Reproductive trajectories over decadal time-spans after fire for eight obligate-seeder shrub species in south-eastern Australia

Annette M. Muir[A,D], *Peter A. Vesk*[B] *and Graham Hepworth*[C]

[A]Arthur Rylah Institute for Environmental Research, Department of Environment and Primary Industries
(formerly Department of Sustainability and Environment), PO Box 137, Heidelberg, Vic. 3084, Australia.
[B]Australian Research Council Centre of Excellence in Environmental Decisions, School of Botany,
The University of Melbourne, Parkville, Vic. 3010, Australia.
[C]Statistical Consulting Centre, Department of Mathematics and Statistics, The University of Melbourne,
Parkville, Vic. 3010, Australia.
[D]Corresponding author. Email: annette.muir@depi.vic.gov.au

Abstract. Intervals between fires are critical for the persistence of obligate-seeding shrubs, and are often used in planning fires for fuel reduction and biodiversity conservation in fire-prone ecosystems worldwide. Yet information about the trajectories of reproductive performance for such species is limited and information is often qualitative. To test existing assumptions about reproductive maturity periods for eight obligate-seeding shrubs (with both canopy and soil seedbanks) in foothill forests of south-eastern Australia, we used a chronosequence approach, with sites from 2 years to >40 years post-fire. Quantitative measurements of flowering and fruiting were used to fit models of reproductive response in relation to time-since-fire for each species. Inferred reproductive maturity for each species, based on modelled times to reach 80% of maximum flower production, varied from 5 to 18 years post-fire. For a subset of three species, models predicted 80% maximum seed production occurring 1–7 years later than flowering. Our results confirmed or extended assumptions about post-fire reproductive maturity for these species, and provided a basis for improved incorporation of plant life-history in ecological fire planning. We infer that increased fire frequency makes one of our study taxa, *Banksia spinulosa* var. *cunninghamii* (Sieber ex Rchb.) A.S.George, vulnerable to decline because of its long reproductive maturity period and serotinous seed storage.

Additional keywords: *Banksia*, fire interval, fire planning, flower production, plant functional type, response curve, seed production.

Received 23 May 2014, accepted 30 July 2014, published online 24 September 2014

Introduction

Fire is important in shaping the species composition and vegetation structure of many ecosystems worldwide (Bond and Keeley 2005), especially open forests in south-eastern Australia (Gill 2012). The response of plants and plant communities to fire depends on the local fire regime and the functional traits of individual plant species (Keith 2012). A fire regime is the sequence of fire intervals, intensities and seasons (Gill 1975) at any point in the landscape (Gill and Catling 2002), and this sequence affects plant survival and recruitment (Whelan *et al.* 2002). The spatial variability of fire regimes also creates mosaics of different vegetation types comprising species with different life history characteristics responsive to fire (Clark *et al.* 2002). Most studies examining the effects of fire regimes on plants have concentrated on fire intervals, because other aspects such as fire intensity are difficult to determine (Gill and Catling 2002).

Species most affected by fire interval are obligate-seeder species, which are killed by fire and persist after fire only as

seed (Pausas *et al.* 2004). Obligate seeders that have had their seed reserves exhausted by disturbance but require long periods to reach reproductive maturity are most vulnerable to repeated frequent fires (Gill and Catling 2002; Bradstock and Kenny 2003). Conversely, intervals between infrequent fires can exceed the lifespan of existing plants or seedbanks of some species (Gill and Catling 2002; Bradstock and Kenny 2003). Fire intensity also affects the survival of adult plants, and many seeds require the direct effects of heat and smoke to germinate (Bell 1999). Additional factors, such as herbivory and weather conditions, can affect recruitment success following fire (Whelan *et al.* 2002). By contrast, resprouting species persist in a vegetative form after fire and can survive more frequent fire disturbance (Pausas *et al.* 2004).

Plant species can be grouped into functional types, on the basis of shared traits or responses to environment or disturbance (Reich *et al.* 2003; Pausas *et al.* 2004; Keith *et al.* 2007). Plant functional-type schemes have been used in fire-prone

ecosystems to hypothesise likely responses of vegetation communities to fire regimes, based on the attributes of their component species (e.g. Menges 2007; Pausas and Lloret 2007; van Wilgen *et al*. 2010; Cheal 2010). The 'plant vital attributes' scheme (Noble and Slatyer 1980; Noble and Gitay 1996) is one plant functional type scheme commonly used in studies of plant responses to fire in Australia, South Africa and USA (e.g. Bradstock and Kenny 2003; Keeley *et al*. 2006; Keith *et al*. 2007; Kraaij *et al*. 2013). Vital attributes refer to the persistence of propagules, mortality of plants and reproductive capacity of surviving plants, patterns of recruitment owing to competition or establishment prerequisites, and times to reach reproductive maturity and for all plants and propagules to die out in a site (Noble and Slatyer 1980; Whelan *et al*. 2002). These attributes are frequently used by Australian land management agencies in planning fire frequencies to optimise the conservation of vascular plant diversity (Fire Ecology Working Group 2004; Bradstock *et al*. 2012). However, the application of the vital-attribute approach in fire planning often relies on subjective information on plant species (DSE 2010*e*) and there have been few empirical studies (Keith 2012).

To address this uncertainty surrounding several of the vital attributes of obligate-seeding shrubs in fire-prone areas of south-eastern Australia, we tested the existing hypothesised reproductive maturity periods for eight obligate-seeder shrubs with canopy and soil seedbanks. We developed empirical models of reproductive characteristics (flowers for each species, fruit for three species) in relation to decadal time-spans after fire, derived predictions from these models about the relationships between time-since-fire and thresholds of reproduction, and then compared these to the existing assumptions about the species' juvenile periods. Implications of these results for planning fire intervals to maintain plant populations are discussed.

Materials and methods

Study area and sites selection

We sampled open forests on the southern side of the Great Dividing Range in the state of Victoria. Target forest types on more exposed slopes were Lowland Forest and Shrubby Foothill Forest, which have eucalypt canopies with an understorey of narrow-leaved shrubs, grasses and herbs (DSE 2011). On more sheltered slopes, Damp Forest was targeted, which has a eucalypt canopy with a tall layer of broad-leaved shrubs, and a ground layer of grasses, herbs and ferns (DSE 2011). Sites were located in two clusters, one in Dandenong Ranges National Park and the other in Bunyip State Park/Kurth Kiln Regional Park. The climate for the two clusters of sites is similar, and is characterised by wet cold winters and dry warm summers. Long-term mean annual rainfall is 1200 mm, the highest rainfall month being August and lowest February (Bureau of Meteorology 2011). Long-term mean monthly temperatures are highest in February (23.3°C) and lowest in July (5.3°C) (Bureau of Meteorology 2011). Study sites were on gentle to moderate slopes, on igneous geology (Parks Victoria 2011*a*, 2011*b*), at elevations of 220–410 m above sea level.

A space-for-time substitution approach was used to assess responses of species to fire over decadal periods. The study area was stratified using spatial databases maintained by the Victorian Department of Sustainability and Environment (DSE 2010*a*, 2010*b*, 2010*c*) to determine target vegetation types and fire histories and to exclude areas subjected to logging in the past 20 years. The study area was further confined to 'Asset Protection' and 'Strategic Wildfire Moderation' fire-management zones (DSE 2006) because these areas have a high likelihood of complete burn coverage. Sites were selected within the following classes representing time since the last fire: 0–3 years, 4–10 years, 11–20 years, 21–40 years and 41 + years. These classes were informed by the timing of growth stages identified by Cheal (2010) for the three target forest types in relation to fire, and undefined after 40 years because of the limits of DSE fire records. Areas were identified with all fire-age-class combinations for each target forest type located within close proximity and with similar environmental conditions (water availability, sun exposure, geographic spread, elevation and aspect) for each species, so as not to confound the responses of the plants to fire with their response to these factors.

Species selection

Shrubs were selected for study because they are prominent in forest communities and are easily identified, and obligate seeders were selected because they are most susceptible to local extinctions from inappropriate fire regimes. These species are killed by fire, recruitment is by seed only, and timing of fires can exhaust their seed supplies before plants reach reproductive maturity. Common species were chosen to enable a good representation of the typical vegetation communities (Cornelissen *et al*. 2003), and because they were detectable in most fire-age classes.

Potential species for the study were identified from the Victorian database of vascular flora (DSE 2010*d*) and subsequent field searches, to identify those species with adequate representation at a range of fire-age sites. Species were selected and categorised according to their mode of persistence following fire (obligate seeder), seedbank type (soil or canopy), length of juvenile period (germination to re-establishment of seedbank adequate to replace parent plants) and individual plant lifespan (Table 1). These factors have been used in classification schemes that predict the response of plants to fire (Whelan *et al*. 2002). Plant functional-type categories used in the study have been adapted from Keith *et al*. (2007), which is a simplified version of the vital-attribute scheme of Noble and Slatyer (1980). Estimates of the responses of individual species in these categories were derived from expert opinion about Victorian plant vital attributes (DSE 2010*e*).

Sampling design

The number of individuals sampled was a balance between obtaining enough replicates to capture the variability of the traits of interest and sampling enough species of interest (Cornelissen *et al*. 2003). We followed Cornelissen *et al*. (2003), who recommended that at least 10 individuals at each site should be measured for plant height (which is more variable than many other plant traits). Individuals were selected using a transect method, modified from Cornelissen *et al*. (2003). Within each fire-age site, a 100-m transect was located where the target species were observed, at least 20 m from a road or track, and

Table 1. Study species grouped into plant functional types
Modified from Keith *et al*. (2007) and DSE (2010*e*) (referred to by their specific name only in the rest of this article)

Seedbank	Juvenile period	Individual plant lifespan	Species and authority
Persistent soil	Moderate (~5 years)	Moderate (<50 years)	*Acacia verticillata* subsp. *cephalantha* (L'Her.) (F.Muell.)
Persistent soil	Moderate (~5 years)	Moderate (<50 years)	*Olearia lirata* (Sims) Hutch.
Persistent soil	Moderate (~5 years)	Moderate (<50 years)	*Pultenaea scabra* R.Br.
Persistent soil	Moderate (~5 years)	Long (>50 years)	*Acacia oxycedrus* Sieber ex DC.
Persistent soil	Long (~10 years)	Long (>50 years)	*Pomaderris aspera* Sieber ex DC.
Persistent soil	Long (~10 years)	Long (>50 years)	*Prostanthera lasianthos* var. *lasianthos* Labill.
Canopy	Moderate (~5 years)	Long (>50 years)	*Hakea decurrens* subsp. *physocarpa* R.Br., W.R.Barker
Canopy	Long (~10 years)	Long (>50 years)	*Banksia spinulosa* var. *cunninghamii* (Sieber ex Rchb.) A.S.George

searched for 10 m on either side. Ten individuals of each target species, haphazardly selected along the transect, were measured at each site. Where species were in low numbers, only five individuals were measured, and where there were fewer than 10 individuals along transects, we searched within the boundaries of the fire-age site. If different age cohorts were present, only the oldest cohorts (largest individuals) were measured. We sampled species at 17 sites representing 14 different time periods since fire (Table 2) and measured 325 plants.

Measurement variables

Data were collected on flowers and seeds because these represent two stages of reproduction. Flower counts were made for all eight target species, and seed counts for four species, between July 2010 and January 2011 and in December 2011. Seed counts for *Banksia spinulosa* and *Pomaderris aspera* were made on the same plants as for the flowers, but for *Hakea decurrens* and *Acacia verticillata*, these counts were on different individuals.

The number of flowers per plant was estimated by using sample units to scale up data (Kirmse and Norton 1985; West 2009). At each fire-age site, a branching unit comprising stems, leaves and flowers was selected for each plant, and then the number of such units bearing flowers was estimated for that plant. The number of flowers on a unit was then counted. For species with more than one flower per inflorescence, the number of flowers per inflorescence was counted and then multiplied by the number of inflorescences on a unit. The number of flowers per unit was finally multiplied by the number of units per plant to obtain an estimate for the whole plant. For *Banksia spinulosa*, the number of inflorescences was counted and then multiplied by an estimate of 100 flowers, because of the difficulty in counting individual flowers.

The number of seeds per plant was estimated in two ways. For the serotinous (canopy-seed) species, the total number of unopened infructescences was counted, because these are considered to represent viable seed (Enright and Goldblum 1999). As in other studies, we assumed that after release, seeds of the woody-fruited Proteaceae generally last only until the next wet season (Lamont and Groom 1998; Campbell *et al*. 2012). However, some fruits may stay unopened for several years after maturity. The number of fruits counted on a plant was multiplied by the estimated number of seeds per fruit. Average seed numbers per fruit for *Banksia spinulosa* were derived from collection of five fruits at each fire-age site, whereas an

Table 2. Summary of time-since-fire sites for each species

Species	Years-since-fire
Lowland forest or Shrubby foothill forest	
Acacia oxycedrus	3, 7, 14, 22, 71
Banksia spinulosa	3, 7, 14, 22, 71
Hakea decurrens	3, 8, 14, 23, 45
Pultenaea scabra	3, 8, 14, 23
Damp forest	
Acacia verticillata	2, 6, 17, 22
Olearia lirata	2, 6, 17, 22
Pomaderris aspera	2, 6, 11, 17, 45
Prostanthera lasianthos	2, 5, 11, 17, 45

assumption of two seeds per fruit was made for *Hakea decurrens* (Barker *et al*. 1996). For the species with soil seedbanks, sample units comprising stems, leaves and infructescences were used, followed by scaling up of data, as outlined for the flower measurements (Kirmse and Norton 1985; West 2009). Estimating flower and seed numbers was more difficult for larger plants, and these results are likely to have greater errors.

The methodology to estimate flower and seed numbers was chosen because it enabled data to be collected fairly rapidly in one season, which may be useful for management-oriented research. Methods used in some other studies of reproductive maturity periods of Proteaceae species have used counts of flowers and seeds on permanently marked plants over several seasons (e.g. Kraaij *et al*. 2013; Enright and Goldblum 1999).

Data analysis

The purpose of the analysis was to build quantitative models of each species measured, in the form of response curves that could be used to understand reproductive maturity patterns following fire. Non-linear regression models were fitted to the relationships between reproduction (response variables) and time-since-fire (explanatory variable). These enabled comparisons to be made with current assumptions about times to reproductive maturity for the species.

Flower and seed numbers were at times very large and skewed to the right, and so numbers were log-transformed. An increment of either 1 or 10 was added before transforming because of the presence of zeros. Gompertz growth curves were used to model the relationship with time-since-fire, using the equation

$$y = \theta_1 \exp(-\exp(\theta_2 - \theta_3 x)).$$

We calculated 95% confidence intervals for the mean (fitted) responses. Various curves were tested for their fit to the relationship, where there is known to be a slow initial response, then a rapid increase followed by a plateau. The sigmoid curve of the Gompertz function (Tjørve 2003) gave the best fit for most species. In the equation above, θ_1 is the upper asymptote, θ_2 sets the displacement in the vertical direction, and θ_3 represents the growth rate. The models were fitted using the statistical package Minitab 16 (Minitab Inc. 2010).

The variable 'time-since-fire' was determined by the year of fire, not by the classes used for the stratification of sites. Sites up to ~15 years post-fire could be recognised confidently as being completely burnt because of the uniform regeneration of plants. The precise number of years since fire was unknown at the oldest sites for all species measured, because detailed fire records date only back to 1970. An estimated time-since-fire was assigned to these sites on the basis of the last major wildfire recorded in the areas.

The final step in the analyses of each species was to predict thresholds for the reproductive variables. The fitted equations from the non-linear regressions were used to estimate the value of response variables for future observations. Predictions were made for the mean time-since-fire that an average plant takes to exceed 80% of its maximum annual flower production (eight species) or 80% of its seed production (three species only) on the log scale. Maximum production was taken as the upper asymptote of the fitted response curve. The threshold of 80% of the estimated asymptote was chosen for biological reasons. For example, at 50%, most species had few or no plants with flowers, whereas at 80%, all species had flowering individuals. Given that flowering is being used to infer reproductive maturity, this is more useful. Asymptotes for *Pomaderris aspera* had very large confidence intervals for both flowers and seeds, because of the model being based on only three non-zero time-since-fire points, and hence predictions were not made or fitted curves presented for this species.

Results

Relationships of reproductive variables to time-since-fire

The eight shrub species displayed similarly patterned trajectories of reproductive output, although their timing differed considerably. The fitted relationships for flowers and seeds showed a rapid increase in production, then a plateau, with the exception of *Pomaderris aspera*. Asymptotes for each species represented the annual flower or seed production for an average plant. Most of the variation in the response variables was explained by the explanatory variable. The flower models had R^2-values between 72% and 94% (Table 3), whereas the seed models had lower R^2 values of between 45% and 85% (Table 3).

The highest maximum flower numbers were recorded for species with soil seedbanks and presumed long juvenile periods (*Prostanthera lasianthos* and *Pomaderris aspera*) (Fig. 1, Table 4). Species with soil seedbanks and presumed moderate juvenile periods (*Acacia oxycedrus*, *Acacia verticillata*, *Pultenaea scabra* and *Olearia lirata*) had fewer flowers at their maximum production (Fig. 1, Table 4). Species with canopy seedbanks (*Banksia spinulosa* and *Hakea decurrens*) had the lowest maximum flower numbers (Fig. 1, Table 4).

Table 3. R^2-values for flowers and seeds models

Species	Flower-model R^2 (%)	Seed-model R^2 (%)
Acacia oxycedrus	91	
Acacia verticillata	94	85
Banksia spinulosa	78	68
Hakea decurrens	72	45
Olearia lirata	84	
Pomaderris aspera	83	82
Prostanthera lasianthos	89	
Pultenaea scabra	72	

The lowest estimated maximum seed production was also for species with canopy seedbanks, being 470 for *Banksia spinulosa* and five for *Hakea decurrens* (Fig. 2, Table 4). In contrast, the maximum estimated seed production for the soil seedbank species *Acacia verticillata* was 2600 (Fig. 2, Table 4).

Predictions for flowering and seeding thresholds

Predictions about the timing of flowering thresholds after fire were made from the data models (Table 4). Species with soil seedbanks and presumed moderate juvenile periods exceeded 80% of predicted mean flower asymptotes within the shortest time-since-fire. Species with soil seedbanks and presumed long juvenile periods exceeded 80% flower asymptotes in the longest periods since fire. Species with canopy seedbanks were intermediate in time to 80% of maximum flower production.

Predictions for seed-production thresholds were made for the two species with canopy-stored seed, and one species with soil-stored seed (Table 4). For the two serotinous species, the gap between the predicted 80% asymptotes for flowers and seeds was 7 years for *Banksia spinulosa* and two years for *Hakea decurrens*. The species with soil-stored seed and a moderate juvenile period (*Acacia verticillata*) exceeded the 80% seed asymptote 1 year after flowers.

Discussion

Reproductive maturity times

There are few published data on times to reproductive maturity after fire for Australian shrubs. Our results on the relationships between reproductive responses and decadal time-spans after fire add to the current knowledge of fire intervals needed for population maintenance of eight obligate-seeding shrub species in south-eastern Australia. The data models either confirmed or extended the hypothesised timing of reproductive maturity (Tables 1, 4) for the species used in this study to represent four plant functional types (shrubs with canopy-stored seed and moderate or long juvenile periods, shrubs with soil-stored seed and moderate or long juvenile periods). For two species (*Banksia spinulosa* and *Prostanthera lasianthos*), existing assumptions were shown to underestimate the time to reach reproductive maturity by up to 10 years.

Times to reproductive maturity for the species with serotinous seedbanks were longer than initially anticipated. Predictions from the data models for *Banksia spinulosa* indicated 80% maximum flower production (on the log scale) at 13 years post-fire and 80% maximum seed production (on the log scale)
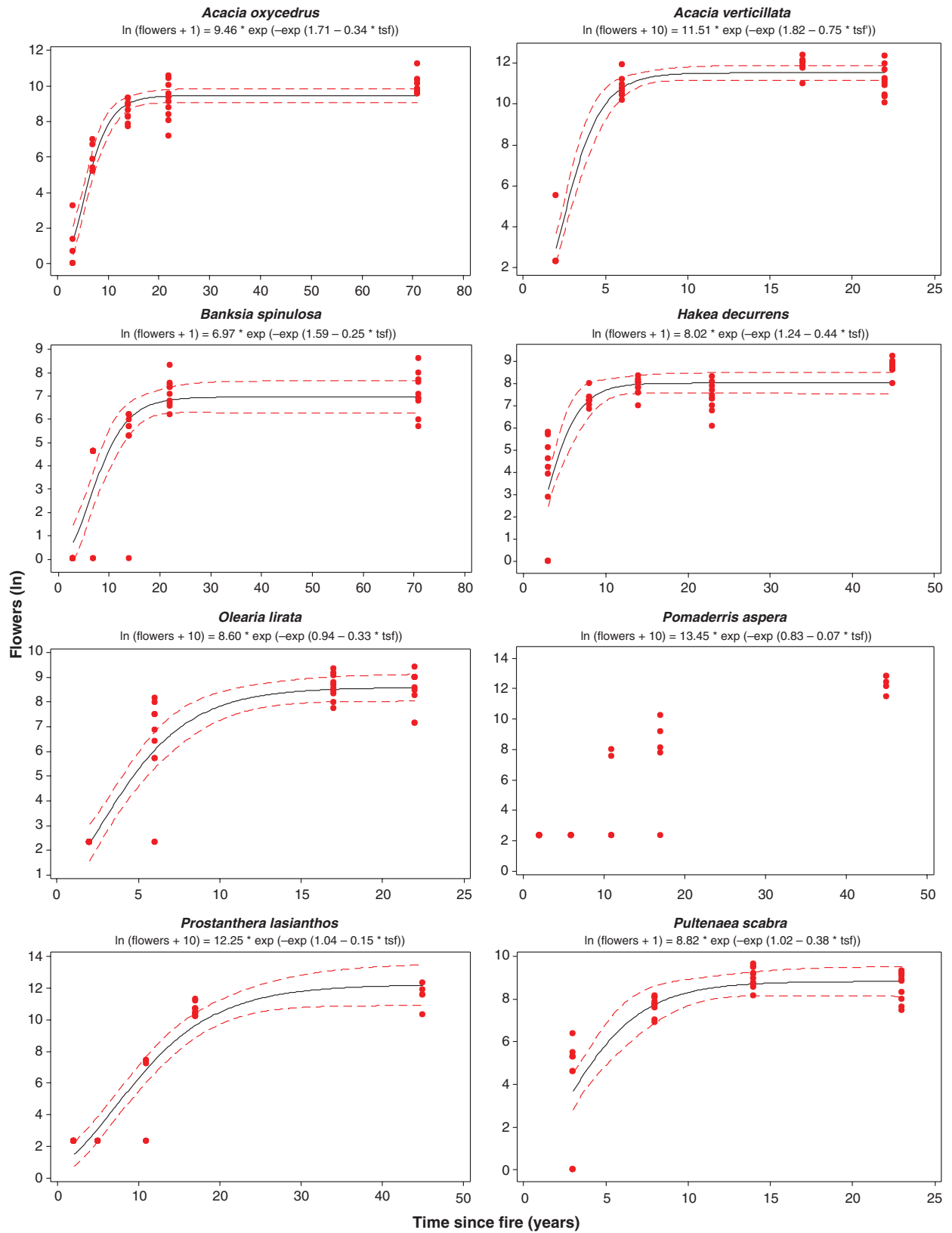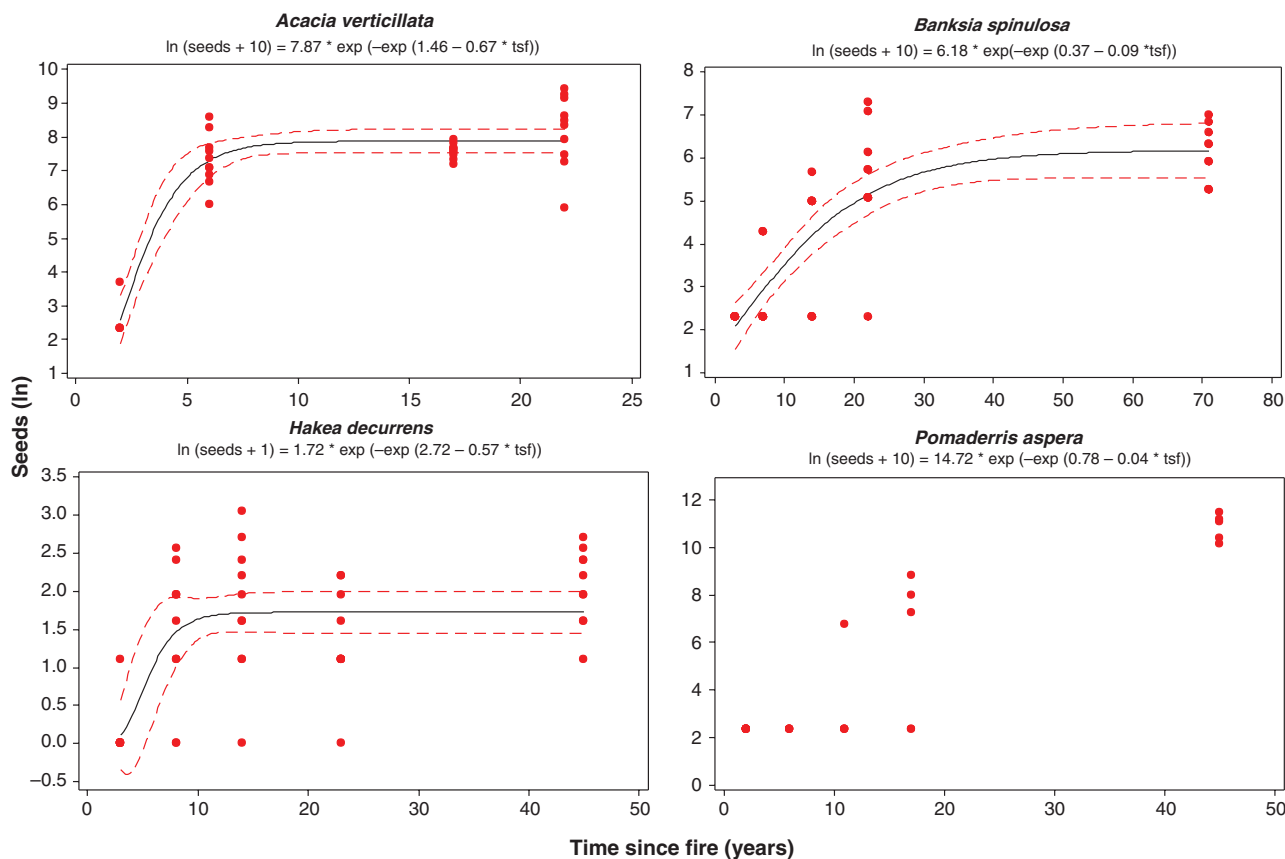
Fig. 1. Relationships between flowers (ln transformed) and time-since-fire. Solid line is the fitted value and dashed lines represent 95% confidence limits. Note for *Acacia verticillata*, *Olearia lirata*, *Prostanthera lasianthos* and *Pomaderris aspera*, values of 2.3 for the response variable represent zero flowers, because of log-transformations.

Table 4.   Flowers and seeds asymptotes (number, back transformed), time (years) after fire to 80% asymptotes of flowers (ln) and 80% asymptotes of seeds (ln)

Species	Flowers asymptote (number) (95% CI in parentheses)	Seeds asymptote (number) (95% CI in parentheses)	Time (years) to 80% of flowers (ln) asymptote: fitted mean (95% CI in parentheses)	Time (years) to 80% of seeds (ln) asymptote: fitted mean (95% CI in parentheses)
Acacia verticillata	99500 (69500, 142400)	2600 (1800, 3700)	5 (4, 6)	6 (5, 7)
Pultenaea scabra	6700 (3300, 13700)		7 (6, 9)	
Olearia lirata	5400 (3100, 9500)		8 (7, 9)	
Acacia oxycedrus	12800 (8600, 19100)		9 (8, 10)	
Hakea decurrens	3000 (1900, 4800)	5 (3, 6)	7 (6, 8)	9 (6, 11)
Banksia spinulosa	1000 (530, 2100)	470 (240, 920)	13 (11, 15)	20 (16, 26)
Prostanthera lasianthos	208300 (53700, 807400)		18 (16, 21)	

Fig. 2.   Relationships between number of seeds (ln transformed) and time-since-fire. Solid line is the fitted value and dashed lines represent 95% confidence limits. Note for *Acacia verticillata*, *Banksia spinulosa* and *Pomaderris aspera*, a value of 2.3 for the response variable represents zero seeds, because of log-transformation.

at 20 years post-fire. Results for *Hakea decurrens* predicted these thresholds at 7 and 9 years following fire. This is comparable to a study in western Victoria where *H. decurrens* did not produce large numbers of fruit until 8–12 years after fire (Enright and Goldblum 1999). Substantial time lags between flowering and seed production have been noted in other studies of *Banksia* (Enright *et al.* 1996) and variation in maturation of *Hakea* and *Banksia* species between different populations (Clarke *et al.* 2009). A study of reproductive responses of

some South African Proteaceae to fire found that flowering had occurred at least once for 90–100% of individuals 11 years after fire (Kraaij *et al.* 2013).

Assumptions about times to reproductive maturity for species with soil seedbanks and moderate juvenile periods were confirmed. These species (*Acacia verticillata*, *Acacia oxycedrus*, *Pultenaea scabra* and *Olearia lirata*) reached a threshold of 80% maximum flowering (on the log scale) between 5 and 9 years after fire, and 80% maximum seed

production (on the log scale) a year later for one of these species. Early reproductive maturity is a recognised floral trait in Australian acacias (Gibson *et al*. 2011).

However, for one of the species with soil-stored seed and a long juvenile period our data indicated that time to reproductive maturity was longer than expected. *Prostanthera lasianthos* exceeded the 80% flowering asymptote (on the log scale) at 18 years. No published data were found on reproductive maturity times for this species. Although predictions were not made for time to 80% maximum flowering for *Pomaderris aspera*, flowering was first recorded at a site that had not had fire for 11 years, suggesting a long juvenile period. This is supported by a study of the soil seedbank in *Eucalyptus regnans* forest in Victoria, where seeds of *Pomaderris aspera* were not present at sites up to 18 years post-fire (Wang 1997).

The use of chronosequences to make inferences about fire-interval thresholds adequate for reproductive maturity has limitations. Flower and seed production can differ among years and sites owing to variations in weather and nutrients (Auld and Myerscough 1986; Copland and Whelan 1989), and fluctuating levels of pollination and herbivory (Vaughton 1990; Vaughton 1991). In particular, the decade of below-average rainfall preceding data collection may have influenced observed responses to fire intervals and also growth and reproduction. Our models could be verified by replicating measurements of the species at other sites, and including additional years of field data.

Seed production

Maximum estimated seed numbers varied greatly among species. Our data on *Banksia spinulosa* var. *cunninghamii* predicted the asymptotic number of seeds per adult plant to be 470, although the actual seed numbers may be lower because of insect predation and other factors. We could find no comparative research on this taxon, but in a study of *B. spinulosa* var. *neoanglica* in New South Wales, a mean of 137.6 seeds per adult plant was recorded (Vaughton 1990). Our results for *Hakea decurrens* predicted the asymptotic number of seeds per adult plant to be five. In contrast, the study of *H. decurrens* recruitment after fire in western Victoria estimated the mean number of viable seeds released per adult to be 42.7 (Enright and Goldblum 1999). The low numbers of seeds in our study may be due to granivory by birds, as the remains of infructescence stems were often observed on *H. decurrens*, and high levels of granivory are common on the woody-fruited Proteaceae because of the highly nutritious seeds (Lamont and Groom 1998). An additional factor in our study of *H. decurrens* compared with that in western Victoria was the collection of data at the end of a 13-year period of below-average rainfall, which was likely to have reduced seed production.

In comparison to species with canopy-stored seed, the species with soil seedbanks had much larger numbers of seed produced per plant. For example, the maximum estimated seed number was ~2600 for *Acacia verticillata*, and high seed numbers are typical of acacias (Gibson *et al*. 2011).

Higher seed output is often related to lower seed mass because of trade-offs in resource allocation (Henery and Westoby 2001;

Campbell *et al*. 2012). In our study, *Pomaderris aspera* had the largest seed output and the smallest mean seed mass (0.56 g: Kew Royal Botanic Gardens 2012). Conversely, *Hakea decurrens* had the smallest seed output and the largest mean seed mass (25.2 g: Kew Royal Botanic Gardens 2012). However mean seed masses for *Banksia spinulosa* (13.45 g: Kew Royal Botanic Gardens 2012) and *Acacia verticillata* (11.49 g: Kew Royal Botanic Gardens 2012) were fairly close although there was a large difference between the seed outputs of these species. This may be explained by the higher accessory costs of fruit structures affecting seed production in *Banksia spinulosa* (Henery and Westoby 2001).

Recruitment

Seed production is not a direct indicator of successful recruitment (Kraaij *et al*. 2013), and measurement of recruitment success would strengthen results from our study. Seedling establishment and population trajectories are limited by granivory, herbivory and unsuitable weather and habitat conditions (Bell 1999; Lamont *et al*. 2007).

Obligate-seeder species with canopy seed storage are reliant on successful germination of seeds after adult plants are killed by fire for population persistence (Noble and Slatyer 1980). A review of woody-fruited Proteaceae in Western Australia reported that following fire, typically less than 5% of seeds become seedlings that survive the first summer (Lamont and Groom 1998). Observations of *Banksia spinulosa* at our study sites indicated that seedling regeneration is low after fires. Seed numbers per adult plant for *Hakea decurrens* are low; however, in the western Victorian study of this species by Enright and Goldblum (1999) an estimated 22.8% of seeds became seedlings. The large seed mass of *H. decurrens* is likely to contribute to high germination and establishment success (Lamont and Groom 1998). Recruitment in the absence of fire has also been reported for *H. decurrens*, associated with adult mortality (Enright and Goldblum 1999). Multi-age stands of *B. spinulosa* have been observed at our study sites, suggesting inter-fire recruitment, and the gradual seed-release mechanism that enables this in other *Banksia* species has been recorded in a study of serotinous shrubs in high-rainfall areas of New South Wales (Clarke *et al*. 2010). In the South African study of Proteaceae (Kraaij *et al*. 2013), the highest recruitment rates were recorded at sites with the longest fire-return intervals (38 years).

Soil seedbanks allow for the persistence of populations between fire events when standing plants are not present (Campbell *et al*. 2012). Germinability is variable for soil-stored seeds, and is likely to be affected by heat and smoke cues, which differ depending on fire intensity (Penman *et al*. 2008) and by depth of seed burial (Brown *et al*. 2003; Wang 1997). Obligate-seeding leguminous shrubs (*Acacia oxycedrus*, *A. verticillata*, *Pultenaea scabra* in our study) typically have partial germination after fire, leaving long-lived viable seed in the soil (DSE 2010e; Gibson *et al*. 2011). This germination response will generally be higher after a moderate-intensity fire than a low-intensity fire (Auld and O'Connell 1991). A study of *Acacia* and *Pultenaea* species in north–central Victoria confirmed that a large portion of seed is retained in

the soil during inter-fire periods (Orscheg and Enright 2011). *Olearia lirata* is also considered to have a long-lived seedbank, with partial germination after fire (DSE 2010*e*).

The two species with long reproductive maturity periods, *Pomaderris aspera* and *Prostanthera lasianthos*, are thought to have long-lived seedbanks (DSE 2010*e*). No published data were found on the germination response and retention of soil-stored seed after fire for *Prostanthera lasianthos*, but a study of *Prostanthera askania* in moist *Eucalyptus* forest in NSW found that germination was related to low-intensity fires (Tierney 2006). In a Victorian study of *Eucalyptus regnans* forest understorey, *Pomaderris aspera* seeds were not found in the soil at sites up to 18 years post-fire (Wang 1997), indicating complete germination after fire and hence reliance on maturation of plants for recruitment.

Fire planning

Data on timing of flower and seed production can help inform planning of fire intervals to maintain plant diversity. Optimum fire intervals for vegetation communities can be derived from the time taken by component species to set seed after fire or senesce without fire (Cheal 2010; Gill and McCarthy 1998). The serotinous obligate-seeder shrubs represented in the present study (*Banksia spinulosa* and *Hakea decurrens*) appear to require fire intervals of between 10 and 20 years if they are to have enough individuals producing seed to maintain populations. Reproductive maturity results for the obligate-seeder shrubs with moderate juvenile periods (*Acacia oxycedrus*, *A. verticillata*, *Pultenaea scabra* and *Olearia lirata*) indicate that fire intervals of about 5 years may be tolerated. Results for the obligate-seeder shrubs with long juvenile periods (*Pomaderris aspera* and *Prostanthera lasianthos*) point to the requirement for much longer fire intervals (at least 20 years). The combined effect of fire and drought on reproductive responses of plant species also needs to be considered in planning appropriate fire intervals.

More frequent fires in Mediterranean-climate ecosystems (Keeley *et al.* 2012) and predicted slower reproductive rates as a result of climate change (Williams *et al.* 2009) may lead to changes in species composition in vegetation communities (Bradstock *et al.* 2012). Where particular fire intervals are repeated, there is the potential for changes in dominance of species with longer or shorter juvenile periods (Gill and Catling 2002). Results from our study indicated that inter-fire intervals of less than 10 years have the potential to favour leguminous shrubs and disadvantage serotinous shrubs and long-maturity shrubs, which all co-occur in foothill forests. These effects may be moderated by the varied responses of species to fire intensity (Bell 1999), and spatial variability allowing the co-existence of plants with different life histories (Clark *et al.* 2002; Menges 2007); however, evidence for appropriate fire mosaics is lacking (Parr and Anderson 2006). Further demographic research on reproductive maturity timing and recruitment of serotinous and long-maturity shrubs would add to knowledge about these plant functional types, strengthen predictions about their responses to fire regimes and provide guidance for fire planning where these species occur.

References

Auld TD, Myerscough PJ (1986) Population dynamics of the shrub *Acacia suaveolens* (Sm.)Willd.: seed production and predispersal seed predation. *Australian Journal of Ecology* **11**, 219–234. doi:10.1111/j.1442-9993.1986.tb01394.x

Auld TD, O'Connell MA (1991) Predicting patterns of post-fire germination in 35 eastern Australian Fabaceae. *Australian Journal of Ecology* **16**, 53–70. doi:10.1111/j.1442-9993.1991.tb01481.x

Barker RM, Barker WR, Haegi L (1996) *Hakea*. In 'Flora of Victoria, Vol. 3. National Herbarium of Victoria'. (Eds NG Walsh, TJ Entwisle) pp. 873–874. (Inkata Press: Melbourne)

Bell DT (1999) Turner review no. 1. The process of germination in Australian species. *Australian Journal of Botany* **47**, 475–517. doi:10.1071/BT98007

Bond WJ, Keeley JE (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution* **20**, 387–394. doi:10.1016/j.tree.2005.04.025

Bradstock RA, Kenny BJ (2003) An application of plant functional types to fire management in a conservation reserve in south-eastern Australia. *Journal of Vegetation Science* **14**, 345–354. doi:10.1111/j.1654-1103.2003.tb02160.x

Bradstock RA, Williams RJ, Gill AM (2012) Future fire regimes of Australian ecosystems: new perspectives on enduring questions of management. In 'Flammable Australia: fire regimes, biodiversity and ecosystems in a changing world'. (Eds RA Bradstock, AM Gill, RJ Williams) pp. 307–324. (CSIRO Publishing: Melbourne)

Brown J, Enright NJ, Miller BP (2003) Seed production and germination in two rare and three common co-occurring *Acacia* species from south-east Australia. *Austral Ecology* **28**, 271–280. doi:10.1046/j.1442-9993.2003.t01-4-01287.x

Bureau of Meteorology (2011) 'Climate statistics for Australian locations. Monthly climate statistics. Summary statistics Mount Dandenong GTV9.' Available at http://www.bom.gov.au/climate/averages/tables/cw_086243.shtml.[Verified 29 March 2011]

Campbell ML, Clarke PJ, Keith DA (2012) Seed traits and seed bank longevity of wet sclerophyll forest shrubs. *Australian Journal of Botany* **60**, 96–103. doi:10.1071/BT11261

Cheal D (2010) 'Growth stages and tolerable fire intervals for Victoria's native vegetation data sets. Fire and adaptive management report no. 84.' (Department of Sustainability and Environment: Melbourne)

Clark JS, Gill AM, Kershaw AP (2002) Spatial variability in fire regimes: its effects on recent and past vegetation. In 'Flammable Australia: the fire regimes and biodiversity of a continent'. (Eds RA Bradstock, JE Williams, AM Gill) pp. 125–141. (Cambridge University Press: Cambridge, UK)

Clarke PJ, Knox KJE, Campbell ML, Copeland LM (2009) Post-fire recovery of woody plants in the New England Tableland Bioregion. *Cunninghamia* **11**, 221–239.

Clarke PJ, Knox KJE, Butler D (2010) Fire intensity, serotiny and seed release in 19 woody species: evidence for risk spreading among wind-dispersed and resprouting syndromes. *Australian Journal of Botany* **58**, 629–636.

Copland BJ, Whelan RJ (1989) Seasonal variation in flowering intensity and pollination limitation of fruit-set in four co-occurring *Banksia* species. *Journal of Ecology* **77**, 509–523. doi:10.2307/2260766

Cornelissen JHC, Lavorel S, Garnier E, Diaz S, Buchmann N, Gurvich DE, Reich PB, ter Steege H, Morgan HD, van der Heijden MGA, Pausas JG, Poorter H (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* **51**, 335–380. doi:10.1071/BT02124

Department of Sustainability and Environment (DSE) (2006) 'Code of practice for fire management on public land: revision 1.' (Department of Sustainability and Environment: Melbourne).

Department of Sustainability and Environment (DSE) (2010*a*) 'Biodiversity interactive map – 3.1.' (Department of Sustainability and Environment: Melbourne). Available at http://mapshare2.dse.vic.gov.au/MapShare 2EXT/imf.jsp?site=bim.[Verified June 2010]

Department of Sustainability and Environment (DSE) (2010*b*) Data source. In 'Firemap'. (Department of Sustainability and Environment: Melbourne). [Verified June 2010]

Department of Sustainability and Environment (DSE) (2010*c*) Data source. In 'Fire history assessment tool (FireHAT)'. (Department of Sustainability and Environment: Melbourne). [Verified June 2010]

Department of Sustainability and Environment (DSE) (2010*d*) Data source. In 'Victorian flora site database' via Flora Information System.(Viridans Biological Databases) with contributions from Royal Botanic Gardens Melbourne. (Department of Sustainability and Environment: Melbourne) [Verified June 2010]

Department of Sustainability and Environment (DSE) (2010*e*) Data source. In 'Plant vital attributes for ecological fire management'. (Department of Sustainability and Environment: Melbourne). [Verified June 2010]

Department of Sustainability and Environment (DSE) (2011) 'Ecological vegetation class benchmarks – Highlands Southern Fall Bioregion.' (Department of Sustainability and Environment: Melbourne). Available at http://www.dse.vic.gov.au/DSE/nrence.nsf/LinkView/43F E7DF24A1447D9CA256EE6007EA8788062D358172E420C4A256D EA0012F71C [Verified March 2011]

Enright NJ, Goldblum D (1999) Demography of a non-sprouting and resprouting *Hakea* species (Proteacea) in fire-prone *Eucalyptus* woodlands of southeastern Australia in relation to stand age, drought and disease. *Plant Ecology* **144**, 71–82. doi:10.1023/A:1009839800864

Enright NJ, Lamont BB, Marsula R (1996) Canopy seedbank dynamics and optimum fire regime for the highly serotinous shrub, *Banksia hookeriana. Journal of Ecology* **84**, 9–17. doi:10.2307/2261695

Fire Ecology Working Group (2004) 'Guidelines and procedures for ecological burning on public land in Victoria.' (Department of Sustainability and Environment: Melbourne)

Gibson MR, Richardson DM, Marchante E, Marchante H, Rodger JG, Stone GN, Byrne M, Fuentes-Ramirez A, George N, Harris C, Johnson SD, Le Roux JJ, Miller JT, Murphy DJ, Pauw A, Prescott MN, Wandrag EM, Wilson JRU (2011) Reproductive biology of Australian acacias: important mediator of invasiveness? *Diversity & Distributions* **17**, 911–933. doi:10.1111/j.1472-4642.2011.00808.x

Gill AM (1975) Fire and the Australian flora: a review. *Australian Forestry* **38**, 4–25. doi:10.1080/00049158.1975.10675618

Gill AM (2012) Bushfires and biodiversity in southern Australian forests. In 'Flammable Australia: fire regimes, biodiversity and ecosystems in a changing world'. (Eds RA Bradstock, AM Gill, RJ Williams) pp. 235–252. (CSIRO Publishing: Melbourne)

Gill AM, Catling PC (2002) Fire regimes and biodiversity of forested landscapes of southern Australia. In 'Flammable Australia: the fire regimes and biodiversity of a continent'. (Eds RA Bradstock, JE Williams, AM Gill) pp. 351–369. (Cambridge University Press: Cambridge, UK)

Gill AM, McCarthy MA (1998) Intervals between prescribed fires in Australia: what intrinsic variation should apply? *Biological Conservation* **85**, 161–169. doi:10.1016/S0006-3207(97)00121-3

Henery ML, Westoby M (2001) Seed mass and seed nutrient content as predictors of seed output variation between species. *Oikos* **92**, 479–490. doi:10.1034/j.1600-0706.2001.920309.x

Keeley JE, Fotheringham CJ, Baer-Keeley M (2006) Demographic patterns of postfire regeneration in Mediterranean-climate shrublands of California. *Ecological Monographs* **76**, 235–255. [Ecological Society of America]. doi:10.1890/0012-9615(2006)076[0235:DPOPRI]2.0.CO;2

Keeley JE, Bond WJ, Bradstock RA, Pausas JG, Rundel PW (2012) 'Fire in Mediterranean ecosystems: ecology, evolution and management.' (Cambridge University Press: Cambridge, UK)

Keith DA (2012) Functional traits: their roles in understanding and predicting biotic responses to fire regimes from individuals to landscapes. In 'Flammable Australia: fire regimes, biodiversity and ecosystems in a changing world'. (Eds RA Bradstock, AM Gill, RJ Williams) pp. 97–125. (CSIRO Publishing: Melbourne)

Keith DA, Holman L, Rodoreda S, Lemmon J, Bedward M (2007) Plant functional types can predict decade-scale changes in fire-prone vegetation. *Journal of Ecology* **95**, 1324–1337. doi:10.1111/j.1365-2745.2007.01302.x

Kew Royal Botanic Gardens (2012) 'Seed information database.' Available at http://data.kew.org/sid/weight.html.[Verified 19 April 2012]

Kirmse RD, Norton BE (1985) Comparison of the reference unit method and dimensional analysis methods for two large shrubby species in the Caatinga woodlands. *Journal of Range Management* **38**, 425–428. doi:10.2307/3899714

Kraaij T, Cowling RM, van Wilgen BW, Schutte-Vlok AL (2013) Proteaceae juvenile periods and post-fire recruitment as indicators of minimum fire return intervals in eastern coastal fynbos. *Applied Vegetation Science* **16**, 84–94. doi:10.1111/j.1654-109X.2012.01209.x

Lamont BB, Groom PK (1998) Seed and seedling biology of the woody-fruited Proteaceae. *Australian Journal of Botany* **46**, 387–406. doi:10.1071/BT96135

Lamont BB, Enright NJ, Witkowski ETF, Groeneveld J (2007) Conservation biology of banksias: insights from natural history to simulation modeling. *Australian Journal of Botany* **55**, 280–292. doi:10.1071/BT06024

Menges ES (2007) Integrating demography and fire management: an example from Florida scrub. *Australian Journal of Botany* **55**, 261–272. doi:10.1071/BT06020

Minitab Inc. (2010) 'Minitab 16 statistical software [computer software].' (Minitab: State College, PA) Available at www.minitab.com

Noble IR, Gitay H (1996) A functional classification for predicting the dynamics of landscapes. *Journal of Vegetation Science* **7**, 329–336. doi:10.2307/3236276

Noble IR, Slatyer RO (1980) The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* **43**, 5–21. doi:10.1007/BF00121013

Orscheg CK, Enright NJ (2011) Patterns of seed longevity and dormancy in obligate seeding legumes of box-ironbark forest, south-eastern Australia. *Austral Ecology* **36**, 185–194. doi:10.1111/j.1442-9993.2010.02135.x

Parks Victoria (2011*a*) 'Parks Victoria education resources. Dandenong Ranges National Park Guide. Geology of the Dandenong Ranges.' Available at http://www.parkweb.vic.gov.au/education/resource_kit/ section4a.htm [Verified 29 March 2011]

Parks Victoria (2011*b*) 'Bunyip State Park management plan. October 1998, amended September 2007.' Available at http://www.parkweb.vic.gov.au/ resources07/07_0164.pdf [Verified 29 March 2011]

Parr CL, Anderson AN (2006) Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. *Conservation Biology* **20**, 1610–1619. doi:10.1111/j.1523-1739.2006.00492.x

Pausas JG, Lloret F (2007) Spatial and temporal patterns of plant functional types under simulated fire regimes. *International Journal of Wildland Fire* **16**, 484–492. doi:10.1071/WF06109

Pausas JG, Bradstock RA, Keith DA, Keeley JE Global Change of Terrestrial Ecosystems Fire Network(2004) Plant functional traits in relation to fire in crown-fire ecosytems. *Ecology* **85**, 1085–1100. doi:10.1890/02-4094

Penman TD, Binns DL, Allen RM, Shiels RJ, Plummer SH (2008) Germination responses of a dry sclerophyll forest soil-stored seedbank to fire related cues. *Cunninghamia* **10**, 547–555.

Reich PB, Wright IJ, Cavender-Bares J, Craine JM, Oleksyn J, Westoby M, Walters MB (2003) The evolution of plant functional variation: traits, spectra and strategies. *International Journal of Plant Sciences* **164**(3), S143–S164. doi:10.1086/374368

Tierney DA (2006) The effect of fire-related germination cues on the germination of a declining forest understorey species. *Australian Journal of Botany* **54**, 297–303. doi:10.1071/BT05111

Tjørve E (2003) Shapes and functions of species-area curves: a review of possible models. *Journal of Biogeography* **30**, 827–835. doi:10.1046/j.1365-2699.2003.00877.x

van Wilgen BW, Forsyth GG, de Clerk H, Das S, Khuluse S, Schmitz P (2010) Fire management in Mediterranean-climate shrublands: a case study from the Cape fynbos, South Africa. *Journal of Applied Ecology* **47**, 631–638. doi:10.1111/j.1365-2664.2010.01800.x

Vaughton G (1990) Predation by insects limits seed production in *Banksia spinulosa* var. *neoanglica* (Proteaceae). *Australian Journal of Botany* **38**, 335–340. doi:10.1071/BT9900335

Vaughton G (1991) Variation between years in pollen and nutrient limitation of fruit-set in *Banksia spinulosa*. *Journal of Ecology* **78**, 389–400. doi:10.2307/2260721

Wang L (1997) The soil seed bank and understorey regeneration in *Eucalyptus regnans* forest, Victoria. *Australian Journal of Ecology* **22**, 404–411. doi:10.1111/j.1442-9993.1997.tb00690.x

West PW (2009) 'Tree and forest measurement.' 2nd edn. (Springer-Verlag: Berlin)

Whelan RJ, Rodgerson L, Dickman CR, Sutherland EF (2002) Critical life cycles of plants and animals: developing a process-based understanding of population changes in fire-prone landscapes. In 'Flammable Australia: the fire regimes and biodiversity of a continent'. (Eds RA Bradstock, JE Williams, AM Gill) pp. 94–124. (Cambridge University Press: Cambridge, UK)

Williams RJ, Bradstock RA, Cary GJ, Enright NJ, Gill AM, Liedloff AC, Lucas C, Whelan RJ, Andersen AN, Bowman DJMS, Clarke PJ, Cook GD, Hennessy KJ, York A (2009) Interactions between climate change, fire regimes and biodiversity in Australia – a preliminary assessment. Report to Department of Climate Change and Department of Environment, Water, Heritage and Arts, Canberra.