Research Article

Mechanisms Enabling a Fire Sensitive Plant to Survive Frequent Fires in South-West Australian Eucalypt Forests

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ABSTRACT

A fire sensitive plant, *Banksia quercifolia* R.Br., that often occurs as thickets embedded in forest landscapes in south-west Australia was exposed to repeated broad-scale fires at short intervals. Fire severity and patchiness was mapped using satellite imagery and the response of the *B. quercifolia* population monitored. Over the study period, the mean interval of fire in the landscape in which *B. quercifolia* occurred was 1.7 yr—almost half the juvenile period of the species—and the landscape fire frequency was six fires per decade. The population increased in response to episodes of fire escape and fire-caused mortality and consequent regeneration. Unlike surrounding vegetation, immature *B. quercifolia* thickets were not flammable under conditions of mild weather and moist fuels, so they burnt at a lower frequency than more flammable vegetation in the surrounding landscape, enabling the species to persist. When the thickets had developed sufficiently to burn, the plants had reached maturity and regenerated readily from seed. However, the juvenile period increased by 58% following a period

RESUMEN

Una planta sensible al fuego, *Banksia quercifolia* R.Br., que frecuentemente se halla en forma de matorrales cerrados integrados a paisajes boscosos en el sudeste de Australia, fue expuesta a fuegos repetidos de gran escala en intervalos cortos. La severidad del fuego y la fragmentación fueron mapeados utilizando imágenes satelitales y la respuesta de la población de *B. quercifolia* monitoreada. Durante el período de estudio, el intervalo medio de fuego en el paisaje en el cual *B. quercifolia* se encuentra fue de 1,7 años—casi la mitad del período juvenil de la especie—y la frecuencia de fuego en el paisaje fue de 6 incendios por década. La población aumentó como respuesta a los episodios del escape de fuego, como así también la mortalidad causada por el fuego y la consecuente regeneración. A diferencia de la vegetación que la rodea, los matorrales de *B. quercifolia* no fueron inflamables bajo condiciones meteorológicas moderadas y combustibles húmedos, por lo tanto se quemaron a una frecuencia más baja que el resto de la vegetación circundante más inflamable, permitiéndole a la especie persistir en el sistema. Cuando los matorrales se habían desarrollado lo suficiente como para quemarse, las plantas alcanzaron la madurez y regeneraron rápidamente de semilla. Sin embargo, el período juvenil se incrementó en un 58% a continuación de un período de preciof 16% below average rainfall, which has implications for fire management in a drying climate.

pitaciones 16% por debajo del promedio, lo cual tiene implicancias para el manejo del fuego en un clima cada vez más seco.

Keywords: fire patchiness, fire sensitive plants, frequent fire, prescribed fire, south-west Australia

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INTRODUCTION

In fire-prone environments, prescribed fire is used to achieve a range of management objectives including fuel hazard reduction, habitat management, catchment management, and for silvicultural purposes (McCaw and Burrows 1989, Walstad *et al*. 1990, Stephens and Ruth 2004). While these forest ecosystems are well adapted to specific fire regimes, they may not be adapted to all potential fire regimes (Gill and McCarthy 1998). Of the elements that compose the fire regime, the interval between fires and fire frequency are of particular concern. Plant life histories and vital attributes, especially the juvenile period of species that are readily killed by fire and depend on seed for regeneration, have been widely used for setting minimum fire intervals below which extinction is likely (Keeley and Zedler 1978, Noble and Slatyer 1980, Kruger and Bigalke 1984, Tolhurst and Friend 2001). This has led to debate about whether frequent burning to manage fuel hazard and mitigate wildfire threat is compatible with long term plant conservation (Cary and Morrison 1995, Enright *et al*. 1996, Bradstock *et al*. 1998, Keeley 2002, Driscoll *et al*. 2010).

A number of scientists studying ecosystems in south-west and south-east Australia have used a variety of models to predict the fate and viability of fire sensitive, usually serotinous, species under various fire interval scenarios (Bradstock *et al*. 1996, Bradstock *et al*. 1998, Enright *et al*. 1998, Groeneveld *et al*. 2008, Nield *et al*. 2009). These models commonly use plant life histories such as juvenile period to model population survival under a range of fire frequencies and invariably demonstrate that fire return intervals close to or less than the plant's juvenile period will likely result in the local extinction (extirpation) of the population. For example, Drechsler *et al*. (1999) used a stage-based model to predict the fate of *Banksia goodii* R.Br. in south-west Australia and concluded that fires should have minimum intervals of 15 to 20 years to ensure the persistence of the population. Similarly, McCarthy *et al*. (2001) modeled the population dynamics of *Banksia ornata* F.Muell. ex Meisn., a fire sensitive serotinous species with a juvenile period of about five years, and concluded that the optimal fire interval to maximize population growth was greater than 30 years.

These models make a number of key assumptions about fire severity, patchiness, plant mortality, seed bank dynamics, and recruitment following fire. Critically, the models assume that fire is a uniform or homogeneous event across the landscape: either it occurred or it didn't, and if it did, then it was lethal to fire sensitive species in the landscape. Jurskis *et al*. (2003) suggest that these assumptions about plant mortality and the uniformity of fire may be unrealistic. Of the few published field studies on this subject, workers in shrublands and savanna woodlands reported that the response of populations of fire sensitive obligate seeders was dependent on fire intensity and patchiness (Ooi *et al*. 2006, Oliveira *et al*. 2015). Most population viability models are unable to accommodate the often complex patchiness in fire behaviour. Variability of fire behaviour, including whether or not fire will spread, depends on the prevailing topography, weather, and fuel conditions. Fuel flammability, as determined by its moisture content, structure, biomass, time since last fire, and consequent fire behaviour, can vary at both landscape and local patch scales (Whelan 1995, Catchpole 2002, Penman *et al.* 2008, Oliveira *et al*. 2015). South-west forest fire management units treated by aerial prescribed burning are generally 3000 ha to 6000 ha and contain a mosaic of vegetation types with different fuel characteristics. Landscape flammability and related fire behaviour reflect the vegetation mosaic (Jurskis *et al*. 2003, Wardell-Johnson *et al*. 2006). In fire-prone regions experiencing a mediterranean-type climate, such as south-west Australia, the flammability of vegetation types can also vary due to topographical variation in fuel moisture content, especially during spring and autumn.

Therefore, the generalisation that repeated fire at short intervals leads to the decline or extinction of fire sensitive species overlooks the spatial and temporal complexity and diversity of fire behaviour in the landscape. Introducing fire into a landscape at short intervals does not necessarily equate to burning the entire landscape at short intervals. Here, "introducing fire" means introducing ignition sources into a landscape (in this case, the 5000 ha London Forest) under fuel and weather conditions conducive to a proportion of the ignitions resulting in spreading fire, the extent and behaviour of which will depend on prevailing fuel and weather conditions.

By dropping incendiaries on a grid pattern across the landscape, aerial prescribed burning enables the delivery of virtually simultaneous ignitions at a density of about one ignition per 2 ha. This ignition pattern ensures that most vegetation types in the landscape will experience one or more ignitions and have the potential to burn. The aim of this study was to quantify the effects of frequent introduction of fire into a forest landscape that contains populations of fire sensitive *Banksia quercifolia* R.Br. as part of the vegetation mosaic. Specifically, the study investigated whether the repeated introduction of fire at intervals less than the juvenile period of *B. quercifolia* results in population decline or extirpation.

METHODS

Study Site

The study was carried out in London Forest, an area of 5000 ha about 40 km north-east of the town of Walpole in south-west Western Australia (34° 47′ S 116° 59′ E). The vegetation comprised a fine scale mosaic of tall eucalypt forests to 40 m, low open woodlands to 15 m, and various heathlands to 2 m, reflecting variability in soil and landform. The major vegetation complexes as defined and mapped by Mattiske and Havel (1998) were Caldyanup (~52 %), which is predominantly heathlands, and Collis and Lindesay, which are various eucalypt forests and woodlands (~48 %). The region experiences a mild climate of cool wet winters and warm dry summers with mean annual rainfall ranging from 900 mm to 1200 mm. An automatic weather station was installed on site for the duration of the study.

B. quercifolia is a woody shrub that grows to a height of about 2.5 m. It occurs along the south coast and adjacent hinterland of south-west Western Australia and its preferred habitat is on the margins of swamps and in the often abrupt ecotone between seasonally wet and densely vegetated heathlands and open eucalypt forests. It was chosen for study because it is one of a small number of species in the region known to be fire sensitive: it is non-lignotuberous, thin barked, and readily killed by fire. It relies on canopy-stored seed for regeneration and, typical of many *Banksias,* it is serotinous (Lamont and Barker 1988, Lamont *et al.* 1991*a*).

B. quercifolia commonly occurs as thickets or in clumps with little or no overstorey provided by other vegetation. There is little or no surface or near surface fuel (as defined by Gould *et al*. 2011) and, typical of many shrublands, the fuel is a discontinuous elevated mix of mostly live vegetation, with the proportion of dead material increasing with the age of the vegetation. This contrasts with the surrounding shrublands, sheoak (*Allocasaurina fraseriana* [Miq.] L.A.S. Johnson) woodlands, and eucalypt forests, where fuel is more continuous, hence more flammable, under mild weather conditions.

Fire History and Patchiness

Since the 1960s, London Forest has experienced low intensity prescribed fires (using the aerial ignition technique) at 6 yr to 8 yr intervals, with the last fires prior to this study being in late spring (November) 1994 and 2002. The patchiness and burn severity (loss of vegetation cover) of fires experienced over the period 2002 to 2008 was mapped from 30 m resolution Landsat satellite data using the Normalised Difference Vegetation Index (NDVI) (Garcia-Haro *et al*. 2001, Li *et al*. 2001). The reliability and limitations of satellite-derived fire mapping have been well documented (Price *et al*. 2003, Oliveira *et al*. 2015).

The intrinsic spatial variability in structure and biomass of live and dead vegetation, and temporal and spatial variability in fuel moisture content associated with topography, results in variability in flammability and fire behaviour potential of vegetation across the landscape. In south-west Australian forests, this variability is most pronounced during mild weather conditions in spring and autumn (after opening rains) when parts of the landscape are dry while other parts remain damp, and it is least evident in summer and early autumn when almost the entire landscape has dried (Burrows *et al*. 2008). Patches that did not burn in the spring (November) 2002 prescribed fire in London Forest are shown in Figure 1 and included a population of some 1.5 ha of mature *B. quercifolia* on the north-east corner of London Forest that was estimated to be eight years old in 2002, based on fire history and the size of the plants.

In early autumn (March) 2003 a wildfire burnt towards London Forest but, because most of it was recently burnt by prescribed fire, the wildfire did not spread through London Forest. However, it burnt the population of *B. quercifolia* that had not burnt during the 2002 prescribed fire. This sequence of fire events provided an opportunity to examine the response of *B. quercifolia* to an intense early autumn wildfire and subsequent frequent low intensity broad-scale prescribed fires.

Landscape Fire Regime Definition

Forman and Godron (1986) defined a "landscape" as a heterogeneous area composed of a mosaic of interacting ecosystems and landforms with similar geomorphology and climate. Approximating this definition, Mattiske and Havel (2002) delineated 29 landscapes in the south-west forest region of Western Australia, ranging from several thousand hectares to ten thousand hectares. Fire regime, as defined by Gill (1981), relates to the history of fire frequency, intensity, and seasonality at a point in the landscape, so it does not adequately describe the regime experienced at the landscape scale, unless the entire landscape burns. Characterising the fire regime experienced at the landscape scale is more complex due to the intrinsic spatial and temporal variability of fuel flammability, especially when fires burn under mild weather conditions or in discontinuous fuels. In determining fire regime components such as fire interval and fire frequency, it is also important to identify the temporal bounds that apply to these measures.

In this study, we characterise the fire regime in London Forest over the time period

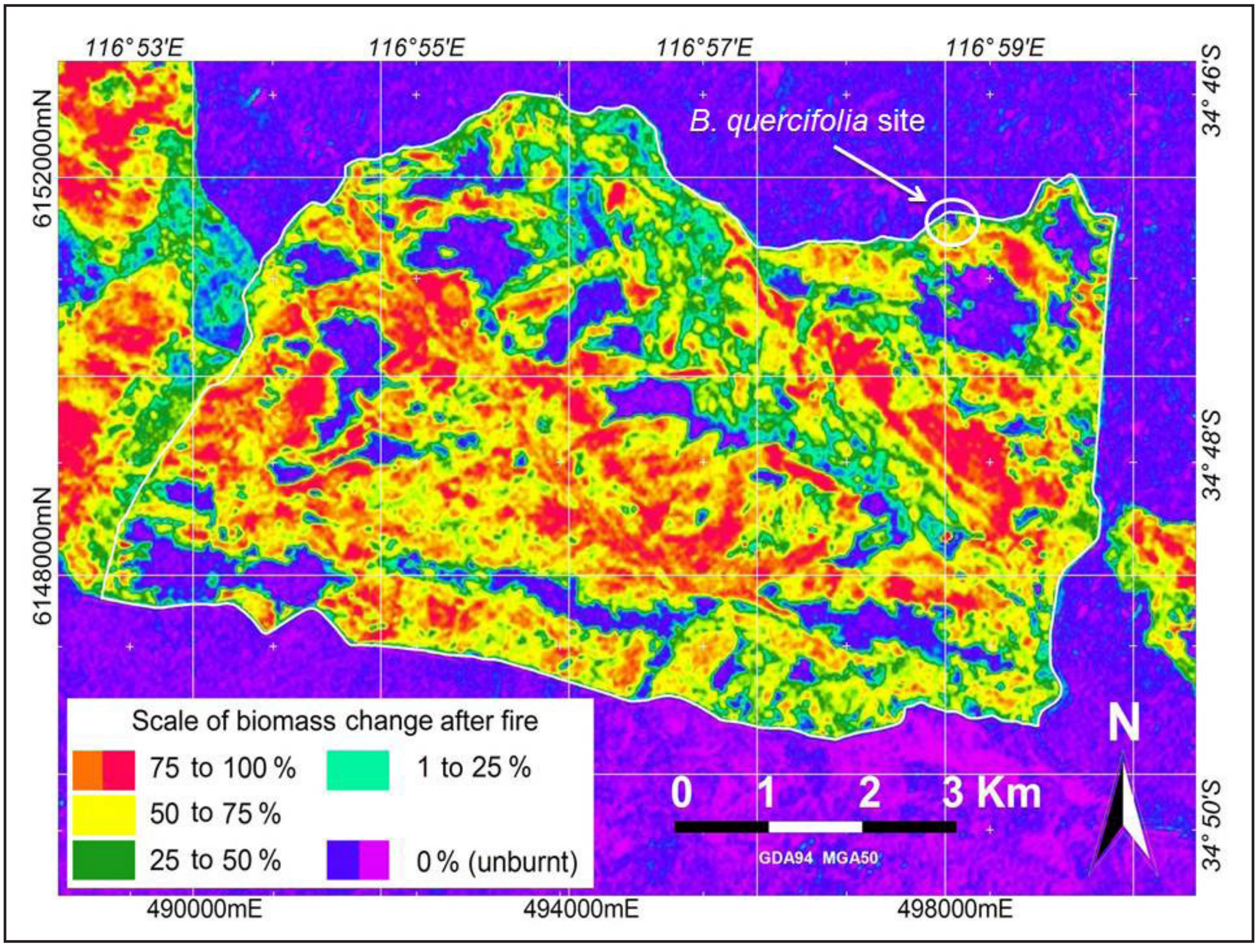

Figure 1. Satellite-derived map of fire severity (extent of vegetation cover removal) following a prescribed fire in the ~5000 ha London Forest landscape in spring 2002. The location of the study population of *Banksia quercifolia* is shown. Note: two categories of unburnt are different reflectances of vegetation in unburnt condition.

from the spring prescribed burn in November 2002 to the spring (November) 2011 assessment, three years after the last introduction of fire in early summer (December) 2008. Having experienced two summers, there was a high probability that most of the surviving regeneration from the 2008 fire would develop to maturity (Enright *et al*. 1998). A final population assessment was made in summer 2015 to confirm that the population had more or less stabilised following the 2008 fire. To characterise the landscape fire regime as it applied to the 5000 ha London Forest, we used measures including the proportions of London Forest burnt at various frequencies, mean landscape fire interval, and mean landscape fire frequency (Table 1). Landscape fire interval and frequency refer to the interval and frequency with which fire was introduced to this landscape (London Forest) and resulted in some portion of the landscape being burnt.

B. quercifolia *Population Assessment*

In March 2004, some 12 months after the wildfire, permanent sample plots were placed in the burnt *B. quercifolia* population. The wildfire defoliated the vegetation and killed all *B. quercifolia* plants. A transect composed of a series of fifteen 5 m × 2 m (10 m^2) plots was

Table 1. The proportion (%) of the area of forest and non-forest vegetation, and of the *B. quercifolia* study area that burnt following five introductions of fire into the London Forest landscape (5000 ha).

Vegetation	Prescribed fire spring 2002	Wildfire summer 2003	Prescribed fire autumn 2005	Prescribed fire autumn 2006	Prescribed fire spring 2008
Forest	84	8		26	38
Non-forest	87	7		11	72
Total London Forest	86	7	5	19	55
Banksia study area	0	100	0	13	61

permanently marked, giving a total sample area of 150 m^2. These plots were assessed in March 2004 and then again several weeks before and after each introduction of fire in 2005, 2006, and 2008. Additional measurements were made in summer 2010, 2011, and 2015. For each 10 m^2 plot, the following data were recorded:

- visual estimate of the proportion (%) of the 10 m^2 plot burnt after each introduction of fire,
- number of dead plants,
- number of live plants (classified as either seedlings or mature plants),
- number of plants flowering or fruiting,
- number of infructescences per plant and number of follicles per infructescence (2004 assessment of wildfire-killed plants only), and
- height of each live plant.

To obtain information about the juvenile period of *B. quercifolia,* a nearby population that had regenerated following the 2003 wildfire in the adjoining Surprise Forest was monitored annually from 2004 to 2011. Juvenile period was deemed to be the time after fire when at least 50% of the population had reached flowering age. To obtain information about the quantity of seed in the canopy-stored seed bank, infructescences were collected from 40 mature plants of varying sizes and ages outside the sample area. Stem diameter, the number of infructescences collected from each plant, the number of follicles per infructescence, and the number of seeds extracted from each infructescence was determined.

In autumn (April) 2005, some three years after the prescribed fire and two years after the wildfire, fire was again introduced to London Forest. This was performed in two ways: (1) on the ground using drip torches to light around the edge of the forest to aid burn security and to attempt to re-burn the young *B. quercifolia* study population that had regenerated following the 2003 wildfire, and (2) by dropping aerial incendiaries on a grid pattern within the forest. As expected, given the young fuel age and the mild weather conditions, there was little ignition and sustained fire spread, with only the most flammable parts of the landscape re-burning (Table 1). Despite attempts to burn the recently regenerated *B. quercifolia* population using a drip torch, the mild conditions and the sparsity of fuel resulted in the population not burning.

This was repeated in autumn (March) 2006, by which time much of the understorey vegetation and fuel in London Forest was four years old and the *B. quercifolia* population was three years old. In addition to aerial incendiaries, a drip torch was again used in an attempt to burn the *B. quercifolia* study population, which, unlike other vegetation types in the landscape, was difficult to burn because of the sparse fuel. However, with increased effort, some patches did burn, particularly two plots beneath a large jarrah (*Eucalyptus marginata*

Donn ex Sm.) tree where leaf litter had re-accumulated. Other plots did not burn. Following a similar procedure, fire was re-introduced in early summer (December) 2008 when most of the *B. quercifolia* population was now 4.8 yr old. The build-up of fuel over this time and persistent attempts at igniting the population using a drip torch ensured that much (61%) of the study area burnt, albeit at low intensity.

RESULTS

Landscape Fire Regime and Fire Patchiness

The variability of fire behaviour during low intensity prescribed fires is reflected in the satellite map of burn severity, or biomass removal, derived using the pre- and post-fire NVDI (Figure 1). Over the period from November 2002, when the first fire was introduced, to February 2011 (8.3 years later) when the *B. quercifolia* population more or less stabilized after the last fire in December 2008, fire was introduced into London Forest and to the *B. quercifolia* population five times (Table 1). From satellite mapping, 1.8% of London Forest did not burn, 2.9% burnt once, 8.8% burnt twice, 84.8% burnt three times, and 1.7% burnt four times. Over the same period, the *B. quercifolia* population burnt three times, but the entire population only burnt once (Table 1). This regime equates to a London Forest landscape fire frequency (the frequency with which fire was introduced into the landscape and some part of the landscape burnt) equivalent to six fires per decade and a mean landscape fire interval of 1.7 yr. Fire frequency and mean fire interval in the *B. quercifolia* population over the same period (8.3 yr) was 3.6 fires per decade and 2.8 yr, respectively. However, the frequency with which the entire (100%) *B. quercifolia* population burnt, as opposed to a part of the population, was equivalent to 1.2 fires per decade. Over this period, the fire frequency and interval at various points in the landscape varied, reflecting the variability in flammability of the vegetation. Fire frequency in the most flammable and least flammable vegetation (fuel) in this landscape was equivalent to 4.8 fires and 1.2 fires per decade, respectively, with the most flammable (burnt most frequently) vegetation being sheoak woodlands and the least flammable being some moist riparian areas, vegetation on rock outcrops, and some heathland vegetation types with sparse fuels.

The proportion of the *B. quercifolia* study area and of the broader landscape (London Forest) that burnt during each of the prescribed fires and the wildfire is shown in Table 1. As satellite mapping was inadequate at fine spatial scales, the proportion of each of the 10 m^2 sample plots burnt was visually estimated, whereas the proportion of the London Forest landscape (5000 ha) that burnt was determined from satellite mapping. The proportion of London Forest that burnt following each introduction of fire (Table 1) reflects the variability in flammability of the different vegetation types. For example, of the area burnt in 2006, ~70% was forest and ~30% was woodlands and heathlands. With the exception of two plots that were affected by jarrah leaf litter, none of the *B. quercifolia* plots burnt.

Response of B. quercifolia *Population*

Before the 2003 wildfire, the study population of *B. quercifolia* comprised even-aged mature plants of similar size. There is no evidence that this species regenerates in the absence of fire (or other disturbance), so the pre-wildfire population was likely eight years old. Details about the age of the population in 1994, and the behaviour and patchiness of the 1994 prescribed fire that burnt and regenerated the population are not available.

The spring 2002 prescribed fire burnt much of the surrounding vegetation, but did not burn the study population (Table 1, Figure 1). However, the early autumn 2003 wildfire did, killing all plants, which regenerated from seed in the first winter post wildfire. Based on the number of infructescences per plant and the number of follicles per infructescence (two seeds per follicle), the ratio of seeds shed after the wildfire to the number of seedlings measured in spring 2004 was calculated to be 32.4:1 (i.e., ~3% of the seed bank successfully developed into seedlings by 18 months after the wildfire). The density of parent plants pre-wildfire, hence the density of seedlings post-wildfire measured in the fifteen 10 m^2 sample plots, was highly variable. Post wildfire, the mean ratio of seedlings-to-parent plants was 9.2:1 (SE = 0.99) (Figure 2).

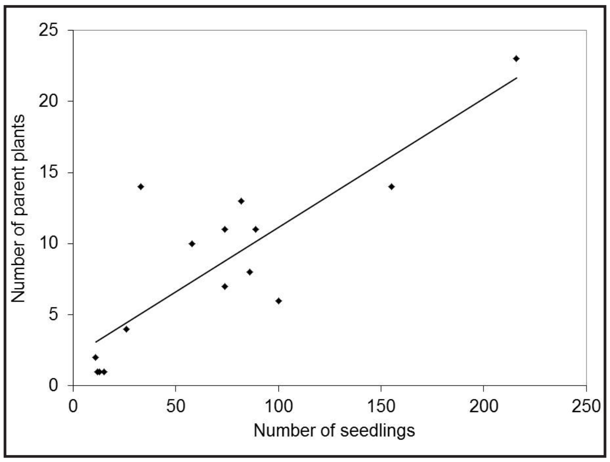

Figure 2. The number of mature (parent) *Banksia quercifolia* plants in each of the fifteen 10 m^2 sample plots before the summer 2003 wildfire versus the number of seedlings measured after the wildfire in spring 2004.

The juvenile period for *B. quercifolia* population in Surprise Forest that regenerated following the early autumn (March) wildfire in 2003 was 3.9 yr, and by ~5.9 yr post fire, about 90% of the population had flowered and set fruit. The larger plants in the even-aged cohort, as measured by stem diameter at ground level, matured earlier than smaller plants. Similarly, there was a direct linear relationship between plant stem size and the number of infructescences per plant, with the largest plants (stem diameter ~10 cm) carrying ~150 infructescences. Plants with a stem diameter less than about 2 cm rarely bore fruit.

An assessment of the London Forest study population in 2015 found that 47% of plants that regenerated following the last fire in December 2008 had not reached flowering age after 6.2 yr, which is about 1.6 times the juvenile period of the plants that regenerated following the early autumn wildfire in 2003. These plants were also significantly smaller than the plants that regenerated following the wildfire (Figure 3). Rainfall in 2003 was 1117 mm and in 2009 it was 758 mm, 24% higher and 16% lower, respectively, than the average rainfall over the study period (904 mm). Importantly for seedling establishment, rainfall in the first three months after post-fire seedfall was 337 mm following the March 2003 wildfire but only 61 mm following the December 2008 prescribed fire.

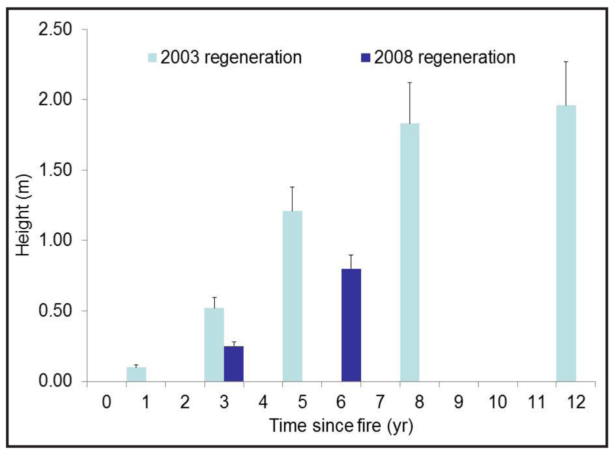

Figure 3. Mean height of *Banksia quercifolia* plants with age for the 2003 and 2008 cohorts of post-fire regeneration when the rainfall in the first three months post fire was 377 mm and 61 mm, respectively.

The fluctuation in the number of plants in each of the 10 m^2 sample plots over the study period is shown in Figure 4. Plant numbers fluctuated due to episodes of fire-caused mortality and post-fire regeneration. As a result of a mean landscape fire interval of 1.7 years, *B. quercifolia* was extirpated (0 plants) in two

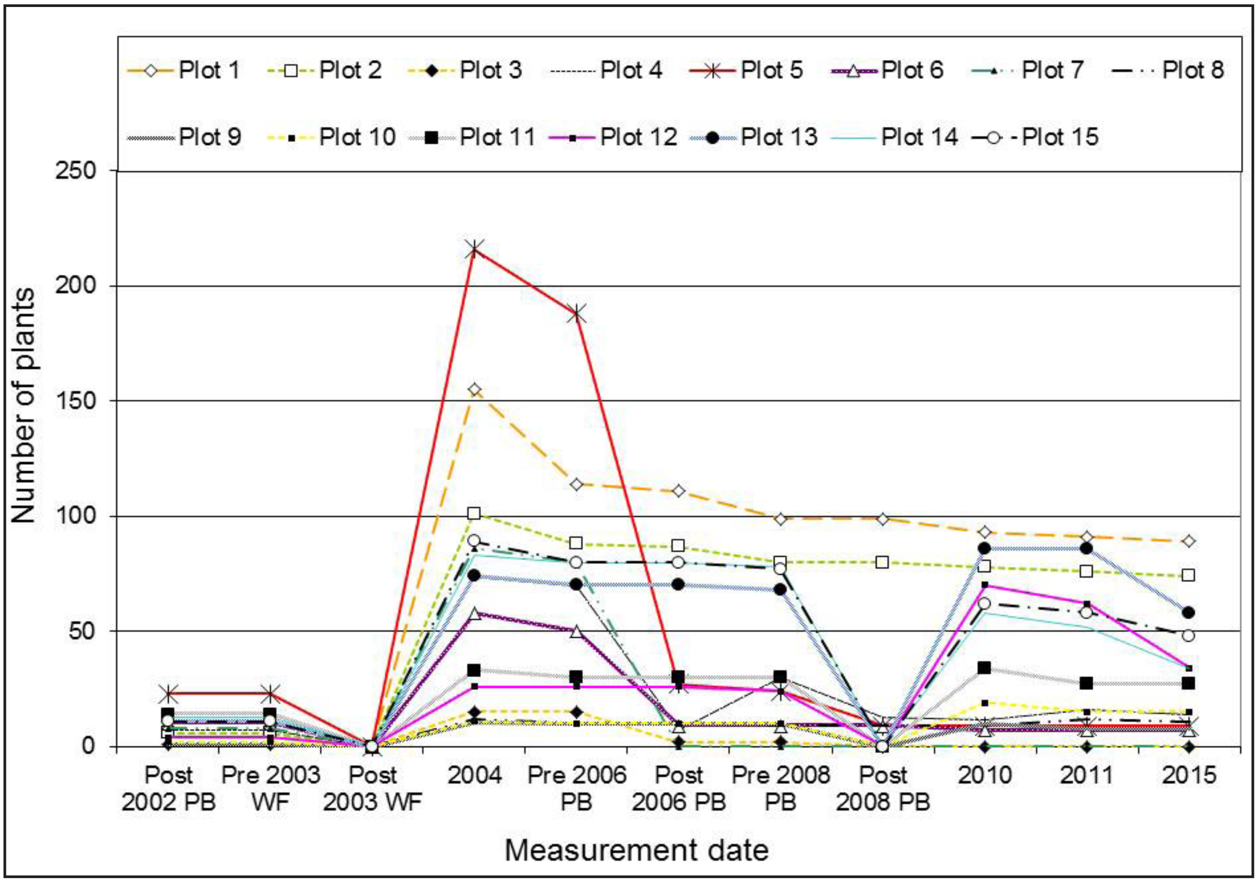

Figure 4. Population fluctuations of *Banksia quercifolia* in fifteen 10 m^2 plots in response to a wildfire (WF) and four prescribed burns (PB) from 2002 to 2011, resulting in a mean landscape fire interval of ~2 yr. The spring 2005 prescribed burn, which burnt ~5% of the landscape (London Forest) and none of the study plots, is not included.

plots, remained unchanged in one plot, decreased in two plots, and increased in ten plots. Cycles of fire escape, and fire-caused mortality and regeneration, resulted in an increase in the study population from the 2002 baseline of 126 plants, to 428 plants in 2015. The population trends graphed in Figure 4 show a 14% overall decline in plant numbers from 2011 to 2015.

As a result of the frequent exposure to fire since 2002, the population changed from an even-aged cohort to one of three age classes. In 2011, 56.5% of the population was two years old, 6.5% was five years old, and 37% was eight years old, representing the three fire-stimulated regeneration events. The changing density of juvenile and mature plants over time is shown in Figure 5. By 2015, there were about equal numbers of mature and juvenile plants.

DISCUSSION

An even-aged population of mature *B. quercifolia* embedded in forest and heathlands in south-west Western Australia escaped a low intensity patchy spring prescribed fire but was then burnt and killed by an intense summer wildfire. The population escaped the prescribed fire because, unlike the surrounding vegetation, the discontinuous fuel typically associated with these populations was not flammable under spring conditions of relatively high fuel moisture content and mild weather. In fire-prone environments, fire sensitive plant species are usually restricted to less flammable

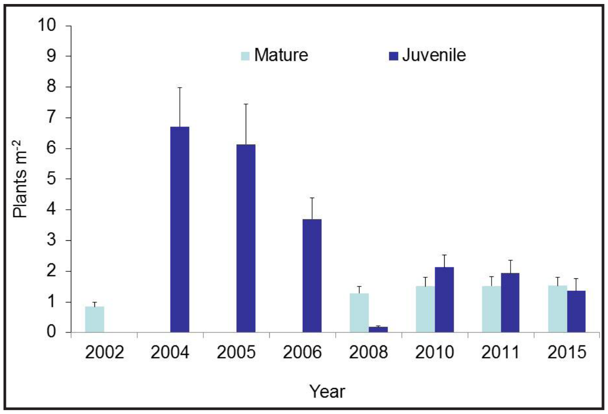

Figure 5. Plant density and maturational structural changes in a population of *Banksia quercifolia* exposed to a summer wildfire and four prescribed fires from 2002 to 2011.

parts of the landscape or form a less flammable fuel complex (Gill and Bradstock 1995, Russell-Smith 2006, Burrows *et al*. 2008) and this is exemplified by *B. quercifolia* thickets. After escaping a low intensity prescribed fire, an intense summer wildfire burnt and killed all plants in the population, but also triggered the release of seed, resulting in dense seedling regeneration following winter rainfall. Of the total amount of seed estimated to have been released, about 3% had germinated and survived as seedlings when measured 18 months after fire, which is similar to other serotinous seeders in this region (Enright and Lamont 1989, Lamont *et al*. 1991*b*). Despite subsequent re-introductions of fire into London Forest landscape at short intervals, the *B. quercifolia* population persisted through cycles of fire escape and fire-caused mortality and recruitment. The extent of successful regeneration following spring and autumn fires was sufficient to ensure that the population increased despite a mean landscape fire interval of 1.7 yr with a landscape fire frequency of six fires per decade. By 2011, the estimated number of seeds in the population's seed bank was about 14% less than the mature population before the 2003 wildfire due to the increased proportion of young plants in the uneven-aged population.

This study demonstrates the importance of spatial variation in fuel flammability and associated local fire behaviour to the survival and persistence of fire sensitive species such as *B. quercifolia* embedded in flammable landscapes. The introduction of fire at intervals shorter than the juvenile period of *B. quercifolia* did not result in the extirpation of the population because, unlike many other vegetation communities, the entire population did not burn each time fire was introduced. While the mean landscape fire interval was 1.7 yr, most of the *B. quercifolia* population did not burn until it was 5.7 yr old when about 61% of the population burnt, even though attempts were made to burn the population about every two years. As the population aged, its composition and structure as fuel also matured. In the early years following fire-stimulated regeneration, subsequent fires burning in the surrounding, more flammable vegetation under mild spring conditions did not burn the *B. quercifolia* population because of a lack of fuel. However, by the time the population was 5.7 yr old, the fuel had developed to the extent that about 61% of the population was burnt and killed during a low intensity prescribed fire. By this time, a high proportion (~90%) of the population had reached maturity, resulting in post-fire seedling regeneration.

The amount of rainfall in the first 12 months after fire had a strong influence on the growth and maturation of post-fire regeneration of *B. quercifolia*. The juvenile period increased significantly from 3.9 yr following the 2003 wildfire to 6.2 yr following the 2008 fire. The 12-month post-fire rainfall was 19% above annual average following the 2003 fire and 16% below average following the 2008 fire. This finding is consistent with Enright *et al*. (2014) who, working in shrublands in a lower rainfall (~500 mm annum^{-1}) region of Western Australia, found that a 20% reduction in post-fire winter rainfall resulted in a 50% increase in the juvenile period of serotinous species.

The species was extirpated from two of the fifteen 10 m^2 sample plots as a result of repeated fires at short intervals burning these plots before the plants had reached maturity. These plots burnt at short intervals because of a localised accumulation of flammable jarrah leaf litter originating from a single large tree near the plots. This highlights the importance of fine-scale variation in fuel continuity, quantity, and, hence, flammability to the survivability of fire sensitive plants. This variability in fuel flammability and consequent fire behaviour is most evident when fires are burning under mild weather, higher fuel moisture content conditions, and in recently burnt fuels, and least evident or non-existent under extreme weather, low fuel moisture conditions, and long unburnt fuels when virtually all vegetation types are likely to burn.

In one of a few published field studies to explore the persistence of fire sensitive plant species in relation to fire patchiness, Ooi *et al*. (2006) reported that fire sensitive *Leucopogon* R.Br. species in the Sydney region of Australia were able to persist under a regime of frequent low intensity, patchy fires. Although *Leucopogons,* unlike *B. quercifolia,* are not serotinous but have a soil-stored seed bank, this finding is consistent with the findings of the current study. Ooi *et al*. also reported that low intensity fires were patchier than high intensity fires and that the proportion of plants killed by fire decreased with increasing patchiness. Although this relationship was not quantified, it is consistent with observations made in the current study. Similarly, Oliveira *et al*. (2015) reported the importance of variability in fire severity and patchiness on the persistence of fire sensitive plant species in northern Australia and, in the same paper, cited studies demonstrating how fauna species also benefit from patchy fires.

Field verification that populations of fire sensitive taxa are able to persist under a regime of frequent fire provided that the fires are patchy is also consistent with modeling by Enright *et al.* (1996) who reported that *Banksia hookeriana* Meisn. was able to persist even if fires occurred at two- to three-year intervals, provided that the fires only burnt a small fraction of the population (i.e., the fires were patchy). That extirpation occurred in two of the fifteen plots studied here also supports the conclusions of Groeneveld *et al*. (2008) that the frequency of lethal fires at the patch level needs to exceed the juvenile period of (serotinous) species if the species is to persist.

Species persistence or population viability models that are not spatially explicit, or that do not take into account the spatial and temporal variability of fire behaviour and subsequent patchiness, will result in erroneous predictions about the likelihood of plant extinctions under various fire regimes. As noted by others (Jurskis *et al*. 2003, Penman *et al*. 2008, Jurskis 2011, Oliveira *et al*. 2015), assuming all fires are lethal to fire sensitive obligate seeders is largely based on observations of intense wildfires rather than low intensity fires. Persistence or population viability models that don't take into account associations between the fire sensitivity or fire resilience of plant species, and the level of risk of ignition and combustion of their habitats, may result in erroneous conclusions.

In the current study, with the exception of two plots that were affected by the localised build-up of eucalypt leaf litter, immature populations of *B. quercifolia* were not able to burn under mild weather and fire behaviour conditions. This mechanism is unlikely to function effectively when the fuel structure of these populations, which usually occur as clumps or thickets with little or no overstorey, has been modified by the presence of an overstorey, by disease, or by weed invasion. Large, fast spreading wildfires burning in long unburnt vegetation and under severe weather conditions may also threaten immature, isolated, small populations of *B. quercifolia* embedded in flammable fuel structures such as forests and heath.

At relatively small spatial scales, infrequent, intense summer fires result in even-aged populations of *B. quercifolia*, whereas frequent, low intensity patchy fires result in uneven-aged populations. This is consistent with Ooi *et al*. (2006) who found that patchy fires created uneven-aged populations of fire sensitive *Leucopogon* species. The south-west Australian forests have been burnt by frequent low intensity prescribed fires, as well as occasional high intensity wildfires, for almost 60 years (Burrows and McCaw 2013) and populations of *B. quercifolia* and other fire sensitive species persist. This history, and the findings of the current study demonstrate that, while fire sensitive species may not depend on frequent, low intensity patchy fire, they are able to persist under such a regime.

CONCLUSION

Understanding the importance of patchiness in fire behaviour associated with frequent, low intensity fires burning under mild weather conditions has important implications for the management of plant species and communities that are sensitive to fire, and for the management of hazardous fuels in the context of the protection of human communities and other assets from wildfire. We have demonstrated how a fire sensitive plant species persisted under a regime of regular introduction of fire into the landscape at short intervals compared with the juvenile period of the species. This regime resulted in relatively low fuel quantities at the landscape scale, which, together with moist fuel and mild weather, resulted in a high level of burn patchiness. Under these conditions, the more flammable parts of the landscape burnt frequently at low intensity, but the less flammable parts, including the *B. quercifolia* population, burnt less frequently. Time to maturity in relation to the interval between fires that burn and kill populations of fire sensitive species such as *B. quercifolia* is important for assessing the persistence of populations in relation to fire. We have demonstrated that this is strongly influenced by post-fire rainfall with juvenile period increasing for plants that germinated following spring fires and that experienced below average rainfall over the next 12 months. In a drying climate, the likelihood of below average rainfall following a fire, and the consequent increase in the maturation time of post-fire regeneration, needs careful consideration by fire managers. Although the frequent introduction of low intensity patchy fires reduces the risk of burning less flammable, fire sensitive vegetation types in the landscape, this could be off-set by an increase in the juvenile period.

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