# Ageing mallee eucalypt vegetation after fire: insights for successional trajectories in semi-arid mallee ecosystems

*Michael F. Clarke*[A,D], *Sarah C. Avitabile*[A], *Lauren Brown*[A], *Kate E. Callister*[A], *Angie Haslem*[A,B], *Greg J. Holland*[B], *Luke T. Kelly*[B], *Sally A. Kenny*[C], *Dale G. Nimmo*[B], *Lisa M. Spence-Bailey*[A], *Rick S. Taylor*[A], *Simon J. Watson*[B] *and Andrew F. Bennett*[B]

[A]Department of Zoology, La Trobe University, Bundoora, Vic. 3086, Australia.
[B]School of Life and Environmental Sciences, Deakin University, Burwood, Vic. 3125, Australia.
[C]Department of Botany, La Trobe University, Bundoora, Vic. 3086, Australia.
[D]Corresponding author. Email: m.clarke@latrobe.edu.au

**Abstract.** A critical requirement in the ecological management of fire is knowledge of the age-class distribution of the vegetation. Such knowledge is important because it underpins the distribution of ecological features important to plants and animals including retreat sites, food sources and foraging microhabitats. However, in many regions, knowledge of the age-class distribution of vegetation is severely constrained by the limited data available on fire history. Much fire-history mapping is restricted to post-1972 fires, following satellite imagery becoming widely available. To investigate fire history in the semi-arid Murray Mallee region in southern Australia, we developed regression models for six species of mallee eucalypt (*Eucalyptus oleosa* F.Muell. ex. Miq. subsp. *oleosa*, *E. leptophylla* F.Muell. ex. Miq., *E. dumosa* J. Oxley, *E. costata* subsp. *murrayana* L. A. S. Johnson & K. D. Hill, *E. gracilis* F.Muell. and *E. socialis* F.Muell. ex. Miq.) to quantify the relationship between mean stem diameter and stem age (indicated by fire-year) at sites of known time since fire. We then used these models to predict mean stem age, and thus infer fire-year, for sites where the time since fire was not known. Validation of the models with independent data revealed a highly significant correlation between the actual and predicted time since fire ($r = 0.71$, $P < 0.001$, $n = 88$), confirming the utility of this method for ageing stands of mallee eucalypt vegetation. Validation data suggest the models provide a conservative estimate of the age of a site (i.e. they may under-estimate the minimum age of sites >35 years since fire). Nevertheless, this approach enables examination of post-fire chronosequences in semi-arid mallee ecosystems to be extended from 35 years post-fire to over 100 years. The predicted ages identified for mallee stands imply a need for redefining what is meant by 'old-growth' mallee, and challenges current perceptions of an over-abundance of 'long-unburnt' mallee vegetation. Given the strong influence of fire on semi-arid mallee vegetation, this approach offers the potential for a better understanding of long-term successional dynamics and the status of biota in an ecosystem that encompasses more than 250 000 km$^2$ of southern Australia.

## Introduction

Fire is an ecological process that shapes ecosystems throughout the world (Bond *et al*. 2005; Bowman *et al*. 2009). It has profound effects on ecosystem function in arid and semi-arid shrublands (Keeley 1995; Pausas and Bradstock 2007) where the prevailing fire regime strongly influences vegetation composition and structure (Noble *et al*. 1980; Bradstock 1989; Noble and Vines 1993). In turn, the vegetation provides resources for fauna, such as food, cover and nest sites (Bos and Carthew 2003; Brown *et al*. 2009). In semi-arid 'mallee' shrublands of southern Australia, the status of many species of animal is influenced by the fire regime (Cheal *et al*. 1979; Gill 1994). For example, the globally endangered mallee emu-wren (*Stipiturus mallee*) primarily occurs in *Triodia*-dominated mallee vegetation that has not been burnt for at least 15 years (Brown *et al*. 2009). The malleefowl (*Leipoa ocellata*) requires vegetation from which fire has been excluded for at least 10 years, and reaches its maximum breeding capacity at sites at least 40 years post-fire (Benshemesh 1989). Clarke *et al*. (2005) suggested that the endangered black-eared miner (*Manorina melanotis*) is most abundant in mallee vegetation not burnt for between 45 and 60 years.

Because different taxa respond to fire in different ways, many fire managers aim to maintain a mosaic of vegetation representing different post-fire age classes (Brockett *et al*. 2001; Bradstock *et al*. 2005; Parr and Andersen 2006; Burrows 2008). However, this requires knowledge of the proportion of vegetation in different age classes within a land-management unit. Such information forms the necessary basis for determining how much of the unit will be subjected to planned burning, or protected by fire suppression (e.g. Fire Ecology Working Group 2002). A major limitation to fire planning throughout most of Australia is that systematic mapping of fires at a regional scale is possible only from 1972 onwards, when satellite imagery

first became widely available. However, many eucalypt forests and woodlands clearly commenced life well before 1972. In the absence of spatially explicit knowledge of when vegetation was last burnt, areas of unknown fire history are often grouped into a single older cohort (e.g. Letnic *et al.* 2004; Driscoll and Henderson 2008; Lindenmayer *et al.* 2008).

Ecologically important components of habitat for faunal species may take decades, or even centuries, to develop (e.g. 144–194 years to develop hollows in blackbutt, *Eucalyptus pilularis*; Mackowski (1984)). Consequently, grouping all areas of unknown 'older' fire history into a single category may fail to distinguish between ecologically significant age classes. In the case of mallee eucalypt species, which resprout multiple stems from a lignotuber following fire, it is not clear whether stems that have not been burnt for some 38 years (i.e. since 1972) should be regarded, ecologically, as 'old'. Holland (1967 cited in Ogden 1978) reported trees of oil mallee (*Eucalyptus oleosa*) to be 150 years of age. This suggests that at least some mallee eucalypts have the potential to persist close to 4-fold longer than the age at which they may be grouped as 'old', on the basis of the current limits of mapping fire history. It clearly would be advantageous to be able to age different cohorts of eucalypts across a land-management unit. Unfortunately, standard dendrochronological techniques are time consuming, expensive and have met with mixed success (Ogden 1978).

Mallee vegetation has a low canopy (generally <5 m), and so almost all fires (prescribed or wildfire) result in the canopy burning and the death of above-ground stems and branches. New stems then arise post-fire from synchronous resprouting from the lignotubers. Consequently, most mallee stems in a particular location are the consequence of a single fire event, unless the fire was patchy or resprouting was in response to insect attack, drought or frost. This offers the possibility that stem diameter may be correlated with time since fire and that this relationship might be used in a predictive fashion to estimate the age of stands of mallee vegetation. This approach has been applied fruitfully to ageing the stems of snow gum (*E. pauciflora* subsp. *niphophila*), a eucalypt that also exhibits a multi-stemmed, 'mallee' growth form, although in a highly seasonal subalpine environment (Barker 1988; Rumpff *et al.* 2009).

The aim of the present study was to examine the relationship between stem diameter and time since fire as a basis for estimating the potential age of stands of mallee for which the time of last fire is not known.

## Materials and methods

### Study area

Data were collected between July and August 2007 at 835 sites, spread across 28 study mosaics (4-km-diameter circles) located in large reserves (>5000 ha) in tree mallee vegetation of New South Wales, Victoria and South Australia (Fig. 1). The locations of mosaics were selected to capture a broad mixture of time since fire age classes within the mosaic (some mostly recently burnt, some with up to four different age classes, others predominantly unburnt for at least 35 years). Mosaics were a minimum of 2 km apart. The locations of sites within each mosaic (up to 30 sites) were chosen to ensure they were representative of the known time-since-fire age classes and the range of landscape

positions (e.g. swale, dune crest, slope of dune) present within the mosaic. Sites were generally at least 200 m apart, and included vegetation ranging from mallee eucalypts over a heathy understorey, to mallee with a predominantly *Triodia* understorey, to more-open stands of mallee with chenopod understorey.

### Collection of initial field data

Data were collected from a total of 835 survey sites. The year of the last fire (and hence time since fire) was determined from fire-history maps for 485 sites, whereas the remaining 350 sites were known not to have been burnt since 1972 (i.e. the earliest available Landsat imagery used in creating the fire-history maps), but otherwise were of unknown age. At each site, data on stem diameters were collected systematically from trees located within 2 m either side of a 50-m transect (as part of a broader collection of vegetation data at each site). The diameter of all stems (dead or alive) of each mallee eucalypt was measured to the nearest cm at ~30 cm above ground. Stems that were <1 cm in diameter were not measured. At each site, stems of the first 10 trees encountered along the transect were measured. Where there appeared to be more than one age cohort of trees at a site (trees whose stems consistently differed by more than ~2 cm in diameter), the first 10 trees of each cohort encountered were measured. The species of each tree was identified. We obtained estimates of the mean annual rainfall for each site from the Australian Bureau of Meteorology.

### Modelling growth in stem diameters for sites of known fire-age

The mean stem diameter was calculated for each individual tree at each site, using only data for live stems. Analyses of changes in stem diameter with time since fire were restricted to data from sites of known fire age (1–35 years post-fire), and for which preliminary inspection of the size distribution of stems suggested a uniform age class at the site ($n = 282$ sites) (i.e. excluding many sites that may have burned patchily). Note that we refer in the present paper to the age of stems rather than trees, because mallee trees generally are not killed by fire; the lignotuber of the tree survives and generates a new cohort of stems.

The relationship between the mean stem diameter of trees and time since fire was modelled separately for each of six species of mallee eucalypts by using generalised linear models (GLMs). The mean annual rainfall at each site was included as a second predictor variable (in addition to time since fire) to allow for a gradient in aridity across the region, which influences productivity of vegetation (Pausas and Bradstock 2007). For all species, data on stem diameter were slightly right-skewed and transformations were ineffective in improving normality. Inspection of residuals revealed that models using raw data for stem diameter and a Gaussian error distribution were not appropriate. Therefore, models were developed using a Gamma error distribution (with an identity link function). The Gamma distribution is appropriate for continuous, positive, right-skewed data with a large coefficient of variation (Bolker 2008), as was the case here. Fitting the models with a Gamma distribution resulted in normally distributed, homogeneous residuals. Exploratory analysis was undertaken to test whether growth in
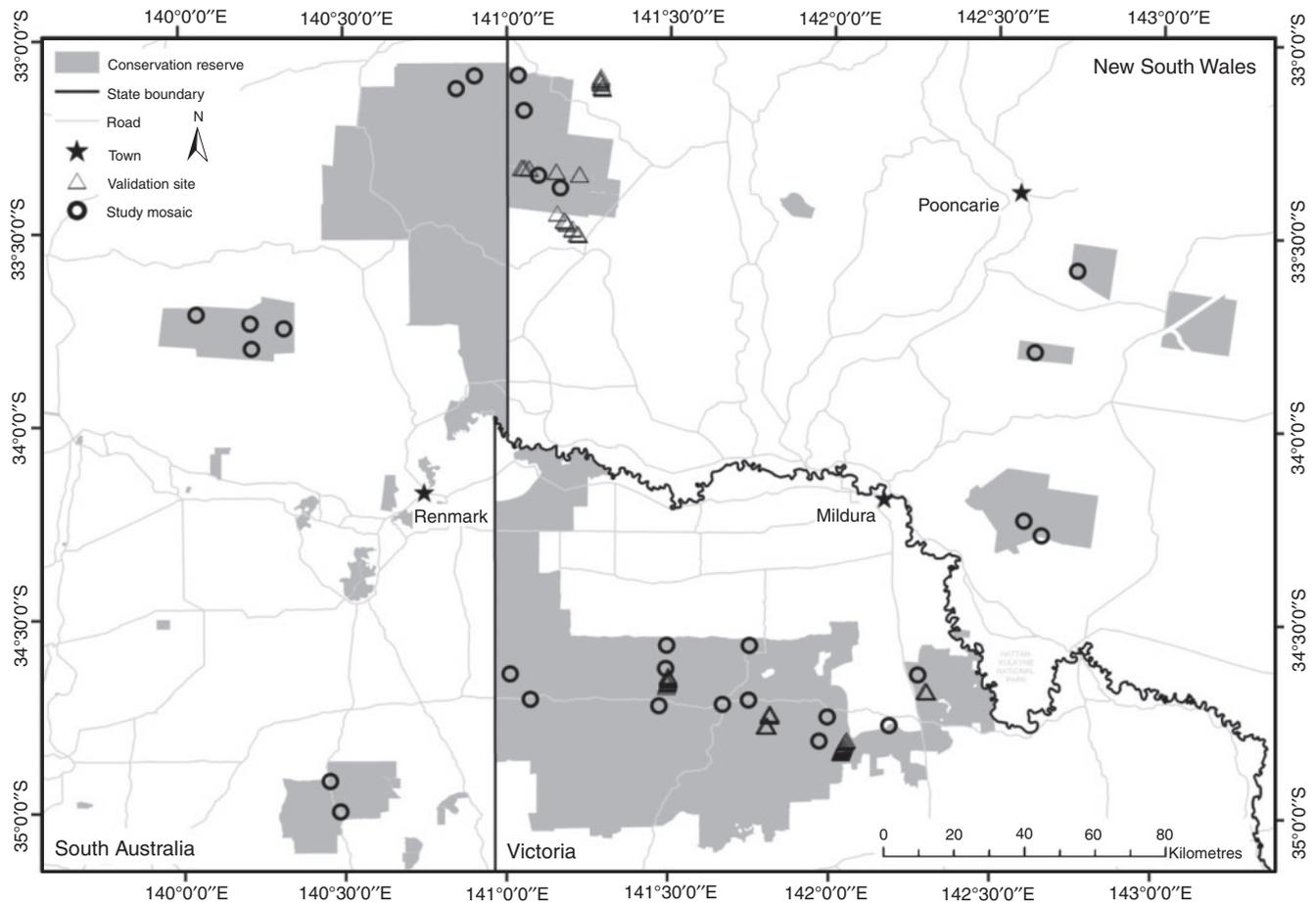
**Fig. 1.** Location of study mosaics and validation sites across the Murray Mallee region, south-eastern Australia.

stem diameter may plateau over time. The following three forms of the variable 'time since fire' were modelled: (1) untransformed, (2) $\log_{10}$ transformed and (3) square-root transformed. Models with the transformed variables did not provide a better fit (i.e. deviance explained) and so the linear models were used. This indicates that growth in mallee eucalypt stems did not begin to plateau over the time period modelled (i.e. up to 35 years). We averaged predictions arising from these species-specific models so as to estimate the time since a site last experienced fire. GLMs were generated with the R statistical program (R Development Core Team 2009).

### Validation of models for predicting post-fire age

To test the ability of this approach to reliably predict the age of mallee eucalypt vegetation beyond the limits of the current fire mapping, we collected additional data in February 2009 at 'validation' sites of known age >35 years since fire. From records of land-management agencies, we identified five areas (across a geographic range of 209 km) where fires had occurred in 1917, 1932, 1951, 1957 and 1964, respectively (i.e. 45–92 years since fire). In each area, multiple sites were located at least 200 m apart to sample spatial variation, including that owing to topographic position. In total, we measured 1894 stems from 636 trees across 88 validation sites, using the field methods outlined above.

We compared the known age of these validation sites with the predictions generated from the GLMs of the mean stem diameter by using correlation coefficients.

### Results

The initial data set comprised measurements of 41 410 stems on 7840 mallee eucalypt trees across 835 sites. Models were developed for six eucalypt species for which samples were adequate (Table 1). A strong linear relationship between stem diameter and time since fire was detected for all six species over the first 35 years of post-fire growth (Table 2, Fig. 2). Even though mean annual rainfall varied by ~100 mm across the study region, it was found to have a significant influence on the stem size of only one species (coefficient $\pm 2 \times$ s.e. did not overlap with zero) where it had a relatively minor influence on stem growth rate (Table 2).

Modelling indicated that individual eucalypt species exhibited different growth rates, with *E. oleosa* subsp. *oleosa* stems growing much faster than those of the other five species, whereas *E. leptophylla*, *E. dumosa* and *E. gracilis* exhibited the slowest growth rates (Fig. 2).

Stem diameter data collected at the additional 88 validation sites of known age of $\geq 45$ years (but not used in the model generation process) were used to test the ability of the models to

**Table 1.    Summary of the numbers of sites of known fire-age, trees and stems used in modelling the relationship between stem diameter and time since fire for six species of mallee eucalypts**

The number of stems does not include stems <1-cm diameter or dead stems

| Species | No. of sites | No. of trees | No. of stems |
|---|---|---|---|
| *E. socialis* | 137 | 266 | 1625 |
| *E. dumosa* | 150 | 386 | 2307 |
| *E. costata* subsp. *murrayana* | 67 | 210 | 912 |
| *E. leptophylla* | 83 | 204 | 1086 |
| *E. oleosa* subsp. *oleosa* | 39 | 93 | 527 |
| *E. gracilis* | 47 | 99 | 550 |
| Total | 282 | 1258 | 7007 |

predict the time since fire. For all six species, the age of stems predicted by using the species-specific models was significantly correlated with the known time since fire for validation sites (Pearson correlation, $r = 0.57–0.79$) (Table 3). To account for differences in species-specific growth rates, while maximising the information used to generate an estimate of the time since fire for each site, we calculated a mean of the predictions from species-specific models for all species at the site. There was a highly significant correlation ($r = 0.71$, $P < 0.001$) between the predicted and actual time since fire at the validation sites, by using this method.

Comparison of the predicted and actual time since fire indicated that the models typically underestimated the time since fire for a site by an average of $23\% \pm 2.1$ (s.e.) (Fig. 3). This suggests that beyond 35 years, the growth rates of stem diameters of mallee trees in the region may slow as the stem ages. The initial models we built to test for non-linear growth of stem diameter with time (i.e. by using square root or log-transformations of diameter – see Materials and methods) did not perform better in predicting the age of validation sites. For five of the six species, predictions from the linear models were more strongly correlated with the actual age of validation sites, than were predictions from models with transformed variables.

Nevertheless, to further examine the possibility that growth rate slows in later years, we generated six new species-specific models on the basis of the combined data from known-age sites (<35 years of age) plus the validation sites (Appendix 1, Table 1). For four of six species, models that used a square-root transformation of time since fire provided the strongest fit, whereas for two species, the linear model was the strongest. We re-estimated the age of sites of unknown age by using an average of the predictions arising from the best new model for each species. The predicted ages of sites when generated by the original models (using data only from sites <35 years of age) and the new models (sites 0–94 years of age) were highly correlated (Appendix 1, Fig. 1); within the bounds of the data from which the models were built (~100 years), the Pearson correlation coefficient $r = 0.94$ ($P < 0.001$). However, predictions of the ages of sites with larger stems (e.g. >12-cm diameter) arising from the new models are likely to have considerable uncertainty; minor changes in stem diameter equate to large changes in the predicted age because of the flattening of the curve resulting from the square-root transformation of age (years).

We based our predictions of the age of sites of unknown age ($n = 346$) on the more conservative original linear models, because (1) these models have been validated and (2) their predictions are highly correlated with those of the alternative models (which have not been validated). The predicted ages were determined by calculating the average of the predictions of time since fire for each tree species at each site (by using the species-specific models in Table 2). Estimates could not be generated for four sites where there was uncertainty over the species of eucalypt present.

The 346 sites of unknown fire history were spread across the majority of the 28 sampling mosaics and were chosen with no knowledge of their likely age other than that they had not been burnt since 1972. If one assumes they are a representative sample of the distribution of pre-1972 age classes in the region, a comparison can be made of the distributions of age classes generated with, and without, the age estimates arising from our models. The age-class structure generated using fire mapping based on Landsat imagery is profoundly truncated (Fig. 4*a*) and suggests a predominance of a single age class across the region (i.e. >35 years since fire).

By contrast, our estimate of the likely age structure of 346 sites falling within the single >35 years age class shows there is not a predominance of a single age class, rather a range of different age classes. This range includes some rare age classes incorporating sites that have remained unburnt for more than 160 years (Fig. 4*b*).

## Discussion

These analyses have demonstrated a strong relationship between the mean stem diameter at a site and time since fire

**Table 2.    Coefficient estimates and standard errors (s.e.) for models of the change in mean stem diameter (cm) in relation to time since fire (years) for six species of mallee eucalypts in the Murray Mallee region**

$D^2$ values represent the percentage of deviance explained by the overall model

| Species | Coefficients for predictor variables | | | | | | $D^2$ |
|---|---|---|---|---|---|---|---|
| | (Intercept) | | Time since fire (years) | | Mean annual rainfall (mm) | | |
| | Estimate | s.e. | Estimate | s.e. | Estimate | s.e. | |
| *E. socialis* | 1.558 | 0.468 | 0.138 | 0.006 | −0.0010 | 0.0019 | 79.5 |
| *E. dumosa* | 1.682 | 0.583 | 0.111 | 0.007 | −0.0016 | 0.0022 | 69.5 |
| *E. costata* subsp. *murrayana* | 1.426 | 0.847 | 0.142 | 0.010 | −0.0009 | 0.0031 | 69.4 |
| *E. leptophylla* | 1.207 | 0.717 | 0.106 | 0.008 | 0.0006 | 0.0028 | 64.6 |
| *E. oleosa* subsp. *oleosa* | 4.495 | 1.482 | 0.194 | 0.018 | −0.0141 | 0.0064 | 79.3 |
| *E. gracilis* | 3.748 | 1.332 | 0.115 | 0.013 | −0.0099 | 0.0052 | 52.2 |
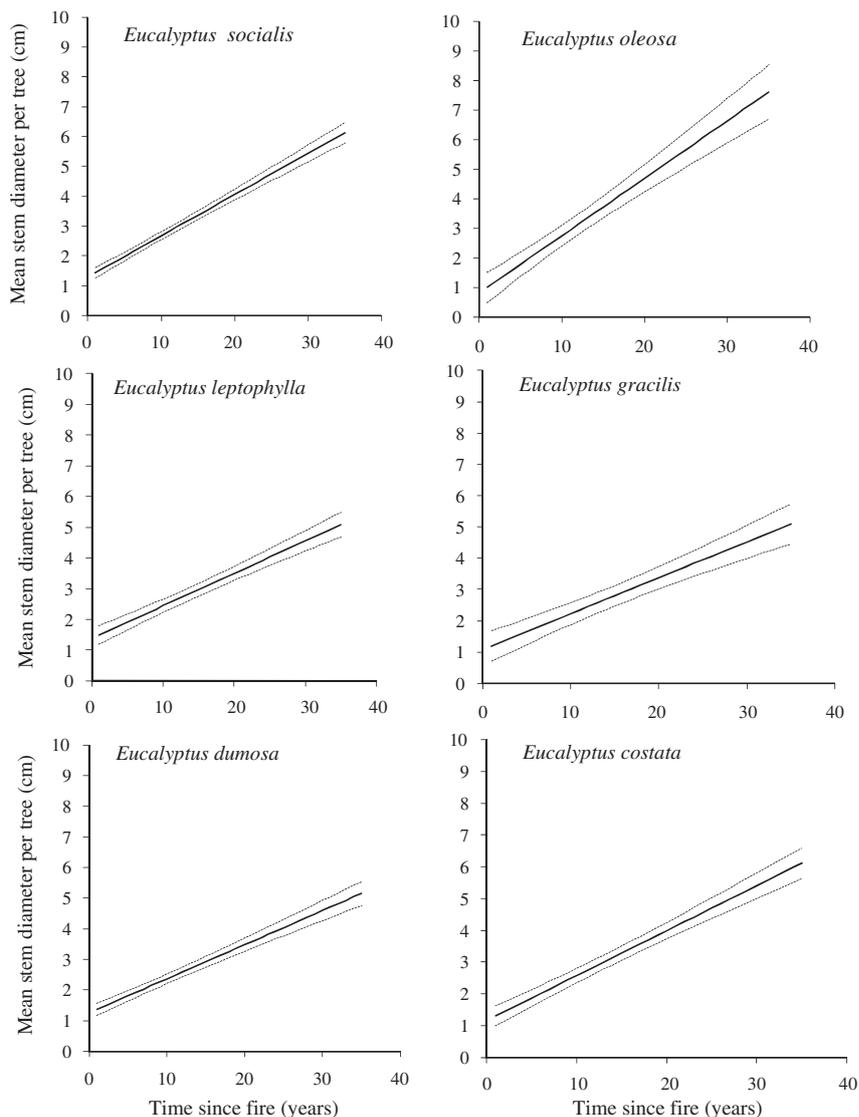
**Fig. 2.** Species-specific models of changes in the mean stem diameter for mallee eucalypts in relation to known time (years) since fire during the first 35 years post-fire (dotted lines indicate 95% confidence intervals).

**Table 3. Correlations between the predicted and actual time since fire for 88 validation sites in mallee vegetation**

Correlation coefficients are presented for each of the individual species models, and for the average of the predicted ages for each species that occurred at the site. The number of stems does not include stems <1-cm diameter

| Species | No. of sites | No. of trees | No. of stems | Pearson correlation ($r$) | $P$ |
|---|---|---|---|---|---|
| *E. socialis* | 42 | 104 | 329 | 0.65 | <0.001 |
| *E. dumosa* | 63 | 232 | 687 | 0.72 | <0.001 |
| *E. costata* | 21 | 95 | 261 | 0.79 | <0.001 |
| *E. leptophylla* | 28 | 72 | 208 | 0.60 | <0.001 |
| *E. oleosa* | 20 | 86 | 259 | 0.55 | 0.011 |
| *E. gracilis* | 14 | 47 | 150 | 0.57 | 0.033 |
| Average for all species present at a site | 88 | 636 | 1894 | 0.71 | <0.001 |

(i.e. the age of the stem) for six species of mallee eucalypts in the Murray Mallee region. Application of the present technique offers a cheaper and more efficient method of estimating the age of mallee vegetation, particularly in areas of unknown fire history, than standard dendrochronological techniques (e.g. Holland 1969). The relationship between the mean stem diameter and time since fire is strong, particularly given potential sources of variation that could arise. First, the potentially localised nature of rainfall events in the semi-arid region could add 'noise' to the growth rates of stems among sites across the region, possibly obscuring clear patterns. However, we found that the mean annual rainfall was of minor importance in predicting growth rates. Second, we assumed that all stems on a site arose after a common fire event. It is unlikely that this is always the case, as an occasional stem may survive a fire and others may arise many years post-fire in response to some other stimulus such as damage by wind or herbivores. Third, we had no way of
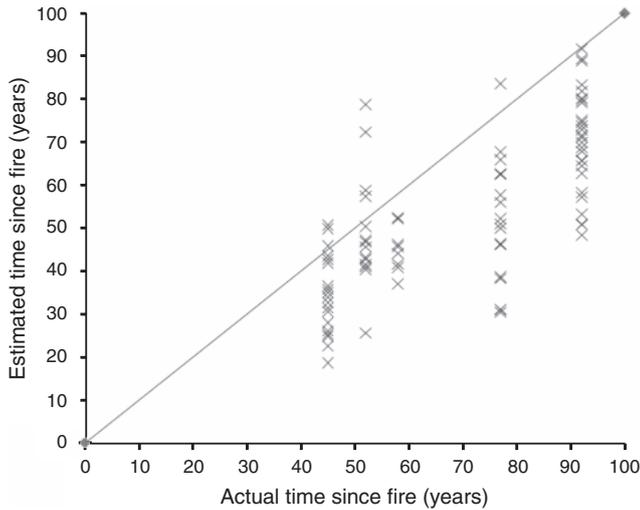
**Fig. 3.** The relationship between the predicted and actual time (years) since fire for validation sites ($n = 88$). The predicted time was based on averages from species-specific models for eucalypt species at each site. The solid line depicts where a 1 : 1 correspondence between the predicted and actual ages of sites would fall.

controlling for variation in the size of the lignotuber from which different trees were sprouting stems. If larger lignotubers have access to more moisture or nutrients, then one might expect this to introduce further variance into growth rates among trees at the same site. Our approach of averaging the age predictions derived from species-specific models, for each species present at a site, and each of these species models being based on the averaged stem diameter for multiple trees at a site, probably reduced the influence of some of this variability.

Examination of interspecific differences in growth rates was not a primary goal of the present study. However, the faster growth rates of *E. oleosa* than, for example, *E. costata*, may well reflect differences in growth form and position in the landscape. *E. oleosa* more commonly occurs in the heavier soils in the swales and *E. costata* more commonly on sandy dune slopes and crests (Sparrow 1989, 1990; Parkes and Cheal 1990). We incorporated this interspecific variation when making predictions of time since fire for sites of unknown age, by calculating the average of the predicted ages for each species at a site. An alternative, potentially simpler, approach could be to model and make predictions on the basis of all stems at a site regardless of tree species. We tested this latter approach (see Appendix – Table 2) and found that although
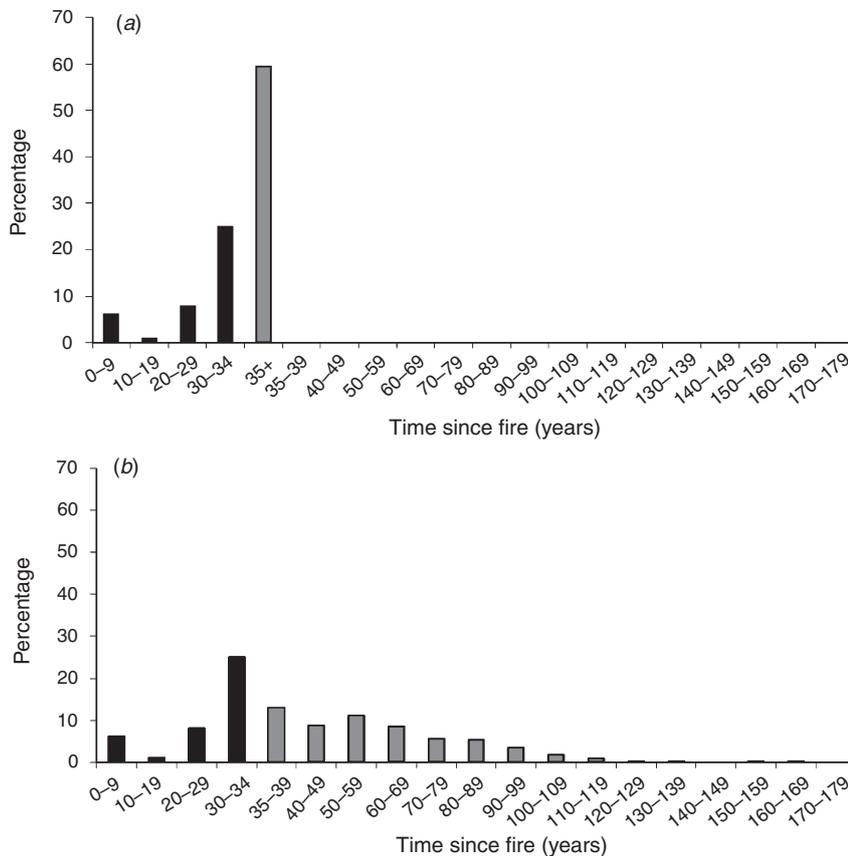


**Fig. 4.** (*a*) Percentage of tree mallee vegetation in the Murray Mallee region of Victoria, NSW and South Australia *known* to fall into particular age classes for time since fire. Percentages were calculated from GIS maps of the region's fire history, derived from all available Landsat imagery for the region (S. C. Avitabile, K. E. Callister, A. Haslem, L. T. Kelly, D. G. Nimmo, S. J. Watson, S. A. Kenny, R. S. Taylor, L. M. Spence-Bailey, A. F. Bennett and M. F. Clarke, unpubl. data.). (*b*) Percentage of tree mallee vegetation in the tri-state region *estimated* to fall into particular age-classes for time since fire. Darker bars depict percentages calculated from GIS maps of the region's fire history (as above). Lighter bars depict the distribution of the >35 years age class, on the basis of the assumption that it is proportional to the age-class distribution of 346 sites whose age was predicted using the stem diameter models.

it was less effective than the species-specific models, it still performed moderately well. For example, for sites of known age of <35 years, a linear model based on mean diameter of all stems at a site (regardless of species) accounted for 52% of variation in the data (Appendix 1), compared with a mean of 69% (range 52–79%) for the species-specific models of the same dataset (Table 2).

Our validated models assumed a linear increase in mean stem diameter with age. This contrasts with much work in dendrochronology that has revealed that the rings on a tree often decrease in width as the tree ages; that is, the rate of growth slows over time (Ogden 1978). However, Barker's (1988) study of *E. pauciflora* showed no sign of the rate of growth of stems slowing before 100 years of age, and possibly before 300 years (although the data are sparse). By assuming a linear increase in the mean stem diameter with age, our models generate conservative estimates of stem age and underestimate the likely age of sites as a consequence. Nevertheless, the models we created by using all available data (Appendix 1) suggest non-linear (slowing) growth rates at older ages for some species. However, these models require validation with independent data, particularly from sites in the older age ranges (e.g. >100 years post-fire).

Although it is clear that mallee vegetation can attain post-fire ages well in excess of 100 years, we believe caution is required in making and using predictions in these older age classes. Linear models of age *v.* mean stem diameter may underestimate such ages, whereas models in which age is transformed (square-root transformation) will have large confidence limits because estimates of the age of sites with larger stems vary greatly, with minor changes in mean stem diameter. At the two sites of greatest predicted age in the present study (tentatively ~160 years), the diameter of the five largest stems ranged from 25 to 40 cm and 30 to 50 cm, respectively. Although this estimate of site age cannot be interpreted as a maximum age of mallee stems in the region, it is consistent with the maximum estimated ages reported by Holland (1967, cited in Ogden 1978) of 150 years for *E. oleosa*, and by Ogden (1978) of 300 years for an *E. pauciflora*, as indicated by a ring count. Even larger stems were encountered in the study region, particularly along roadsides in otherwise cleared landscapes (M. Clarke, pers. obs.). After allowing for the likely superior soils in the cultivated regions (Land Conservation Council 1987) and the possibility of slightly faster growth rates, these roadside trees are likely to be very old and contain resources (e.g. hollows) less common in the younger vegetation in conservation reserves. Note that the models presented here are not appropriate for estimating the age of individual stems of mallee eucalypts. Rather, they are most appropriately used to predict the age of mallee vegetation at a site because they are based on the mean stem diameter of all trees of a particular species at a site.

A primary goal in fire ecology is to understand how the distribution and abundances of organisms change with time following a fire (Friend 1993; Fox *et al.* 2003; Torre and Diaz 2004), and then to understand the processes that drive those changes. Many such analyses have been constrained by the limited fire history available for most sites (rarely >40 years before present) (e.g. Fire Ecology Working Group 2002), thus restricting the focus to shorter-term changes in ecosystems following fire (Clarke 2008). Our approach makes it possible to determine the time since fire efficiently for sites in mallee shrubland up to at least 100 years post-fire, and therefore to identify ecological changes that may occur more slowly, or much later, in successional pathways. Only when we have a more complete picture of a successional pattern will we be able to understand the key ecological processes that drive changes during succession (Lunt 2002). This approach will allow a more precise quantification of the age-class preferences of many species of the mallee fauna, for example, the malleefowl (Benshemesh 1989) and black-eared miner (Clarke *et al.* 2005), that previously have simply been classified as favouring vegetation greater than 40 years of age. It will also enable a more comprehensive examination of the time periods over which key ecological resources used by faunal species (e.g. litter layers, *Triodia* hummocks, tree hollows) develop following a fire (A. Haslem, L. T. Kelly, D. G. Nimmo, S. J. Watson, S. A. Kenny, R. S. Taylor, S. C. Avitabile, K. E. Callister, L. M. Spence-Bailey, A. F. Bennett and M.F. Clarke, unpubl. data).

These analyses also challenge current understanding of the age-class distribution of mallee vegetation across the study region (e.g. Fire Ecology Working Group 2002). In contrast to a perception that conservation reserves in the region currently contain a disproportionate abundance of 'older' mallee vegetation (>35 years post-fire, Fig. 4a), the present results suggest a more diverse distribution of sites in this age category, and that mallee vegetation older than 100 years of age is quite rare. Given that several threatened species in mallee ecosystems are reported to prefer long-unburnt habitats (e.g. Emison and Bren 1989; Bradstock and Cohn 2002; Clarke 2005), spatially explicit maps showing the location and sizes of stands of mallee vegetation of different age classes, including those up to an estimated 100 years post-fire, would be a valuable resource for management. We are currently developing such a map for the Murray Mallee region in south-eastern Australia by using our study sites and their predicted ages as 'training sites' for a modelling analysis using remote-sensing imagery (P. Griffioen, unpubl. data).

This simple approach to estimating the age of mallee vegetation at sites offers great potential for studying long-term successional changes in mallee ecosystems. This approach could also be applied in other states and in other contexts, with appropriate calibration for local species and climatic variation. Given that mallee shrublands and woodlands occupy some $250\,420\,km^2$ in southern Australia (National Land and Water Resources Audit 2001), there is scope for greatly enhancing our current understanding of ecosystem function across a significant portion of the continent.

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**Appendix 1.   Coefficient estimates and standard errors (s.e.) for models of the change in mean stem diameter (cm) per site in relation to time since fire for six species of mallee eucalypts in the Murray Mallee region**

Models are based on data from sites of known time since fire ranging from 0 to 94 years. Alternative models are presented for which time (years) is modelled in linear form and square-root transformed (sqr). $D^2$ = the percentage of deviance explained by the model

| Species | (Intercept) Estimate | (Intercept) s.e. | Years since last burnt Estimate | Years since last burnt s.e. | Mean annual rainfall (mm) Estimate | Mean annual rainfall (mm) s.e. | $D^2$ |
|---|---|---|---|---|---|---|---|
| *E. socialis* (linear) | 1.212 | 0.506 | 0.121 | 0.005 | 0.001 | 0.002 | 80.2 |
| *E. socialis* (sqr)[A] | 1.960 | 0.460 | 0.961 | 0.035 | −0.007 | 0.002 | 82.0 |
| *E. dumosa* (linear)[A] | 1.690 | 0.546 | 0.102 | 0.005 | −0.001 | 0.002 | 78.7 |
| *E. dumosa* (sqr) | 1.962 | 0.542 | 0.841 | 0.037 | −0.007 | 0.002 | 76.4 |
| *E. costata* subsp. *murrayana* (linear) | 1.140 | 0.908 | 0.118 | 0.008 | 0.001 | 0.003 | 68.8 |
| *E. costata* subsp. *murrayana* (sqr)[A] | 1.088 | 0.780 | 0.961 | 0.051 | −0.004 | 0.003 | 73.7 |
| *E. leptophylla* (linear) | 1.092 | 0.742 | 0.096 | 0.007 | 0.001 | 0.003 | 66.1 |
| *E. leptophylla* (sqr)[A] | 1.861 | 0.719 | 0.796 | 0.050 | −0.006 | 0.003 | 66.8 |
| *E. oleosa* (linear) | 2.373 | 1.838 | 0.134 | 0.014 | −0.004 | 0.008 | 67.0 |
| *E. oleosa* (sqr)[A] | 5.792 | 1.385 | 1.278 | 0.090 | −0.025 | 0.006 | 80.0 |
| *E. gracilis* (linear)[A] | 3.530 | 1.219 | 0.109 | 0.009 | −0.009 | 0.005 | 71.2 |
| *E. gracilis* (sqr) | 4.693 | 1.189 | 0.917 | 0.071 | −0.018 | 0.005 | 69.1 |

[A]Model that provides best fit to data for each species.

**Appendix 2.   Coefficient estimates and standard errors (s.e.) for models of the change in mean stem diameter (cm) per site in relation to time since fire for mallee eucalypts in the Murray Mallee region**

Models are based on data recorded from all mallee eucalypts at a site, regardless of species. Models are presented for datasets based on sites of <35 years since fire and 0–94 years since fire, respectively. In each case, alternative models are presented for which time (years) is modelled in linear form and square-root transformed (sqr). $D^2$ values represent the percentage of deviance explained by the overall model

| Dataset | (Intercept) Estimate | (Intercept) s.e. | Years since last burnt Estimate | Years since last burnt s.e. | Mean annual rainfall (mm) Estimate | Mean annual rainfall (mm) s.e. | $D^2$ |
|---|---|---|---|---|---|---|---|
| Sites <35 years since fire (linear)[A] | 2.292 | 0.805 | 0.122 | 0.007 | −0.003 | 0.003 | 0.520 |
| Sites <35 years since fire (sqr) | 1.183 | 0.879 | 0.884 | 0.053 | −0.004 | 0.003 | 0.486 |
| Sites 0–94 years since fire (linear)[A] | 3.272 | 0.754 | 0.099 | 0.004 | −0.005 | 0.003 | 0.661 |
| Sites 0–94 years since fire (sqr) | 1.326 | 0.754 | 0.915 | 0.036 | −0.005 | 0.002 | 0.660 |

[A]Model that provides best fit to data for each dataset.
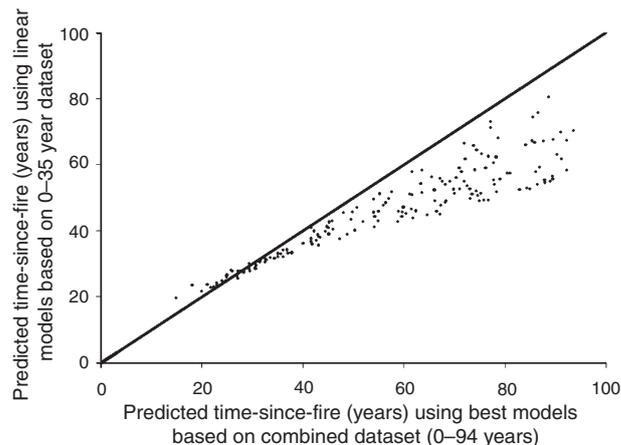


**Appendix 3.**   Relationship between the predictions of two methods of generating time-since-fire predictions by using (1) the average across species of the best linear or square-root species-specific models from the combined dataset of 0–94 years (*x*-axis) and (2) the average across-species time-since-fire predictions from the linear species-specific models built only on 0–35-year data (*y*-axis) (Pearson's correlation ($r$) = 0.94, $P < 0.001$). The solid line depicts where a 1 : 1 correspondence between predicted ages of sites determined by each model would fall.