

Impact of high-severity fire in a Tasmanian dry eucalypt forest

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Abstract. Dry eucalypt forests are believed to be highly fire tolerant, but their response to fire is not well quantified. We measured the effect of high-severity fires in dry eucalypt forest in the Tasmanian Midlands, the driest region on the island. We compared stand structures and fuel loads in long-unburnt (>15 years since fire) and recently burnt (<5 years since fire) sites that had been completely defoliated. Even in unburnt plots, 37% of eucalypt stems and 56% of acacia stems ≥ 5 cm in diameter were dead, possibly because of antecedent drought. The density of live eucalypt stems was 37% lower overall in burnt than in unburnt plots, compared with 78% lower for acacias. Whole-plant mortality caused by fire was estimated at 25% for eucalypt trees and 33% for acacias. Fire stimulated establishment of both eucalypt and acacia seedlings, although some seedlings and saplings were present in long-unburnt plots. The present study confirmed that eucalypts in dry forests are more tolerant of fire than the obligate seeder eucalypts in wet forests. However, there were few live mature stems remaining in some burnt plots, suggesting that dry eucalypt forests could be vulnerable to increasingly frequent, severe fires.

Additional keywords: epicormic shoots, *Eucalyptus*, fire tolerance, fuel loads, mortality, resprouting, stand structure, tree biomass, wet eucalypt forest.

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Introduction

Dry eucalypt forests and woodlands occupied large areas of temperate southern Australia before European settlement. The landscapes throughout this range were typically a mosaic of grassy eucalypt woodlands between treeless grasslands in the valleys, and dry eucalypt open forests on the hills (Yates and Hobbs 1997); here we collectively refer to these eucalypt open forests and woodlands as dry eucalypt forests. Following colonisation, these dry eucalypt forests were targeted for agricultural development, and by 1995, $\sim 500\,000$ km² had been cleared (Yates and Hobbs 1997; Bradshaw 2012). Across Tasmania, $\sim 13\,700$ km² remains of eucalypt forest and woodland with 20–50% cover (ABARES 2014).

The Tasmanian Midlands represent the southern terminus of Australia's dry eucalypt forests. It is the second-oldest agricultural area in Australia. As in similar areas of dry eucalypt forest in mainland Australia, the vegetation has been largely cleared, and what remains is heavily fragmented (Kirkpatrick 1991; Bradshaw 2012; Romanin *et al.* 2015). Only 16% of the Midlands remains under native vegetation, mostly in steep, rocky areas unsuitable for cultivation (Fensham 1989). Tree cover is continuing to decrease as a result of tree dieback, agricultural intensification and grazing pressure from introduced herbivores (Kirkpatrick 1991; Neyland 1999; Davidson *et al.* 2007; Close *et al.* 2009; Prior *et al.* 2013; Romanin *et al.* 2015). Climate change poses a further threat to the tree cover that remains (Williamson *et al.* 2014). One

factor that is not well understood is the role of fire in maintaining the openness of the vegetation, with some anthropologists arguing that this was an artefact of Aboriginal burning (Jones 1969; Gammage 2011); however, this contention is based on historical anecdote, and has not been rigorously demonstrated (Bowman 2012). Regardless of past fire history, it is not clear how to manage fire in this fragmented landscape to best protect its remaining biodiversity. As a consequence, many remnants have been left unburnt by planned fires, rendering them vulnerable to high-intensity wildfires.

The effects of fires in wet eucalypt forests are well documented (McCarthy *et al.* 1999; Ashton 2000, and references therein; Lindenmayer and McCarthy 2002; Benyon and Lane 2013; Bowman *et al.* 2014), but there has been less research on the effects of fire on trees in dry eucalypt forests in temperate Australia (Williams *et al.* 1994; Gill 1997; Hobbs 2002; Lunt *et al.* 2012; Fairman *et al.* 2015). In dry eucalypt forest, fires can occur frequently, as low-intensity ground fires as well as high-intensity, canopy-consuming fires, and there is the potential to safely reduce fuel loads using prescribed fire (Penman *et al.* 2007; Leonard *et al.* 2014). This is in contrast to wet eucalypt forests, which switch quickly from their usual state of being too wet to burn, to burning at high intensity in hot, windy conditions after unusually dry periods (Bradstock 2010; Leonard *et al.* 2014). Associated with the contrasting fire regimes in the two forest types are divergent ecological responses to fire. Wet eucalypt forests are dominated by

obligate seeders and depend on infrequent, intense stand-replacing fires to occur within the lifespan of the dominant trees, whereas in dry eucalypt forests, most mature trees survive the surface fires and many eucalypts survive the canopy-destroying fires by resprouting (Gill and Ashton 1968; Christensen *et al.* 1981; Bowman and Kirkpatrick 1986; Gill 1997; Clarke *et al.* 2005; Burrows 2013). These forests are regarded as fire tolerant and even benefited by fire, in that long-term absence of fire in these forests has been implicated in the premature decline of overstorey eucalypts (Jurskis 2005; Close *et al.* 2009), as well as a decrease in understorey species richness (Penman *et al.* 2009). The stimulation by fire of eucalypt seedling germination and establishment is well known (Potts 1986; Yates *et al.* 1996; Gill 1997; Clarke and Davison 2001; Hill and French 2004; Bailey *et al.* 2012), and fire also increases the density of eucalypt resprouts in dry eucalypt forests (Gill 1997; Hill and French 2004). However, surprisingly few studies have quantified the mortality and resprouting responses of trees after fire in these forests (Fairman *et al.* 2015). Survival of eucalypts has been reported as being similar to, or only slightly lower (<5%), in recently burnt than in long-unburnt dry eucalypt forests (Potts 1986; Wardell-Johnson 2000; Croft *et al.* 2007; Pickup *et al.* 2013). Gill (1978) measured the impact of fire on small *Eucalyptus dives* trees in south-eastern New South Wales; all survived the fire, but lost 30–50% of their initial height. In *E. marginata* forest in southern Western Australia, frequent, low-intensity fires had little impact on the trees, whereas a single, high-intensity fire damaged many, but killed few, trees (Abbott and Loneragan 1983). However, despite the renowned fire tolerance of resprouter eucalypts, Fairman *et al.* (2015) cited several instances where a single wildfire killed substantial numbers of resprouter eucalypts; it is worth noting that such severe impacts had not previously been documented in the scientific literature.

Resprouting allows plants to survive disturbance. For example, Strasser *et al.* (1996) reported that in six eucalypt species, only 0–12% of trees, but 33–82% of stems, were dead following a crown-scorching fire in dry eucalypt forest in the Australian Capital Territory. Resprouting can be categorised as aerial (e.g. epicormic), basal (e.g. from a lignotuber) and below ground (Clarke *et al.* 2013). Aerial resprouting, which is common in eucalypts from dry forests, is especially advantageous because it allows them to re-establish an extensive leaf surface that is higher, and can intercept more light, than the leaves of basal resprouters and reseeders (Burrows 2013; Clarke *et al.* 2015). A study in dry eucalypt forest in northern New South Wales following a 3-year drought found that survival was similar in unburnt trees and those that had also experienced a severe wildfire; however, burnt trees tended to resprout from lignotubers, whereas unburnt trees typically resprouted from the trunk and canopy (Croft *et al.* 2007), which would allow unburnt trees to regain their initial size more quickly.

Motivated by the need to better understand the fire ecology and management of dry forests, the aims of the present study were to (1) quantify the stem and whole-plant mortality of acacia, eucalypt and other tree species following canopy-defoliating fire in dry eucalypt forest and woodland in the Tasmanian Midlands; (2) examine the extent of seedling

establishment and resprouting in eucalypts and acacias, the most dominant tree genera in the region; and (3) compare fuel loads in burnt and nearby unburnt transects.

Materials and methods

Study region

The northern part of the Tasmanian Midlands lies on the Tamar graben, an extensive plain bordered to the east and west by low but rugged mountains (Fig. 1). The climate is cool temperate, with rainfall spread uniformly throughout the year (Köppen Cfb; Kottek *et al.* 2006); however, the area receives only a mean of ~500–700 mm annual rainfall, making it the driest part of the state. Temperatures at the town of Ross (42.0°S, 147.5°E; 186-m elevation) vary from a mean daily minimum of 1.4°C in July to a mean daily maximum of 24.5°C in January (Bureau of Meteorology 2015). Soils are highly variable, and range from shallow, moderately fertile soils derived from basalt and dolerite, to infertile soils on the original Tertiary surfaces, which have been subjected to long periods of laterisation (Fensham 1989).

The natural vegetation of the Midlands comprises *Eucalyptus viminalis*, *E. pauciflora* and *E. ovata* open forest and woodland on Quaternary sands and alluvium, and *E. amygdalina* open forest and woodland on Tertiary deposits (Resource Planning and Development Commission 2003). This region was one of the first in Australia to be developed for agriculture, and like similar grassy woodlands elsewhere in temperate Australia, it has been extensively cleared (Fensham 1989; Kirkpatrick 1991; Romanin *et al.* 2015). Most surviving remnants are <5 ha in size and concentrated on steep slopes, and on sand and Jurassic dolerite substrates (Gilfedder and Kirkpatrick 1998). These remnants are important for nature conservation; however, their condition and biodiversity values are strongly affected by fire and grazing management and the nature of the surrounding vegetation (Gilfedder and Kirkpatrick 1998; Davidson *et al.* 2007; Close *et al.* 2008). In addition, rural tree decline and secondary clearing, accelerated by irrigation development, continue to erode tree cover in the region (Close and Davidson 2004; Prior *et al.* 2013; Romanin *et al.* 2015).

Site selection and fire history

Because natural woodland in the Midlands is highly fragmented, the number of fires and the area burnt in any one year are usually small (Kirkpatrick and Gilfedder 1995). For obvious ethical and practical reasons, we could not plan high-severity fires and measure vegetation before and after burning in remnant dry forests. However, a series of canopy-defoliating fires in February 2009, February 2011, February 2012 and January 2013 afforded the opportunity to document fire effects in remnant dry eucalypt forest in the northern part of the Midlands. We did this by comparing 14 recently burnt and 20 long-unburnt sites. All study sites were located in the vicinity of 41.8°S and 147.4°E, at an elevation of between 177 and 256 m, with a slope of <5° (Fig. 1). The sampled vegetation included woodland and open forest (*sensu* Specht *et al.* 1974) and was dominated by *Eucalyptus* species such as *E. amygdalina*, *E. viminalis* and *E. pauciflora*. These species can all basally resprout after fire, but *E. pauciflora* has thin

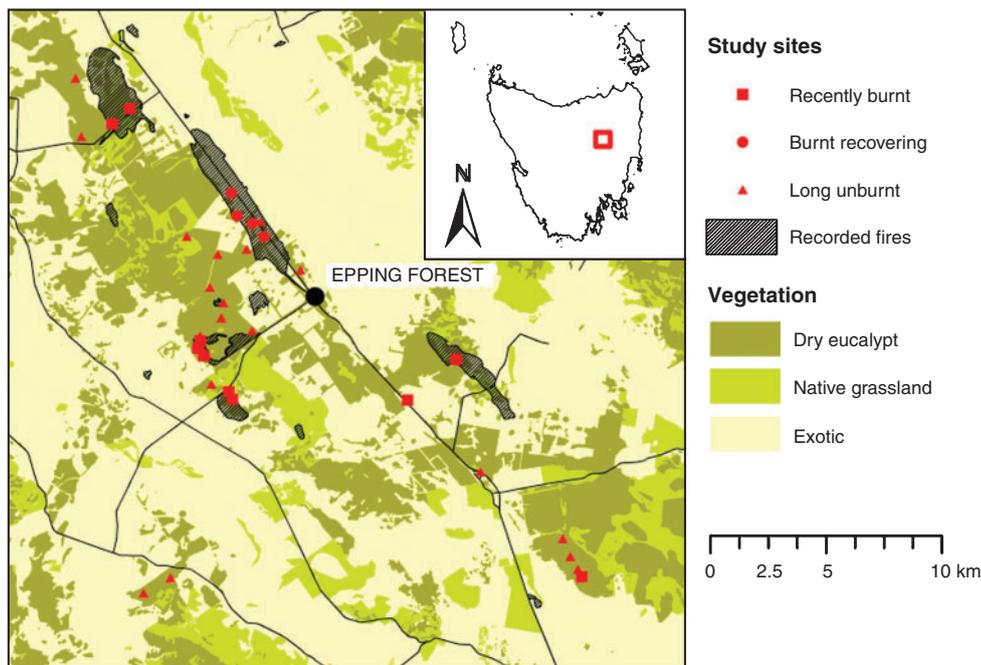


Fig. 1. Map of study area in the vicinity of Epping Forest (41.76°S, 147.35°E), showing location of stand structure sites in relation to vegetation and fire history. We distinguished between recently burnt (0.5–2 years since fire) and recovering burnt sites (4.5 years since fire) for analyses of sapling density and fuel loads.

bark and is a poor epicormic resprouter (Strasser *et al.* 1996; Pickering and Barry 2005). There was a mix of small trees in the midstorey, including *Acacia dealbata*, *Allocasuarina verticillata*, *Banksia marginata* and *Exocarpos cupressiformis*, and a variable ground cover of C₃ grasses (average 20% cover of live grass, range 2–60%), herbs (average 7% cover), *Lomandra*, sedges and bracken. No other species of acacia were recorded; hence, the term ‘acacia’ refers to *Acacia dealbata*.

Our recently burnt study sites were selected using the fire-history mapping provided by the Tasmanian Fire Service. This is based on ground and helicopter surveys, and includes larger and more intense fires, whereas smaller fires on private land that do not require Fire Service intervention are less well represented. We targeted sites for which we were able to obtain landholder permission to sample; that were at least 100 m from a major road and 30 m from tracks or fencelines; at least 300 m apart from each other; that had experienced recent crown fire; and that were reasonably homogeneous in their vegetation and fire severity. We sampled all the burnt areas that met these criteria. The fires at our study sites were all sufficiently severe to completely defoliate the vegetation, and kill some or most overstorey trees, and were, therefore, of moderate to high severity (Keeley 2009). Typical remnant forest recovering from fire is shown in Appendix 1, available online as supplementary material to this paper. So as to obtain a geographically representative sample of recently burnt vegetation, we had to sample areas burnt by fires between 0.5 and 4.5 years before sampling, which took place in July and August 2013. Although adding variability to some of our measurements, this chronosequence allowed us to make some preliminary inferences about post-fire recovery, which need

to be tested using a larger sample size that can control for edaphic variability. Long-unburnt sites (>15–20 years after fire, according to landholder testimony) were selected to be similar to burnt sites in physical characteristics and tree-species composition. Our field observations confirmed that only recently burnt sites contained scorched trees. Charred trees were much more numerous in the burnt plots, although a few were also present in the long-unburnt plots, being indicative of past fire.

We were able to describe fire weather at each site on the day it burnt by calculating the McArthur forest fire-danger index (FFDI), which incorporates temperature, humidity, wind speed and antecedent rainfall and evaporation (Dowdy *et al.* 2009). The FFDI on the day of most fires was between 16 and 20, corresponding to high fire-danger conditions (Dowdy *et al.* 2009). For one site, FFDI was 34, corresponding to a very high fire danger. These values are far higher than the regional mean summer FFDI of 5, and the summer 90th percentile of 9, calculated using data collected since 1970 from meteorological stations within the Midlands, following the methodology of Williamson *et al.* (2016). We also estimated fire intensity at each site using satellite records, although we acknowledge their coarse spatial and temporal resolution in comparison to the size of the forest remnants and duration of the fires. To do this, each site was attributed with the sum of the fire radiative power (FRP) for all MODIS collection 5 MCD14DL active fire detections (Giglio *et al.* 2006) for a window spanning 16 days before the established fire day to 16 days after the fire day, within a 4-km radius of the site. This showed that a mean FRP for these fires was 56 MW (range 8–237 MW).

Measurement of tree density, survival and resprouting

At each site, we established a plot 100 m long and 20 m wide, from which we collected data on tree size, density and species composition. Seedling-density data (individuals <1.5 m tall) were collected on only the centre 4-m width of the plots (or the centre 2 m, if seedlings were very dense, i.e. >1 m⁻²). All individuals were identified according to genus, and to species level, where possible. The heights of seedlings, and the diameter at breast height (DBH) of 'saplings' (≥1.5 m tall and <5 cm in DBH) and 'trees' (≥5 cm in DBH) were measured. We noted the presence of live epicormic shoots on the main stem, live basal sprouts, scorching and charring, whether the tree was fallen, and whether it was a stump, whether it was cut or broken. We recorded the status of each individual as 'alive, no epicormics' (if the main stem had live foliage), 'epicormically resprouting' (main stem with live epicormic resprouts), 'basally resprouting' (main stem dead but live basal resprouts present) or 'dead' (main stem dead and no live resprouts). For analyses of survival, 'live stems' included those with live epicormic resprouts, and 'live whole plants' included those with live epicormic or basal resprouts.

Statistical analyses

Our statistical approach was based on generalised linear modelling, multi-model inference and model selection using Akaike's information criterion modified for small sample size (AICc) (Burnham and Anderson 2002) using the statistical software R (R Core Team 2015). For each analysis, we constructed candidate model sets to compare the global model, containing all terms of interest, with simpler models containing all subsets of these terms. Where we were specifically interested in testing for an interaction, we added an additional model containing this interaction. We considered the interaction to be strongly supported if the AICc of the interactive model was ≥2 lower than that of the next-best model. If the interaction was not well supported, we dropped this model and calculated w_i (the summed w_i of all the models containing the term) for all terms based on the additive models (full subsets regression; Burnham and Anderson 2002). Model terms were considered to be important if w_i exceeded 0.73 (Burnham and Anderson 2002).

Tree density and stand structure

Density data were calculated on a plot basis, and were all log-transformed (density per ha + 1) for analysis to normalise the data. Aboveground biomass was calculated using the allometric equations from Bowman *et al.* (2014), which were modified from the equations of Keith *et al.* (2000) for dry eucalypt forest. We tested whether the densities of live, dead and resprouting trees, aboveground carbon in live and standing dead trees, live- and dead-stand basal area, and the percentage contribution of eucalypts to stem numbers and basal area were related to differences in fire history (long-unburnt compared with recently burnt plots) by comparing the linear model containing the term 'fire history' with the null model.

We then examined the densities of live seedlings and saplings in relation to time since fire. Inspection of the raw data showed that sapling density was highest ~4.5 years after the fire, which we interpreted as fire stimulating establishment of seedlings,

some of which recruited to the sapling class between 1.5 and 4.5 years after the fire. There was statistical support (lower AICc) for using three fire-history categories for analysis of sapling (but not seedling) data: 'recently burnt' (<2 years since fire), 'recovering' (4.5 years after fire) and 'long-unburnt' (>15 years after fire). For seedlings and trees, we used just two categories, namely burnt versus unburnt. We compared models with and without the term 'fire history' for densities of seedlings, saplings and trees of all species combined, eucalypts only and acacias only, using data from all plots.

To test for differences in the occurrence of individual species between burnt and unburnt plots, the presence/absence of seedlings, saplings and trees of individual species was analysed by comparing binomial general linear models (GLM) with and without the term 'fire history'. For species in which seedlings, saplings or trees occurred in more than half the plots, we then tested whether density was related to 'fire history' by using linear models, considering only those plots where the species was present, to avoid using zero-inflated data.

Stand structures were compared between burnt and unburnt plots by binning counts of live eucalypt, acacia and *Banksia marginata* trees into 10-cm-diameter bins, up to the largest diameter class for that fire history. The data were over-dispersed, and so we used negative binomial GLMs in the package glmmADMB (Skaug *et al.* 2014). Plot was used as a random effect to account for the spatial correlation in the data. Preliminary modelling showed that the slopes of the log (count)–diameter relationship varied between burnt and unburnt plots, so we fitted a separate log(count)–diameter model for both, and tested for conformity to the negative exponential distribution and, hence, likely frequent recruitment at a regional level (Prior *et al.* 2011).

Survival and resprouting

Survival and resprouting were considered only for stems with DBH of ≥5 cm, because dead trees smaller than this are likely to be consumed or fall after fire. We calculated both stem survival (main stem with live foliage, including live epicormic resprouts) and whole-plant survival (live main stem, or live basal resprouts). Stem mortality, therefore, includes whole-plant death and stem death with basal resprouting. Overall estimates of fire-induced stem (and whole-plant) mortality were based on comparisons of densities of live stems (and whole plants) in burnt and unburnt plots. This was because there were many dead trees even in the unburnt plots (as detailed in the Results section), so we could not assume that most of the dead trees in the burnt plots were killed by fire. We also considered it likely that dead trees were less likely to remain standing in burnt than unburnt plots, and, hence, mortality estimates based on percentages of live standing trees were likely to be biased.

We did examine the proportion of main stems that were alive in relation to diameter and genus by using binomial GLMs, which maximise statistical power by treating each tree as an observational unit. However, we acknowledge that survival estimates based on proportions of live standing trees could be biased, given that small trees are more likely than large trees to fall or be consumed by fire. We tested whether there was an

interaction between fire and genus, controlling for tree size, using the binomial GLM 'stem alive ~diameter + genus × fire' with plot as a random factor to account for the spatial correlation in the data. (Live stems were rated '1', and dead stems, including those with basal resprouts, as '0'). Only acacias and eucalypts were present in sufficient numbers to include in this analysis, which we restricted to stems <40 cm in diameter, so that similar-sized trees were compared. The proportion of live whole plants was then analysed in the same way.

Basal resprouting (as a proportion of dead stems) in relation to DBH and genus (acacia versus eucalypt) was similarly analysed using binomial GLMs, with plot as a random effect. We also used binomial GLMs, with plot as a random effect, to test whether there was a relationship between epicormic resprouting (as a proportion of all eucalypts ≥ 5 cm in DBH) and stem diameter in burnt eucalypts. The density of basally resprouting trees in relation to fire history was examined using linear models.

Fuel loads

Fuels were sampled from a subset of 11 recently burnt and 11 long-unburnt sites, using the methods described by Bowman *et al.* (2014). At each of these sites, we established three 30-m-long transects. The transects at recently burnt sites were located ~100 m from the fire boundary. Canopy cover was measured with a densitometer at the start and midpoint of each transect. Canopy height, slope and aspect were measured with a clinometer.

Fine litter (<6 mm), standing grass, standing herbs and shrubs (woody plants, including saplings, to 4 m tall) were collected separately from 1-m² quadrats and weighed. At least two quadrats were measured in each transect (0 m and 14 m), but where fuels were very patchy, three or four quadrats were measured. Moisture content, measured on subsamples of the fuels, was used to convert fresh weights to dry weights. Woody fuels were measured as counts (of four size classes) of vertical planar intercepts along the 30-m transect (Brown 1974). For the four size classes of woody fuels, we assessed 4 m, 4 m, 8 m and the full 30 m of the transect respectively. Volume of the three smallest size classes was estimated using the average radius for the size class, and an angle correction of 1.13. For the largest size class, the volume of each piece of

woody debris was measured directly. A density of 0.48 g cm⁻³ was assumed for the two smaller size classes, and 0.40 g cm⁻³ for the two larger size classes. Here, we present results for the finest class (<6 mm) and total load of woody fuels.

Differences between burnt and unburnt transects in loads of the various fuel categories were tested using linear mixed-effects models with site as a random effect to account for spatial autocorrelation in the data. We also tested whether a trend could be detected in fuel loads of burnt plots as a function of time since fire.

Results

Density in relation to fire history and growth stage

The study plots were dominated by eucalypts, in terms of both abundance and basal area (Table 1). *Eucalyptus amygdalina* was the most common species, and was present in 31 of the 33 plots. Other abundant species were *E. viminalis*, *E. pauciflora*, *Banksia marginata* and *Acacia dealbata* (Appendices 2 and 3). Canopy height and cover at unburnt sites averaged 22 m and 44% respectively, placing the vegetation in the open-forest category. Even in unburnt plots, 41% of the standing trees ≥ 5 -cm DBH had dead main stems (Table 1), which makes it more difficult to detect effects of fire, species and tree size on mortality. The effect of fire history on overall tree density varied according to growth stage and genus (Appendices 2 and 3). Burnt plots contained fewer live trees (Table 1), but had many more seedlings than did unburnt plots (Fig. 2), as described below.

Burnt plots contained 63% fewer live stems ≥ 5 -cm DBH than did unburnt plots, and 44% fewer live whole plants (Table 1). Live basal area was 34% lower in burnt than unburnt plots (Table 1). There were far more top-killed, basally resprouting trees in the burnt than unburnt plots (54 versus 0.5 per ha; Table 1). Dead-stem density, dead whole-plant density and dead basal area were all higher in burnt than in unburnt plots, but these differences were not statistically important because of high variability (Table 1). Aboveground tree biomass was 14% lower in burnt than in unburnt plots, but again this difference was not statistically important (Table 1). Eucalypts comprised a higher percentage of live stems ≥ 5 -cm DBH in burnt than in unburnt plots (86% versus 51%), suggesting that

Table 1. Summary of stand basal area and density of trees ≥ 5 cm in diameter at breast height of all species in relation to fire history

The density of live and dead stems and whole plants and top-killed, basally resprouting trees is shown, as well as the percentage contribution of eucalypts to live basal area and live tree density. Standard errors indicate variation among plots. w+ is for the term 'Fire history'; values >0.73 are shown in bold

Parameter	Unit	Unburnt		Burnt		w+
		Mean	s.e.	Mean	s.e.	
Live-stand basal area	m ² ha ⁻¹	25.3	1.6	16.7	2.6	0.96
%Eucalypts	%live basal area	89	3	96	1	0.71
Dead-stand basal area	m ² ha ⁻¹	9.6	1.6	14.7	2.7	0.59
Live stem density	ha ⁻¹	283	24	105	17	1.00
%Eucalypts	%live-stem density	51	5	86	5	1.00
Live whole-plant density	ha ⁻¹	283	24	159	34	0.99
Dead-stem density	ha ⁻¹	200	37	277	45	0.61
Dead whole-plant density	ha ⁻¹	200	37	223	27	0.40
Basally resprouting-tree density	ha ⁻¹	0.5	0.5	54	32	1.00
Aboveground tree biomass (includes standing dead trees)	t ha ⁻¹	304	24	262	15	0.37

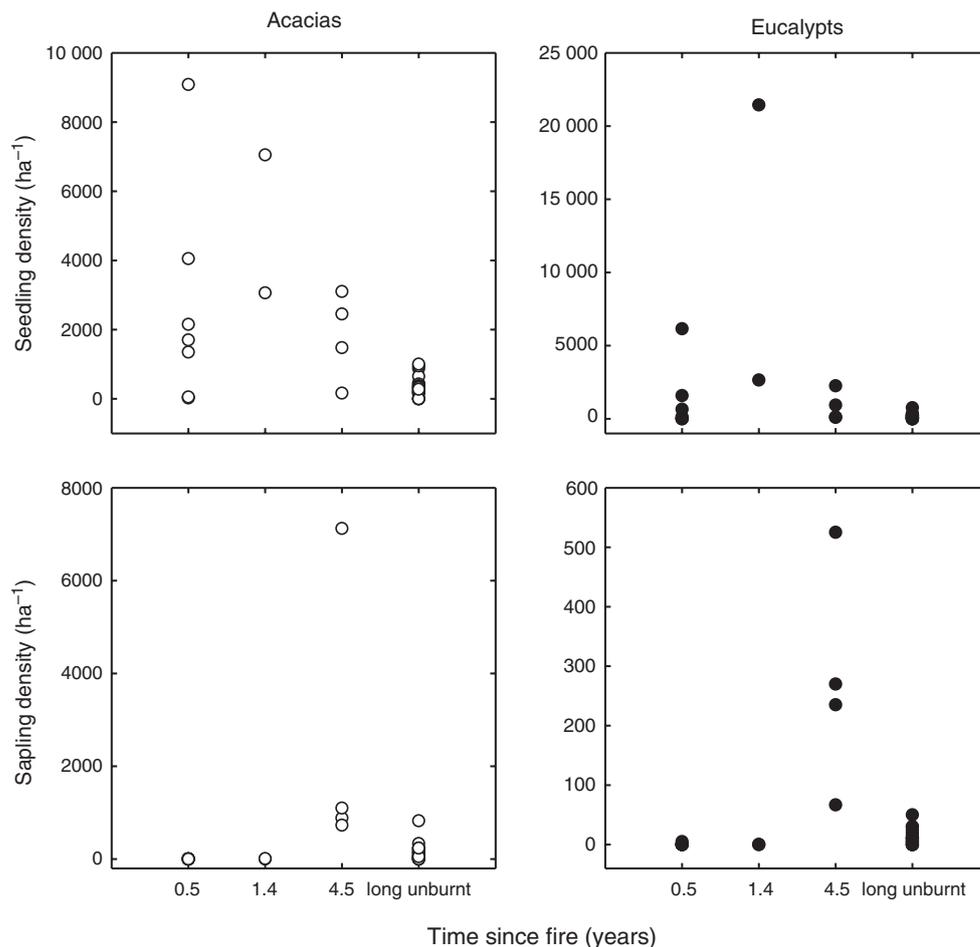


Fig. 2. Density of live acacia (○) and eucalypt (●) seedlings and saplings in each plot in relation to time since fire. Note the different scales on the y-axes. Fire history influenced density of acacia seedlings ($w^+ = 0.95$), acacia saplings ($w^+ = 1.00$) and eucalypt saplings ($w^+ = 1.00$), whereas there was only weak support for differences in eucalypt seedling density ($w^+ = 0.65$).

fire disproportionately killed non-eucalypt species (Table 1). In burnt plots, live-stem density was 78% lower for acacias, 37% lower for eucalypts and 97% lower for other species than that in unburnt plots. Live whole-plant density was 33% lower for acacias, 25% lower for eucalypts and 96% lower for other species.

The density of seedlings and saplings was influenced by time since fire. In general, the number of seedlings was highest 0.5 years after the fire, and decreased after that (Fig. 2). By contrast, saplings were far more abundant in plots burnt 4.5 years ago than in long-unburnt plots, whereas they were almost absent in plots burnt less than 2 years ago (Fig. 2). There was statistical support for these trends in acacia seedlings ($w^+ = 0.95$), eucalypt saplings ($w^+ = 1.00$) and acacia saplings ($w^+ = 1.00$), but only weak support for differences in eucalypt seedling density ($w^+ = 0.65$). There was more acacia than eucalypt regeneration, especially in unburnt plots, despite a higher density of eucalypt than acacia trees (Fig. 2).

There were obvious differences between burnt and unburnt plots in the presence and densities of live seedlings, saplings and trees for some individual species (Appendices 2 and 3). For example, *Acacia dealbata* seedlings and saplings were

found in most plots, and trees were found in 95% of the unburnt, but only 54% of burnt plots. Density of live *A. dealbata* seedlings was higher in burnt than unburnt plots, sapling densities were highest in recovering plots and tree densities were higher in unburnt plots (Appendix 3). Live *Banksia marginata* seedlings, saplings and trees were present in most unburnt plots, but not in any of the burnt plots (although dead *B. marginata* saplings and trees were found in 5 burnt plots). *Eucalyptus viminalis* trees with live stems were found in 85% of unburnt plots, but only in 38% of burnt plots.

When data from all unburnt plots was combined, stand structures of eucalypt, acacia and *Banksia marginata* trees all conformed to a negative exponential distribution (Appendix 4), with the count-diameter model explaining 11.2%, 14.4% and 11.6%, respectively, of the deviance. This is consistent with frequent recruitment at a regional level. Eucalypts and acacias in the burnt plots also approximately conformed to the negative exponential distribution, but the fit was not as good as in the unburnt plots (respectively 9.8% and 3.4% deviance explained). Eucalypt stand structures at 14 of the 20 individual unburnt plots and 7 of the 13 burnt plots also conformed to a negative exponential distribution.

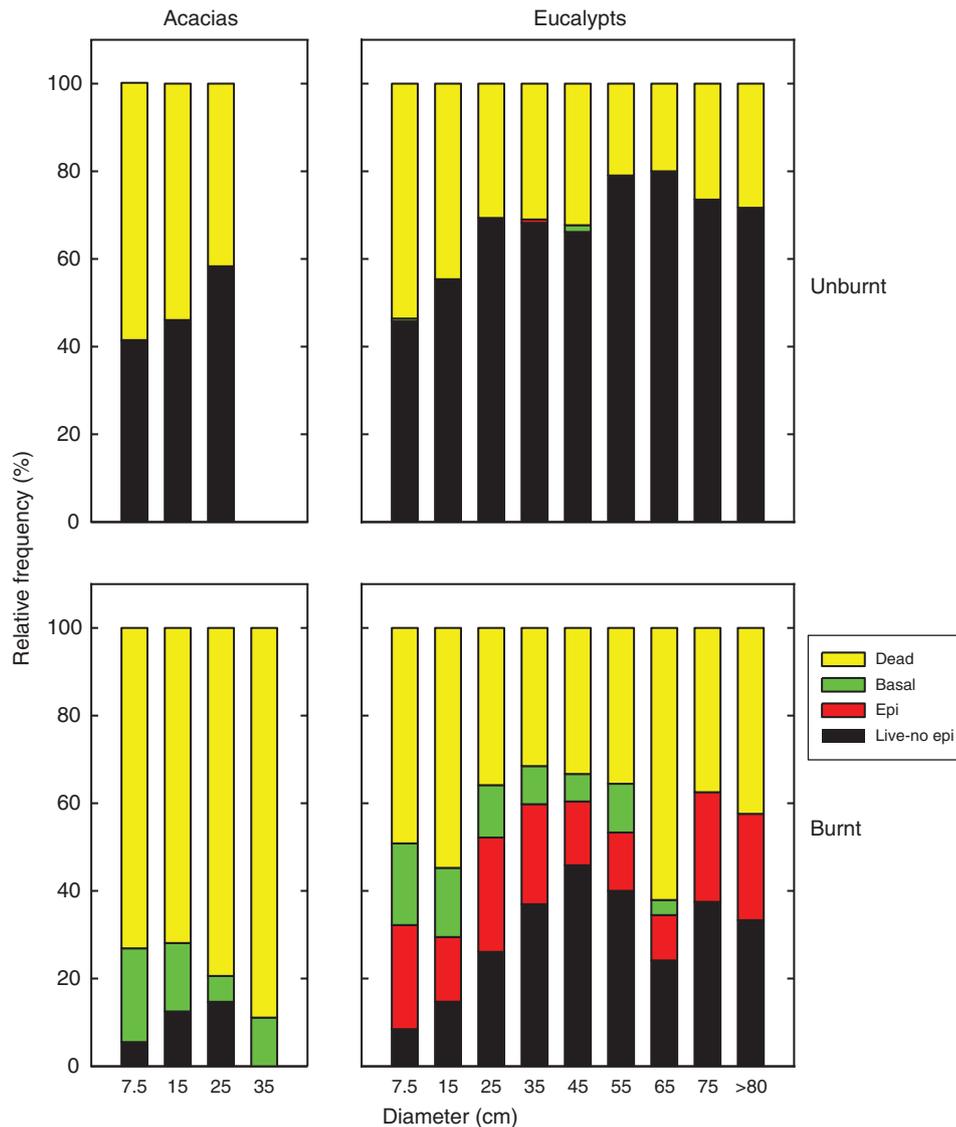


Fig. 3. The relative frequency of live stems with no epicormic sprouts, live stems with epicormic sprouts, basally resprouting dead stems and dead stems with no resprouts (i.e. dead whole plants), as a function of diameter and according to genus and whether located in burnt or unburnt plots. All stems ≥ 5 cm in diameter at breast height (DBH) were binned into 10-cm-DBH classes for graphical presentation, whereas diameter was a continuous variable in the modelling. Eucalypt stems survived fire better than did acacias ($w_i = 1.00$ for the model with the interaction between fire and genus, controlling for diameter). There was a negative relationship between percentage basal resprouting and diameter, and more resprouting in eucalypts than in acacias ($w_i = 0.99$). There was no relationship between diameter and epicormic resprouting for eucalypts in the burnt plots ($w_i = 0.51$).

Proportional survival of stems and whole plants

The proportion of stems that were alive was influenced by fire history, tree size and genus (w_i for this model was 1.00). A higher proportion of eucalypt than acacia stems of ≥ 5 -cm DBH were alive in both unburnt and burnt plots (Fig. 3). On average, 63% of eucalypt stems and 44% of acacia stems were alive in long-unburnt plots, compared with 48% of eucalypts and only 9% of acacias in recently burnt plots. However, the proportion of live stems was highly variable in both burnt and unburnt areas; for example, in four burnt plots, more than 63% of eucalypt stems were alive (the average for unburnt plots), suggesting the fire had caused little, if any, stem mortality. However, at two sites, fewer than 10% of eucalypt stems were

alive. Whereas every burnt plot contained some live mature eucalypt stems, there were no live acacia stems in 50% of burnt plots.

The proportion of live stems increased with tree size to ~ 25 cm in DBH; more than half of small stems (< 10 -cm DBH) were dead, even in unburnt plots (Fig. 3). Tree size did not appear to influence stem survival during the fires, given there was no statistical support for an interaction between tree diameter and fire history. Eucalypt stems appeared to survive fire better than acacia stems, because there was a strongly supported interaction between genus and fire history ($w_i = 1.00$), even when diameter was controlled for in the model.

The proportion of whole plants that were alive was similarly influenced by fire history, tree size and genus (w_i for this model was 1.00), although the effect size was generally smaller than for stems (Fig. 3). On average, whole-plant survival was 64% for eucalypts and 44% for acacias in long-unburnt plots, compared with 58% of eucalypts and 27% of acacias in recently burnt plots. In three burnt plots, fewer than 40% of eucalypt whole plants were alive. There were no live acacia whole plants in three burnt plots.

Resprouting

There were large differences between burnt and unburnt plots in the numbers of trees with epicormic and basal resprouts (Fig. 3). In unburnt plots, of a total of 1932 live and dead stems, there was only one with epicormic resprouts, and two with basal resprouts. The density of basally resprouting trees was 107 times higher in burnt than unburnt plots (Table 1). Epicormic shoots were found only on eucalypts, and on only 0.2% of live eucalypt stems in unburnt plots, compared with 42% in burnt plots. (By our operational definition, dead stems had no epicormic shoots). There was no relationship between epicormic resprouting and DBH in eucalypts in burnt plots ($w^+ = 0.51$). In the burnt plots, we were able to identify to species level only 36% of the 214 dead whole eucalypts, so we cannot reliably compare resprouting rates among eucalypt species. However, it is worth noting that we identified 66 *E. amygdalina* and 25 *E. viminalis* trees with epicormic resprouts, but observed no epicormically resprouting *E. pauciflora* trees, consistent with other reports of poor epicormic resprouting in *E. pauciflora*.

In burnt plots, basal resprouting was more common in dead (17.5%) than live (11.9%) stems ($w^+ = 0.90$). In the burnt plots, the proportion of dead main stems that basally resprouted was negatively related to stem diameter ($w^+ = 0.99$; Fig. 3). There was also more basal resprouting in eucalypts than in acacias, controlling for diameter ($w^+ = 0.99$; Fig. 3), but the overall difference between the two genera was small (of dead main stems, 20% basally resprouted in eucalypts, compared with 18% in acacias).

Fuel loads

Burnt plots contained a shallower depth and smaller load of litter fuels and less woody fuels of all size categories than unburnt plots; fuel loads were 57% lower for litter fuels and 51% lower for total woody fuels (Fig. 4, Appendix 5). Grass loads were, on average, 21% lower in burnt than unburnt plots, and increased with time since fire; the regression equation indicated that grass loads in burnt plots would recover fully in 4.7 years (Fig. 4, Appendix 5). There was statistical support for an increase in shrub mass with time since fire, but shrub mass tended to be lower in long unburnt than recently burnt plots (Fig. 4, Appendix 5). Note that not all shrub mass represents available fuel. All other fuels also tended to increase with time since fire, but the differences did not receive strong statistical support.

Discussion

The present opportunistic study showed that fires that burnt intensely, albeit not under extreme or catastrophic fire-weather

conditions, caused significant whole-tree mortality in dry forest remnants. There were consequent changes in the structure and species composition compared with similar forests that had not been burnt for over 15 years. As outlined below, these findings are significant as they challenge the view that dry forests are highly resilient to fire compared with wet forests. They also highlight the need for active fire management in dry forest fragments to conserve their biodiversity and other values such as catchment protection and visual amenity.

It is widely held that dry eucalypt forests are more tolerant of fire than are wet eucalypt forests, which are often dominated by obligate seeders; yet, there have been few quantitative comparisons of fire responses in these two forest types (Fairman *et al.* 2015). We were able to directly compare the impact of fire on trees in the dry eucalypt forest in the Midlands with those in in wet eucalypt forest dominated by *Eucalyptus delegatensis*, using a recent study in the Australian Alps that employed the same measurement protocols (Bowman *et al.* 2014). As expected, the impact of fire was much lower in the Midlands dry eucalypt forest (detailed comparisons are given in Appendix 6). For instance, the density of mature live eucalypt stems (>20-cm DBH) was 94% lower in burnt than in unburnt plots in the Alps, compared with only 22% in the Midlands. In the Alps, only 2 of 10 plots contained any live eucalypts following a single fire, compared with the Midlands, where there were surviving eucalypts in every plot. The difference could be partly due to the higher maximum fire intensities in the wet eucalypt forests, which have a much higher standing biomass and fallen woody-fuel loads than do the dry eucalypt forests. Using the same methods as in the current study, we estimated mean FRP in the Alps to be 112 MW, compared with 56 MW in the Midlands. Biological factors such as bark thickness and resprouting are also likely to be important in explaining better survival of the species in the dry eucalypt forest (Lawes *et al.* 2011; Clarke *et al.* 2015). In contrast, stimulation of regeneration appeared more pronounced in the Alps than the Midlands, in line with infrequent, stand-replacing fires in the Alps and multiple eucalypt cohorts associated with more frequent, less severe fire in the Midlands. Our results are also consistent with those of a study in 'damp' eucalypt forest showing a more severe impact of fire on the obligate-seeder *Eucalyptus regnans* than the resprouters *E. cypellocarpa* and *E. obliqua* (Ashton and Martin 1996).

A striking feature of the Midlands dry forest was the large number of standing dead trees present. Even in long-unburnt plots, of the standing stems ≥ 5 -cm DBH, on average, 41% were dead (36% of eucalypts, and 57% of acacias). Eucalypt die-back is a well known phenomenon in the Midlands, but many of the suggested causes (such as increased insect attack and possum browsing, changed microclimate, soil compaction and decreased infiltration of water, and nutrient enrichment and grazing of regeneration) apply particularly to scattered paddock trees (Neyland 1999). Neyland (1999) commented that the largest forest remnants are relatively unaffected by tree decline, except on their margins, whereas over 75% of isolated paddock trees had died in the previous four decades. Davidson *et al.* (2007) examined the health of eucalypts in bushland remnants in the Midlands, and found that grazing history was the primary determinant of tree health; sites that

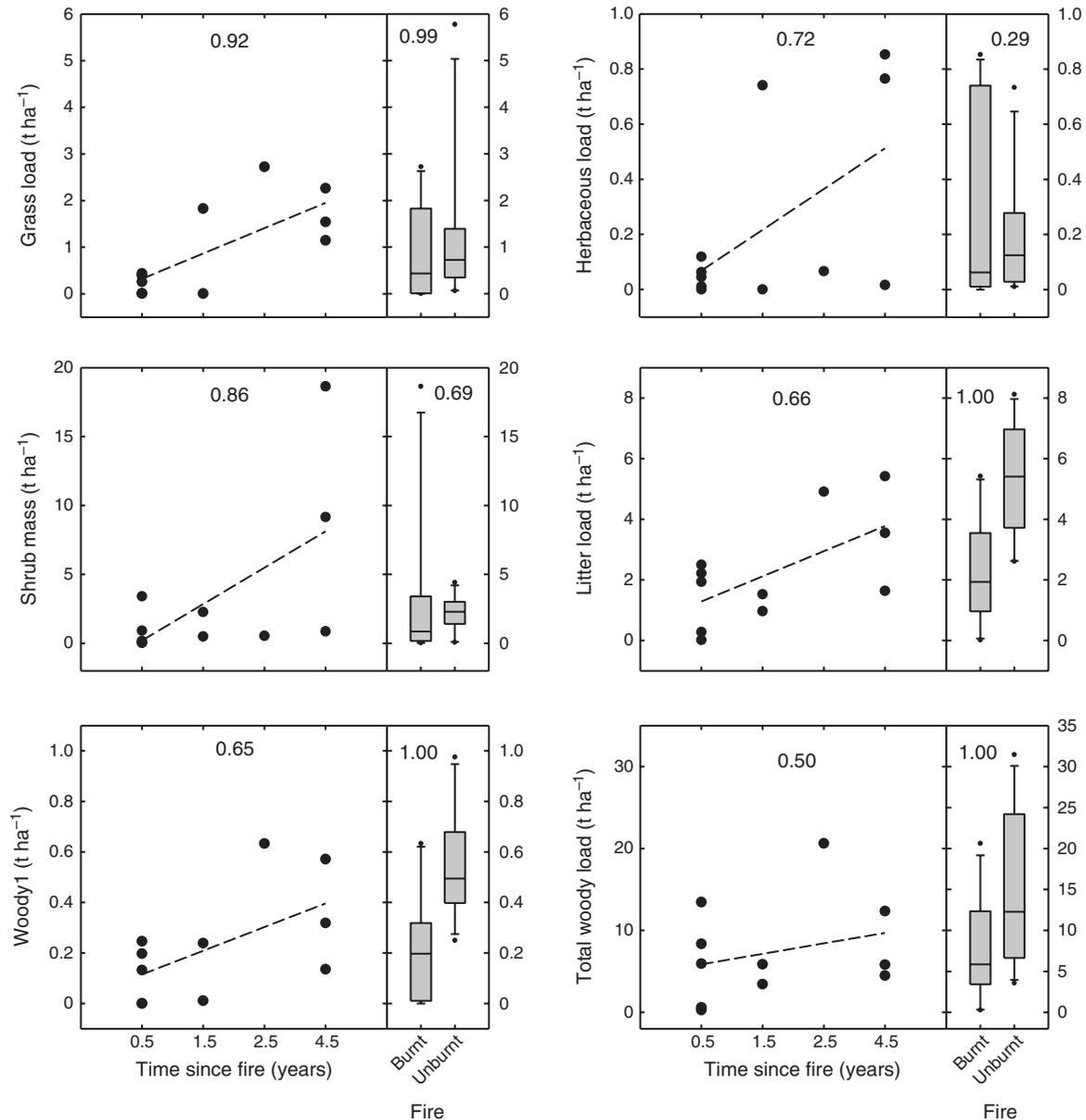


Fig. 4. Fuel loads in relation to time since fire and fire history. The scatterplots with regression lines show the change in fuel loads with time since fire in the burnt plots. The boxplots compare fuel loads in all burnt plots and long-unburnt plots. The numbers are the w^+ values for the terms 'time since fire' (left-hand panels) and 'fire history' (right-hand panels); values >0.73 are considered statistically important. Woody1 is the finest (<6 mm) fraction of woody fuels. Note the different scales on the y -axes.

were ungrazed or only lightly grazed were generally healthy. They concluded that the eucalypt species present in the Midlands could tolerate the drying and warming climate of the previous 30 years. The sites in our study were lightly grazed or ungrazed, and the moderately high live basal area ($25 \text{ m}^2 \text{ ha}^{-1}$) and the presence of eucalypt seedlings and saplings at many unburnt sites suggested that the health of the unburnt remnants was generally satisfactory, despite the large number of dead trees. It is possible that, relative to other areas of Australia, standing dead trees persist for longer in Tasmania because there is less termite activity; unlike in other states, termites do not cause damage to buildings in Tasmania

(Termite Research Centre 2016), and they could also be less active in native forests.

The presence of so many dead stems makes it more difficult to accurately quantify mortality caused by fire. We estimated stem (and whole-plant) mortality caused by fire by comparing densities of live stems (and whole plants) in burnt and unburnt plots. This allowed us to account for other causes of mortality, such as drought, that affect both burnt and unburnt plots. However, we acknowledge that there could be a positive interaction between drought stress and fire that exacerbated the effects of the fire. Considering all species and all stems ≥ 5 cm in DBH, there was an estimated overall stem mortality of 63%

following the fires in dry eucalypt forests in the Midlands (37% for eucalypts and 78% for acacias). Corresponding estimates for fire-induced whole-plant mortality were 44% overall, 25% for eucalypts and 33% for acacias. This value for eucalypts is considerably higher than the 0–5% reported for dry forests in several other studies (Potts 1986; Wardell-Johnson 2000; Croft *et al.* 2007; Pickup *et al.* 2013), and higher than the 15% reported for evergreen eucalypts in a northern Australian savanna as a result of an unusually severe fire (Williams *et al.* 1999). Although fire appeared to have little impact on eucalypt survival at some sites, at two sites, fewer than 10% of eucalypt stems were alive. At three sites, fewer than 40% of whole eucalypt plants were alive, in accord with anecdotal reports of widespread death of resprouter eucalypts after single, high-severity fires (Fairman *et al.* 2015). Hence, although the Midlands dry eucalypt forest was more fire tolerant than the wet eucalypt forest in the Alps, burning substantially reduced the overall densities of live stems and whole plants.

Eucalypts were more tolerant of fire than were acacias. Some live eucalypt stems were found in all burnt plots, but there were no live acacia stems in half of our burnt plots. Not only were eucalypts less likely than acacias to be top-killed in the burnt plots, they were more likely to basally resprout if they were top-killed. In addition, there were no live *Banksia marginata* trees, seedlings or saplings in any burnt plots, suggesting that fire locally eliminated this species. Very low post-fire seedling emergence has been reported elsewhere in this species, apparently related to decomposition or herbivory of buried seed (Williams and Clarke 1997). Similar marked differences in fire-induced mortality among eucalypts, acacias and other species have been reported in tropical eucalypt savannas (Prior *et al.* 2009; Lawes *et al.* 2011; Bond *et al.* 2012), and these have been attributed to the deeply embedded epicormic strands found in eucalypt stems (Burrows 2013). Bark thickness and moisture content could also play a role (Gill and Ashton 1968; Vines 1968; Wardell-Johnson 2000).

Densities of seedlings and saplings were low in unburnt plots, but an order of magnitude higher in burnt plots. The difference was especially pronounced for eucalypts, consistent with findings by Bailey *et al.* (2012) that canopy gaps and ashbeds are important for establishment of eucalypt seedlings in forest and woodland remnants in low-rainfall agricultural areas of Tasmania. Stimulation of eucalypt seedling establishment by fire has also been reported in dry eucalypt forests in other parts of temperate Australia (Yates *et al.* 1996; Clarke and Davison 2001; Hill and French 2004). However, it is noteworthy that there were some eucalypt seedlings and saplings in unburnt plots, in contrast with wet eucalypt forest, where there is virtually no seedling regeneration in the absence of disturbance (Ashton and Attiwill 1994; Gill 2012; Bowman *et al.* 2014). These combined results are in line with infrequent, stand-replacing fires in the wet forest and multiple eucalypt cohorts associated with more frequent, less severe fire in the dry forest.

Dry eucalypt forests have the potential to carry frequent, low-intensity ground fires (Leonard *et al.* 2014). However, dry eucalypt forest in agricultural areas is so fragmented that the number of fires and the area burnt in any one year are usually small, even though an entire individual fragment may get burnt.

For example, Kirkpatrick and Gilfedder (1995) found that only 9% of forest remnants in the Midlands had been burnt within 5 years, and 72% had been unburnt for more than 20 years. In addition, stock grazing has replaced fire as the major ecosystem driver over much of the grassy woodland areas of temperate eastern Australia (Hobbs 2002). The many interactions among fire, grazing and weed invasion remain poorly understood, and are likely to be especially important in these fragmented and highly modified systems (Hobbs 2002; Davidson *et al.* 2007; Lunt *et al.* 2007; Close *et al.* 2009). It has been suggested that more control burning may be required to improve health of dry eucalypt forest (Jurskis 2005; Close *et al.* 2009), as well as to reduce fuel accumulation and risk of wildfire during extreme fire weather (Duff *et al.* 2013; McCaw 2013). The rate of accumulation of grass, herb and litter fuels in our study was $\sim 4.5 \text{ t ha}^{-1}$ in 4.5 years, very similar to the $1 \text{ t ha}^{-1} \text{ year}^{-1}$ reported by Fensham (1992) in Tasmanian grassy forest. This means that fine fuels, which are a major driver of surface fire regimes (Gill and Zylstra 2005), can recover to levels found in long-unburnt forest within 6–7 years (see Fig. 4). However, burning more frequently than every 10 years was weakly correlated with poor tree health in similar forests in the Midlands (Davidson *et al.* 2007). Frequent fire could also increase the number of exotic species and the exotic–native species ratio of Tasmanian lowland forests (Gilfedder and Kirkpatrick 1998). Thus, there is a potential conflict with regard to fire management between biodiversity conservation and hazard reduction in the Midlands, as noted by Morrison *et al.* (1996) for eucalypt woodlands in the Sydney region. Given the fragmented nature of the habitat, it will be critical to preserve some unburnt vegetation to conserve biodiversity (Gill and Williams 1996; Berry *et al.* 2015; Doherty *et al.* 2015). By excluding fire entirely from a fragment, as has often been the practice, there is a risk that it will be burnt entirely in a high-severity fire, as was the case for the burnt sites in our study. Therefore, we advocate using small, patchy fires to reduce fuel loads and the risk of destructive fires, while maintaining long-unburnt habitats within each fragment (Ross *et al.* 2002; Boer *et al.* 2009; Doherty *et al.* 2015; Trauernicht *et al.* 2015). However, we stress that fire-management interventions must be based on adaptive management principles, whereby the ecological effects of fire management are monitored and subsequent burning is modified in light of research findings.

The high stem mortality apparent in some of the Midlands plots demonstrates that fire effects on eucalypts are more complex than indicated by the dichotomy of fire-sensitive obligate seeders versus fire-tolerant resprouters. In addition, there are unanswered questions about what fire frequencies and intensities can be tolerated. Indeed, Fairman *et al.* (2015) considered that like obligate seeder forests, resprouter forests could be converted to non-forest or shrubland if severe wildfires become more frequent. Climate change is likely to increase both fire frequency and severity (Bradstock *et al.* 2012; Enright *et al.* 2015), as well as to reduce seedling regeneration (Mok *et al.* 2012) and slowing tree growth rates, leading to ‘interval squeeze’ in the dry eucalypt forests of south-eastern Australia (Enright *et al.* 2015). Further research needs to explore the interplay among fire intensity, species type (and their traits such as bark thickness and regeneration strategies), antecedent climate, management history and the physical environment. Much of

this research will necessarily be opportunistic, like this study, given the ethical and practical difficulty in experimentally setting high-intensity fires in dry forests. We cannot afford to be complacent about fire in dry eucalypt forests; although, relative to the wet eucalypt forests, they are fire tolerant, their tolerance is not boundless.

Supplementary material

Figures showing a typical remnant forest recovering from fire; details of differences between burnt and unburnt plots in the presence and densities of live seedlings, saplings and trees for some individual species; size-class distributions for various trees >1.5 m tall in unburnt and burnt plots; a summary of results from the fuel survey and a comparison of the impact of fire history and region are available on the Journal's website.

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