weather zone</td>
<td>Char height</td>
<td>2.02 0.69 −11.00</td>
<td>31_{2,31}</td>
<td>&lt; 0.001</td>
<td>131</td>
<td>0.64</td>
</tr>
<tr>
<td>Char height</td>
<td>Density</td>
<td>1.49 0.73 −0.02</td>
<td>26_{2,31}</td>
<td>&lt; 0.001</td>
<td>134</td>
<td>0.60</td>
</tr>
<tr>
<td>Stem tip diam.</td>
<td>Basal area</td>
<td>1.06 0.34 −3.57</td>
<td>6_{2,34}</td>
<td>0.006</td>
<td>64</td>
<td>0.22</td>
</tr>
<tr>
<td>Stem tip diam.</td>
<td>Density</td>
<td>0.92 0.41 −0.01</td>
<td>5_{2,34}</td>
<td>0.01</td>
<td>66</td>
<td>0.19</td>
</tr>
</tbody>
</table>
Similar trends were found for stem tip diameter, but these models explained less of the variance (Table 1). *Eucalyptus* abundance in the outgoing quadrat did not affect fire intensity (based on char height or stem tip diameter) in any model. Thus, changes in fire intensity associated with changes in vegetation composition were driven by *Callitris*, not *Eucalyptus* abundance.

**Callitris** survival

*Callitris* survival was so low in the extreme fire-weather zone (4%) that logistic regression models were only developed for the low-moderate fire-weather zone. In this zone, *Callitris* survival was negatively related to char height on the tree trunk and positively related to tree diameter (DBH) and tree height (Table 2; Fig. 5). *Callitris* DBH was a slightly better predictor of *Callitris* survival than tree height, as indicated by AIC values and by the higher proportion of correctly classified cases when fitted values were compared to actual values (Table 3). When char heights exceeded 1 m, most *Callitris* died and all surviving trees were > 25-cm DBH.

**Fuel characteristics**

In most cases, *Callitris* and *Eucalyptus* basal areas were comparable between the burned and the unburned area, where the fuel samples were taken. The exception was in the *Callitris* patches, where *Callitris* basal area was greater in the unburned than the burned area ($X^2 = 4.74, P = 0.03$, means = 19.7 versus 12.7 m$^2$ ha$^{-1}$). As a consequence, fuel characteristics in the *Callitris* patches may be overestimated.

Six of the nine fuel characteristics differed significantly between *Callitris* patches and the *Eucalyptus* matrix in the adjacent unburned area (Table 4). Shrub cover, shrub density, litter depth, bare ground and *Eucalyptus* leaf litter cover were significantly greater in the *Eucalyptus* matrix than in *Callitris* patches ($P < 0.05$). In contrast, *Callitris* leaf litter cover was significantly greater in *Callitris* patches than in the *Eucalyptus* matrix (Table 4). Other fuel characteristics, shrub height, fine fuel weight and total ground fuel weight did not differ significantly between the two vegetation types ($P > 0.05$).

**Discussion**

The results highlight an important mechanism by which feedbacks between vegetation and fire can enhance the ability of fire-sensitive species to persist in flammable landscapes. By modifying vegetation and fuel structure, patches of fire-sensitive *Callitris* reduced fire intensity, and thereby reduced *Callitris* mortality, enhancing population persistence. However, fire-weather conditions ultimately determined the success of this feedback loop, which was less effective under extreme fire-weather conditions. Although fire intensity in *Callitris* patches was lower than

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**Table 2.** Models of *Callitris* survival in relation to fire intensity (char height on *Callitris*) and *Callitris* size in the low-moderate fire-weather zone. Survival = $B_0 + B_1$ Intensity + $B_2$ *Callitris* Size + $B_3$ Intensity $\times$ *Callitris* Size. Based on Akaike information criterion (AIC), $B_3$ Intensity $\times$ *Callitris* Size was not included in the models.

<table>
<thead>
<tr>
<th>Intensity</th>
<th><em>Callitris</em> Size</th>
<th>Coefficients</th>
<th>$X^2_{\text{adj}}$</th>
<th>$P$</th>
<th>$R^2$</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Char height</td>
<td>DBH</td>
<td>$B_0$</td>
<td>$B_1$</td>
<td>$B_2$</td>
<td>0.3</td>
<td>177 (2)</td>
</tr>
<tr>
<td>Char height</td>
<td>Height</td>
<td>2.5</td>
<td>3.3</td>
<td>0.6</td>
<td>169 (2)</td>
<td>$&lt; 0.001$</td>
</tr>
</tbody>
</table>

**Table 3.** Comparison of the actual and the fitted values for live and dead *Callitris* for the survival models.

<table>
<thead>
<tr>
<th>Survival Model</th>
<th>Fitted</th>
<th></th>
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<tbody>
<tr>
<td>Dead</td>
<td>Alive</td>
<td>Correct (%)</td>
</tr>
<tr>
<td>Char height + DBH</td>
<td>Actual dead</td>
<td>83</td>
</tr>
<tr>
<td>Char height + Height</td>
<td>Actual dead</td>
<td>78</td>
</tr>
<tr>
<td>Char height + DBH</td>
<td>Actual live</td>
<td>7</td>
</tr>
<tr>
<td>Char height + Height</td>
<td>Actual live</td>
<td>8</td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td>91</td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td>87</td>
</tr>
</tbody>
</table>

**Fig. 5.** Probability of *Callitris* survival in relation to fire intensity (char height) and tree size (diameter at breast height, DBH) in the low-moderate fire-weather zone.
in the *Eucalyptus* matrix during these conditions, the difference was not enough to significantly increase the probability of *Callitris* survival. Thus, although patch structure contributed to spatial heterogeneity of fire intensities in both fire-weather zones, it only enhanced *Callitris* survival under low-moderate fire-weather conditions.

In flat landscapes, fire intensity is influenced by weather and fuels (Catchpole 2002; Boer et al. 2008), with their relative importance varying among ecosystems (Bessie & Johnson 1995; Hely et al. 2001; Turner et al. 2003). In this study, fuels influenced fire intensity in both fire-weather conditions. Evidence of fuels influencing fire intensity across a range of weather conditions has also been recorded in mixed boreal forests (Hely et al. 2001).

**Vegetation composition and fire intensity**

Under low-moderate fire-weather conditions, vegetation composition strongly influenced fire intensity and stand flammability. Since *Eucalyptus* were relatively evenly distributed throughout the study area, the concentration of *Callitris* in patches was responsible for the reduction in incoming fire intensity within 10 m of patch edges. Fire intensity declined with increasing *Callitris* basal area, and the decline in fire intensity was greatest where *Callitris* basal area reached 20 m² ha⁻¹. Since large trees contribute most to basal area, this indicates that flammability was lowest in stands dominated by large *Callitris*.

By contrast, in extreme fire-weather conditions there was no evidence of vegetation composition influencing fire intensity and stand flammability at the scale of the paired quadrats. However, when the fire intensity data were pooled across the landscape, fire intensity was lower in *Callitris* patches than the *Eucalyptus* matrix. This suggests that vegetation composition affected fire intensity during extreme fire-weather conditions at a larger spatial scale than was apparent in the paired quadrats.

Stand flammability is influenced by surface litter and above-ground fuel levels, which control the potential for fires to ignite, spread laterally and propagate into tree crowns (Catchpole 2002). In this study, ground fuel biomass was similar in both vegetation types, but litter composition differed greatly, being dominated by *Callitris* and *Eucalyptus* litter respectively, in each vegetation type. Other studies have found greater fuel biomass beneath *Eucalyptus* species, due to contributions from woody material and grasses (Clayton-Greene 1981; Bowman & Wilson 1988). Grasses are unlikely to have played a significant role in our study area, as grass biomass was low during drought conditions. We recorded similar levels of ground fuels in both vegetation types, which may be explained by the ubiquity of *Eucalyptus* across vegetation types and differences in specific leaf area, which influence leaf longevity (Lusk et al. 2003; Prior et al. 2003). Leaves of higher specific area, such as *Eucalyptus*, have a shorter leaf life span, and are likely to make a larger contribution to leaf litter than leaves of a lower specific area such as *Callitris* (Lusk et al. 2003; Prior et al. 2003).

Higher covers of *Callitris* and *Eucalyptus* leaf litters in their respective vegetation types may also have influenced flammability through differential spatial packing (Schwil & Ackerly 2001; Scarff & Westoby 2006). Despite comparable fine fuel biomass, the needle-like leaves of *Callitris* resulted in tightly packed, shallower leaf litter in the *Callitris* patches than in the matrix, which in experiments by Scarff & Westoby (2006) resulted in lower flammability. Greater shrub cover in the *Eucalyptus* matrix is also likely to have increased fire intensity by increasing elevated fuel levels (Cheney 1981; Alexander et al. 2006; Thompson & Spies 2009). The above mechanisms for reducing fire intensity are likely to be intensified in older *Callitris* stands, which may explain why flammability declined as *Callitris* basal area increased. Old stands may accumulate a more uniform, deeper layer of non-flammable litter, which may inhibit regeneration of other, more flammable plants (Facelli & Pickett 1991).

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**Table 4.** Results of Kruskal-Wallis tests on the effects of vegetation type (*Eucalyptus* matrix, *Callitris* patches) on ground fuel characteristics.

<table>
<thead>
<tr>
<th>Shrub cover (%)</th>
<th>Eucalyptus matrix</th>
<th>Callitris patches</th>
<th>X²</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>24.1</td>
<td>2.8</td>
<td>9.70</td>
<td>0.003</td>
<td></td>
</tr>
<tr>
<td>5.5</td>
<td>1.0</td>
<td>7.40</td>
<td>0.007</td>
<td></td>
</tr>
<tr>
<td>52.1</td>
<td>23.9</td>
<td>5.80</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td>0.7</td>
<td>67.2</td>
<td>20.57</td>
<td>&lt; 0.001</td>
<td></td>
</tr>
<tr>
<td>20.4</td>
<td>16.2</td>
<td>5.23</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td>23.4</td>
<td>10.3</td>
<td>6.19</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td>0.6</td>
<td>0.4</td>
<td>2.74</td>
<td>0.10</td>
<td></td>
</tr>
<tr>
<td>8040</td>
<td>8178</td>
<td>0.07</td>
<td>0.79</td>
<td></td>
</tr>
<tr>
<td>17186</td>
<td>18474</td>
<td>0.20</td>
<td>0.65</td>
<td></td>
</tr>
</tbody>
</table>

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**Callitris survival**

Differences in fire intensity have consequences for the survival of Callitris. Only 4% of Callitris survived fire in the extreme fire-weather zone, since most of their foliage was either scorched or burned, and like most conifers, Callitris do not resprout following this level of damage (Gill 1981; Bond & Midgley 2001; Russell-Smith 2006). Given this susceptibility, regular high-intensity fires have led to declines in the persistence of non-serotinous, non-resprouting woody plants in favour of sprouters or serotinous, non-resprouters in a range of ecosystems (e.g. Prior et al. 2007; Pausas et al. 2008). By comparison, Callitris survival was relatively high, reaching 58% in the low-moderate fire-weather zone. Callitris survival increased as char height (a surrogate for fire intensity) declined, and as tree diameter (a surrogate for bark thickness and tree height) increased. The survival of other non-serotinous, non-resprouting conifers (Rodrigo et al. 2004, 2007), including Callitris intratropica, is similarly affected by these factors (Bowman et al. 1988; Russell-Smith 2006).

In low-moderate fire-weather conditions, Callitris survival was higher in Callitris patches (46%), since they experienced lower fire intensities than the adjacent Eucalyptus matrix (12%). When char heights on Callitris exceeded 1 m, most Callitris died, with survival restricted to trees > 25-cm DBH. Since trees with larger diameters contribute significantly more to basal area, larger Callitris were more likely to be less flammable than smaller Callitris in low-moderate fire-weather conditions. Indeed, larger diameter trees are usually taller and have fewer lower branches, reducing the vertical continuity of fuels (Alexander et al. 2006; Thompson & Spies 2009). The oldest and largest Callitris in our study, which established from 1890 to 1911 (Austin & Williams 1988; Norris et al. 1991; Whipp 2009), characteristically had no lower branches (Whipp 2009). Schwilk & Ackerly (2001) suggest that branch shedding is an evolved trait that reduces the flammability (and thereby enhances survival) of non-serotinous Pinus.

Callitris stands burned by high-intensity fires remain vulnerable to subsequent low-intensity fires, until Callitris grow large enough to modify fuel levels and reduce stand flammability. Predictions of an increase in the frequency of extreme fire-weather days under global warming (Lucas et al. 2007) suggest that flammability differences may be overridden by fire-weather in the future, encouraging resprouting Eucalyptus to profit over non-resprouting Callitris.

**Conclusions**

These results demonstrate that flammable feedbacks, mediated by low flammability fuel traits of dominant trees, can provide an important mechanism for enhancing the survival and persistence of slow-growing, non-serotinous, fire-sensitive trees in highly flammable landscapes. This is likely to be particularly important in relatively flat landscapes (such as the study area), where topographic fire refugia (e.g. rock outcrops) do not exist. In addition to enhancing species persistence, this feedback loop is also likely to modify the spatial patterning of fire-sensitive trees, by creating sharp boundaries between stand types rather than gradual gradients in abundance, although this requires further research. This fire–vegetation feedback loop is less effective in increasing the survival probability of Callitris under extreme fire-weather conditions, when fire intensity is greater. Stands burned by high-intensity fires remain vulnerable to subsequent low-intensity fires, until Callitris grow large enough to modify fuel levels and reduce stand flammability. Predictions of an increase in the frequency of extreme fire-weather days under global warming (Lucas et al. 2007) suggest that flammability differences may be overridden by fire-weather in the future, encouraging resprouting Eucalyptus to profit over non-resprouting Callitris.

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