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Fire-stimulated reproduction in the resprouting, non-serotinous conifer Podocarpus drouynianus (Podocarpaceae): the impact of a changing fire regime

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Abstract

Species with fire stimulated reproduction (fsr) are common in Mediterranean climate ecosystems. We investigated how season of, and time since, fire affects seed production in *Podocarpus drouynianus* F. Muell., a dioecious resprouting coniferous shrub endemic to the jarrah (*Eucalyptus marginata* Sm.) forests of southwestern Australia, and if the now largely managed fire regime in these forests poses a risk to its persistence. We hypothesised that, like other species showing fsr, seed production in *P. drouynianus* would be limited to the first few years following fire and seed set would be lower after spring burns. Mature plants regenerated rapidly from buried stem tissue (lignotuber) after fire, producing abundant sporophylls in autumn 12–18 months later. Stands burnt in autumn showed peak seed production 1 year later, while for those burned in spring, peak seed production was delayed until the second autumn after fire. Limited seed production occurred for up to 3 years following fire, but no seed production was observed in longer unburnt (>10 years since fire) stands. While we did not observe a significant impact of fire season on seed production, seed weight and viability were lower for spring-burnt plants. Population-level effects associated with plant density may also have negative impacts on *P. drouynianus* demography, with females within a small population burnt in autumn producing very few seeds 12 months following fire. Interactions between climate change, fire regimes

and fire management practices need to be considered in order to best safeguard the long-term persistence of this conifer species.

Introduction

The importance of fire on ecosystem properties and function has been extensively documented (Bond and Van Wilgen 1996). Much of the flora in fire-prone, Mediterranean-type ecosystems has evolved adaptive traits in response to a regime of frequent fires (Gill 1981) with fire-promoted flowering in perennial plants one of the key responses (Lamont and Downes 2011). If fire-stimulated reproduction (fsr) occurs only in the first 1–2 years after fire, and is followed by a period of dormancy or only vegetative growth through the remainder of the inter-fire period, the species is considered to exhibit obligate fsr (Lamont and Downes 2011). Up to 154 different species within the Mediterranean regions of Australia and South Africa are thought to exhibit obligate fsr (Lamont and Downes 2011). Such species may be particularly susceptible to changes in fire regimes that are discordant with their flowering phenologies and associated cueing and resource availability.

Prior to the settlement of Australia by aborigines, forests in southwestern (SW) Australia are thought to have experienced fires of moderate to high intensity, on average every 30–100+ years (Enright and Thomas 2008). Conditions in SW Australia are normally conducive to fires over a 4–8 month period, with lightning strikes a major source of ignition during summer and early autumn, resulting in intense and wide-spread fires (McCaw and Hanstrum 2003). The arrival of aborigines in the late Pleistocene instituted an anthropogenic fire regime, with a shortened fire interval in heavily occupied areas of 10–15 years (Hassell and Dodson 2003) or less. Fires were typically ignited from October to June, with most recorded for the hottest months from December to March (Abbott 2003). Current land management practices by forestry and conservation authorities favour a regime of short interval burns,

delivering low intensity fires in spring or autumn that reduce surface layer fuels and are readily suppressed (Enright and Fontaine 2014).

Current fire regimes in SW Australia are predicted to shift on a landscape scale as a result of climate change, and at a local scale are being altered as a result of habitat loss and fragmentation (Williams et al. 2001). Modelled future climates within the region (Bates et al. 2008) project a decline in rainfall and an increase in temperature. These climate shifts will result in increasingly prevalent severe fire weather conditions, increasing the likelihood of ignitions, with more frequent fires over a longer fire season (Bradstock et al. 2002). Species whose reproductive strategies have evolved in response to recurrent (predominantly summer) fires are potentially threatened by changes to fire regimes that are discordant with their life histories.

Most fsr species produce a soil seed bank with germination cued by fire. However, a small number of species that flower post fire do not have a soil seed bank and must recruit new individuals within one to two seasons after flowering e.g., *Doryanthes excelsa*, *Telopea speciosissima*(Denham and Auld 2002) and *Xanthorrhoea* spp. (Taylor et al. 1998; Lamont and Downes 2011). Some fsr species show reduced flowering and shoot growth following spring burns as compared to summer–autumn burns (Bowen and Pate 2004) with explanations including reduced fire intensity that fails to cue flowering, and less time for development of the regenerating shoots (Bowen and Pate 2004). Shifting season of fire occurrence may impact on long term demographic success in fsr species by restricting the acquisition of resources for the next reproductive episode, especially under increasingly dry conditions. Despite this, the link between burn season, time-since-fire and plant demography is poorly understood, especially for obligate fsr species which may be particularly vulnerable to decline since they have only a narrow window of opportunity for reproduction linked to the time of fire.

Little is known about the ecology of *Podocarpus drouynianus* F. Muell. (though see Chalwell and Ladd 2005; Ladd and Enright 2011), the only member of the Podocarpaceae found in south western Australia (Enright and Hill 1995). Although fire-tolerant, *P. drouynianus* retains some life history characteristics of its fire-sensitive relatives, such as large recalcitrant seeds, but resprouts rapidly after fire from a lignotuber, with most vigorous shoot regrowth observed in the first year following fire

(Chalwell and Ladd 2005). *Podocarpus drouynianus* is the most phylogenetically ancient obligate fsr species in Western Australia and has significant biodiversity and commercial value, with young foliage routinely harvested from the wild for use in floral arrangements (Ladd and Enright 2011). *Podocarpus drouynianus* also has a key dispersal mutualism with the emu (*Dromaius novaehollandiae* Latham) and seed is a favoured component of its diet when available (Chalwell and Ladd 2005). Given the conservation and commercial value of the species, and with altered fire regimes continuing to threaten the persistence of flora in the region (Myers et al. 2000), it is important to understand how fire season and time-since-fire may impact the phenology and reproductive biology of *P. drouynianus* (and other obligate fsr species). The aims of this study were to:

(1) Determine the extent to which *P. drouynianus* seed production is linked to time since fire.

(2) Identify whether, as has been seen for other fsr species (Bowen and Pate 2004; Lamont and Downes 2011), season of fire affects seed production—we hypothesise that spring fires lead to lower seed production.

Methods

Study species

Podocarpus drouynianus is a dioecious, non-serotinous shrub that grows in the wetter areas (>900 mm annual rainfall) of fire-prone forests of SW Australia (Chalwell and Ladd 2005). The species is unusual within the Podocarpaceae, being one of only two fire-tolerant species in Australia (*P. spinulosus* in eastern Australia being the other; Gibson et al. 1995). Female and male sporophylls are borne in the leaf axils of the new shoots, with seeds ripening and shed in autumn (Chalwell and Ladd 2005; Lamont and Downes 2011). The production of a small amount of seed in the second year after fire has been observed in some instances, and plants growing in open fields and gardens may show seed production in most years (likely reflecting higher resource availability). Seeds of *P. drouynianus* are recalcitrant, germination coinciding with the arrival of winter rains (Chalwell and Ladd 2005). As the species has likely evolved under a regime of summer–autumn fires, our

hypothesis is that spring burns are likely to be inimical to reproduction as there is a shorter time available for the production of new reproductive structures after a spring burn than for fires in summer or autumn. Further, we predict that there is little seed production in the second year after fire regardless of fire season. No seeds are produced by plants in long unburnt forest areas so recruitment of new individuals is restricted to a narrow window of 18 and 24 months after fire.

tudy sites

Podocarpus drouynianus occurs in the moist (annual rainfall >900 mm) jarrah (*Eucalyptus marginata*) forests of southern SW Australia, with small outlier populations in the northern jarrah forest at Dwellingup and Sawyers Valley (Fig. 1). Initially, eight 50 × 50 m and two 30 × 30 m (where plant density was very high) sample plots were established near Nannup in southern SW Australia in February–March 2012 (Fig. 1). Nannup has a mean average annual rainfall of 946 mm, with approximately 500 mm falling in winter, and approximately 200 mm in autumn and spring respectively (Australian Bureau of Meteorology; BOM 2014). Plots were located in areas burnt by prescribed fire by the Western Australian Department of Parks and Wildlife (DPAW) in different seasons (autumn vs. spring) over the previous 2 years. Four further 50 × 50 m monitoring plots were installed during March 2013 to encompass additional areas of the Nannup forest block, including areas long unburnt (>10 years since last fire). *Podocarpus drouynianus* was also surveyed in adjacent areas at Forest Grove and Burnham (near Nannup) that had been burnt by separate ignitions (Table 1). Due to the low density of *P. drouynianus* in these areas, a random survey of individuals was conducted. Each monitoring plot was located in a site burnt by a separate prescribed fire, with the exception of one site (Rosa) that was burnt by wildfire following escape of a prescribed burn. The distance between plots at Nannup varied. Plots in adjacent forest blocks burnt in different seasons were separated by <500 m, while all other plots were placed within forest blocks >5 km apart.

Sample plots were also established during March 2012 in the northern outlier population at Sawyers Valley (31°55′S, 116°13′E) in areas burnt by prescribed fire by DPAW in late autumn and early spring of 2011. Sawyers Valley has a mean average annual rainfall of 1042 mm, with similar seasonal distribution to that at Nannup (Mundaring Weir weather station, BOM 2014). At this site, two

25×25 m plots were located in the spring burn area and four 25×25 m plots in the autumn burn area. The larger number but smaller size of plots at this site reflects the limited size and spatial distribution of the *P. drouynianus* population. Since plots within the spring and autumn areas at Sawyers Valley were each burned by a single fire, data were aggregated into a single sample for each fire season to avoid pseudo-replication.

Demography

During the initial census of plots in February–March 2012, we recorded the sex of each reproductive individual. Plants without sporophylls were classified as being of unknown sex. Population structure was described based on lignotuber size, estimated as the mean of lignotuber crown width (i.e., where stems emerge from the lignotuber) for the longest axis, and width at right angles to this. The number of intact and damaged (eaten by granivores) seeds on each female was counted. We collected five intact seeds from each of 10 individuals selected at random in each plot for viability testing. For three of the plots, fewer seeds were collected (17, 34 and 20 in total, respectively) owing to low seed production at these sites. There were no seeds at one site. The weights of each seed and podocarpium were recorded. Seeds were cut in half and considered viable if a healthy-looking torpedo-shaped green embryo was present in the female gametophyte.

During the March 2013 census we revisited established plots to obtain estimates of the current seed crop. For the additional plots installed at Nannup in 2013 we also determined the demographic parameters as described above.

Data analysis

We used a generalised linear mixed model, with parameter estimation via penalised quasi-likelihood (PQL) methods to assess the impact of burn season, year of burn, study site, time-since-fire and mean lignotuber width (and the interaction between these main factors) on seed production of *P. drouynianus*. Individual monitoring plots were included in the model as a random effect and the Poisson family error function was selected. We used PQL for the model fits due to considerable overdispersion within the count data (Bolker et al. 2009). Analysis was conducted using

the *glmmPQL* function within the 'MASS' package (Venables and Ripley 2002) within R version 2.15.2 (R Core Team 2012). The model with all parameters (minus non-significant interaction effects) is presented to provide a clear overview of the impact of main factors on seed production following Burger et al. (2012) who also used glmmPQL to fit overdispersed ecological data. Mean seed weight between burn season (pooled by study site) for material collected during the 2012 census was compared using a *t* test, assuming unequal variance. Potential seed viability of the collected seeds was compared between autumn 2011 and spring 2010 burnt sites at Nannup using a *t* test, assuming unequal variance. For the 2012 census data, Female:Male sex ratios were compared using Chi-squared analysis, with the null hypothesis of a 1:1 ratio (Ornduff 1985). The proportion of plants producing sporophylls from the autumn- and spring-burn data (pooled across study site and time-since-fire) were compared using Chi-squared analysis.

Results

Mean seed weights (for seed collected from the 2012 census) between burn seasons were significantly different ($t_{125} = 13.8$, $P < 0.001$), with seeds sampled from areas burnt by prescribed fire in autumn heavier (1.9 ± 0.1 g SE) than those from areas burnt in spring (0.9 ± 0.1 g). Seed cut tests indicated that almost 100 % of seeds sampled from areas prescribed burnt in autumn were viable. Conversely, a smaller percentage (89 ± 1 %; $t_2 = 11.0$, $P < 0.01$) of seeds sampled from the spring burn areas was viable.

Population size structures at Nannup were all skewed to the left, with a predominance of individuals <50 cm mean lignotuber diameter (Fig. 2). Population structure at Sawyers Valley differed markedly from that at Nannup with a much higher proportion of small individuals and fewer large (>150 cm lignotuber diameter) individuals (Fig. 3). There was no difference in the mean lignotuber width for reproductive individuals among study sites (Fig. 4).

Determination of sex was only possible where plants carried reproductive structures at the time of census. There was no clear size threshold at which individuals reached reproductive stage, with a few

small individuals (smallest reproductive individual had a mean lignotuber diameter of 4 cm) producing sporophylls, and no indication that males became reproductive at a different size from females. The proportion of plants that produced sporophylls was higher in populations in the first 2 years following autumn burns (53 ± 4 %) in comparison to spring burns (34 ± 7 %; χ^2 = 106.6, df = 1, $P \leq 0.01$), though sporophyll production was low (ca. 25 %) 3 years following autumn burns (Fig. 5). The proportion of female to male individuals at Nannup was not significantly different from 1.0 (1.02 ± 0.18; χ^2 = 0.05, df = 1, P = 0.83). The proportion of female to male individuals at Sawyers Valley was also not significantly different from 1.0 (0.95; χ^2 = 0.02, df = 1, P = 0.88).

Seed production was significantly linked to time-since-fire and mean lignotuber width, with seed production decreasing sharply after 1 year since fire and a greater number of seeds recorded with increasing lignotuber size (Fig. 6; see Table 2 for model parameters). The largest seed crop was produced at each site 12–18 months following fire, irrespective of fire season and the year during which the fire occurred. While fewer seeds were produced per female following spring burns, the difference was not significant (Table 2). No seeds were produced nor could the sex of the plants be determined for the three long unburnt (>10 years since last fire) plots at Nannup. Neither the site nor year of the burn significantly affected seed production (Table 2).

Discussion

Podocarpus drouynianus exhibits fire-stimulated reproduction (fsr), with sporophyll production decreasing sharply, to almost zero, >2 years following fire. While the season of burn was not found to substantially impact seed production, the number of plants producing sporophylls was significantly higher following autumn burns, relative to spring burns. Considering the 1:1 male/female sex ratio observed at both Sawyers Valley and Nannup, a greater proportion of females became reproductive following autumn burns in comparison to spring burns. No seeds were recorded from individuals that were burnt in spring and surveyed in autumn 6 months after fire at either Nannup or Sawyers Valley,

nor did long unburnt individuals in undisturbed forest produce seeds. Seeds produced from autumn-burnt plants were heavier (1.9 g) and had higher viability (100 %) in comparison to spring-burnt plants (seed weight 1.1 g and 89 % viable).

The relationship between environmental cues and reproductive initiation in fsr species is not simple, but a significant impact of fire season on floral phenology has been recorded for several species exhibiting fsr in SW Australia. *Stirlingia latifolia* (Proteaceae), a common shrub of the jarrah forests, is noted to have prolific inflorescence production following summer/autumn fires, with only half the number produced following spring fires (Bowen and Pate 2004). Flowering of some grass tree species, *Xanthorrhoea* spp. (Xanthorrhoeaceae), is also significantly influenced by fire season. *Xanthorrhoea preissii* produced only 40 % as many inflorescences following spring burns compared with flowering after autumn burns (Lamont et al. 2000) while in *X. fulva* there were 20 % fewer flowering plants after a winter compared to a summer fire (Taylor et al. 1998). Both *S. latifolia* and *X. preissii* co-occur with *P. drouynianus*, *P. drouynianus* might be expected to display similar seasonally-influenced seed production. In the absence of such an observation, it should be considered that divergent reproductive strategies may benefit individual species by limiting competition.

Seeds from some fsr species (e.g., *X. preissii, P. drouynianus*) do not form a soil seed bank and germination occurs normally in the second winter after fire, soon after the seeds are shed (Ladd and Enright 2011; Lamont and Downes 2011), taking advantage of open space and resources available in the first few years following fire. *Podocarpus drouynianus* seeds germinate relatively quickly after seed release from the plant to coincide with winter rains (Chalwell and Ladd 2005). Other taxa, such as *Telopea* in eastern Australia, show a more delayed response, producing and liberating seeds up to 2.5 years after fire by which time considerable vegetative regrowth has occurred (Denham and Auld 2002). Many other fsr species such as *S. latifolia* accumulate a soil seed bank and although seeds are produced in the first year after fire, they remain dormant in the soil until the next fire when smoke triggers a germination response (Bowen and Pate 2004).

Seed size is often inversely correlated with post-dispersal seed longevity, and environmental factors may further affect seed survival (Schutte et al. 2008). The smaller seed sizes observed following the spring burns is unlikely to result in greater seed longevity, rather it may reflect a depleted resource pool available for seed set following greater overstorey canopy development. Given that seeds such as those of *P. drouynianus* are often under significant predation pressure in the post-burn environment (Bond 1984; Ladd and Enright 2011), poor seed production, coupled with comparatively reduced viability as a result of spring burning, may adversely affect recruitment of the species. Reduced seed size observed in spring burnt plants may also negatively impact potential recruitment. We observed a relatively small seed size overall (1.4 g) in comparison to the 2.85 g reported by Chalwell and Ladd (2005), likely attributable to reduced rainfall prior to the census years. Additionally, substantial variation in seed production between sites of the same burn history was observed. These local nuances in resource availability may impact seed size and potential germinability (Schutte et al. 2008). As the size and weight of seeds increases, so does seedling resilience to shading and competitive stress (Baker 1972; Stanton 1984). Seedlings of *P. drouynianus* established from the smaller seeds that are dispersed following spring burns may be less successful in the post-burn environment, having to compete with many other resprouter and seeder species (Bell 2001). The post-burn environment also varies with season of burn, with spring fires generally cooler than autumn fires, and consuming a smaller proportion of both live and dead biomass (Harrington 1993). Variation in fire intensity with season may be the cause of our observed fewer reproductive plants following spring burns. Improved seedling recruitment may be related to the increased intensity of hot autumn fires that ashes a greater proportion of biomass and releases more resources for establishment. Nutrient and moisture availability are influenced by intensity and season of burn, fuel load and other fire characteristics (Bond and Van Wilgen 1996), so that small seeds and germinants of *P. drouynianus* may be disadvantaged in a less open, less nutrient-rich post-burn environment following spring fires or in unburnt vegetation if the seeds are transported beyond the burned area. The spatial variability in fire temperatures encountered during prescribed burning (Hobbs and Atkins 1988) further reduce the efficacy of cool spring burns in combusting fuel and providing a suitably beneficial post-fire landscape for seedling recruitment.

The pyrogenic reproduction displayed by *P. drouynianus* is analogous to masting in other conifers. This has been argued as an adaptation to satiate seed predators (Chalwell and Ladd 2005; Archibald et al. 2012), but will also produce an attractive display for seed dispersers and may also increase the density of pollen (Smith et al. 1990), in an understorey wind pollinated plant like *P. drouynianus*. Denham and Auld (2002) report that the eastern Australian fsr species *Doryanthes exselsa* and *Telopea speciosissima* (which are not frugivore dispersed) suffer severe seed predation and that masting failed to satiate seed predators. In these two species seed is shed passively and seeds are smaller than in *Podocarpus*. Emus consume and carry *P. drouynianus* seeds long distances internally without harming them, and so may void them in unburnt areas where they escape seed predators (Chalwell and Ladd 2005). Their large seed size may be an advantage to seedling establishment under competition in unburned sites, and rapid lignotuber development in seedlings (Ladd and Enright 2011) means plants are well prepared to survive by resprouting when the next fire occurs. Cessation of seed production after two seasons may reflect a transfer of resources to lignotuber storage in preparation for the next fire, which may be more advantageous than continuing sporophyll production that may not lead to successful seed set or attract seed dispersers.

This study found that *P. drouynianus* exhibits fsr, producing seeds in the first 1-2 years after fire, but almost no seed during the inter-fire period there-after. While much attention has been paid to the vulnerability of fire-killed species to shortened fire intervals (Enright et al. 1996; Keeley et al. 1999; Westerling et al. 2011), resprouting species have been largely treated as uniformly highly resistant to altered fire regimes. However, some proportion of any resprouter population will be killed by fire, with further individuals dying during the subsequent inter-fire period, so that population maintenance still ultimately depends on adequate seedling recruitment. Here we illustrate that abundant seed production generally occurs 12–18 months following fire, irrespective of season of burn but declines rapidly after this time, and that seed size and viability is relatively reduced after spring in comparison to autumn fires. While many resprouter species return to a pattern of annual seed production within a few years of fire, and accumulate seed stores over the ensuing inter-fire interval, obligate fsr species have only one major opportunity per fire cycle to produce seeds, so that the time since fire in relation

to flowering and fruiting phenology is critical. Changed fire frequency and timing as a result of the managed use of fire to reduce fuel loads, further exacerbated by climate change, habitat loss and fragmentation (which may also exclude fire, resulting in negative demographic effects), may threaten *P. drouynianus*.

Land management agencies increasingly have to make decisions about fire regimes for asset protection and biodiversity conservation purposes in an environment where climate change is resulting in significant shifts in synoptic weather patterns (Hughes 2003) and fire hazard (Williams et al. 2009). In SW Australia, not only has temperature increased and rainfall decreased over the past 40 years, but rainfall has become less reliable, and is commencing later in winter (Yu and Neil 1993). Species that exhibit obligate fsr may face severe demographic consequences if the outcome of the interaction between climate change and altered fire regimes are not thoroughly considered as part of adaptive management strategies (Thomas et al. 2004). As a species with recalcitrant seeds, a delay in the commencement of winter rainfall likely threatens the recruitment success of *P. drouynianus*, with germinating seeds potentially drying out before the seedling can fully develop.

Species with constrained reproduction and recruitment will be less resilient to alterations in rainfall reliability and changed fire regimes than species that spread their seed production and recruitment more evenly through time, e.g., taking advantage of good rainfall years when they occur. Thus adaptive management programs in relation to the use of fire for biodiversity management need to take account of variations in the biology of different species such as that associated with obligate fire stimulated flowering and fruiting as illustrated here for *P. drouynianus*.

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Fig. 1 Distribution (*shaded areas*) of *P. drouynianus* in southwestern Australia. *Lines* are isohyets
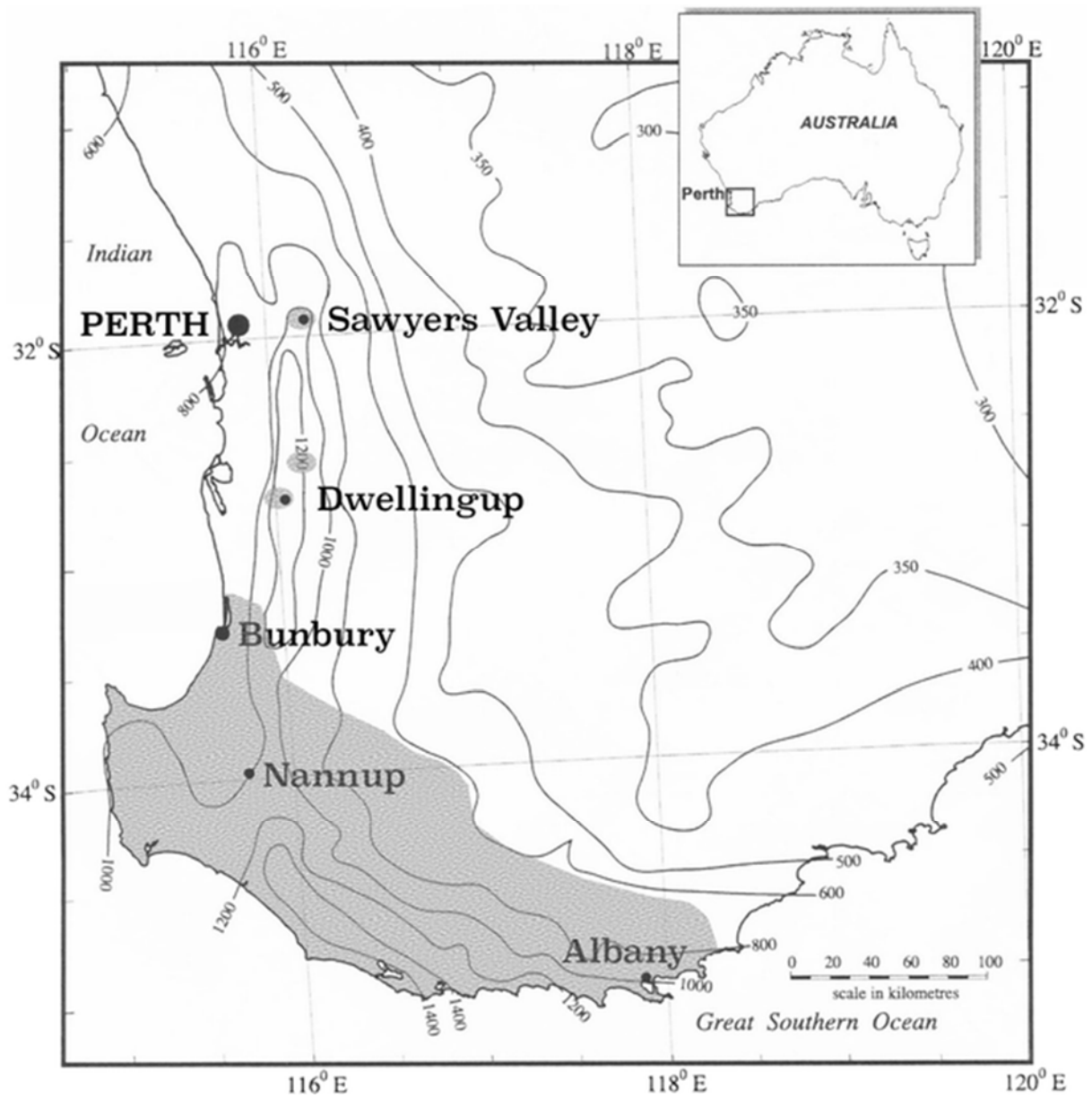
Fig. 2 Size-class (lignotuber width) and sex distributions for *P. drouynianus* populations from the Nannup (**a**) River Road (autumn 2010 fire), (**b**) Layman, Rosa, Milyeannup North (spring 2010 fire), (**c**) Whicher, Sollya, Milyeannup (autumn 2011 fires), (**d**) Cundinup, Brockman (spring 2011 fires), and Sawyers Valley (**e**) autumn 2011 fire, and (**f**) spring 2011 fire areas, SW Australia
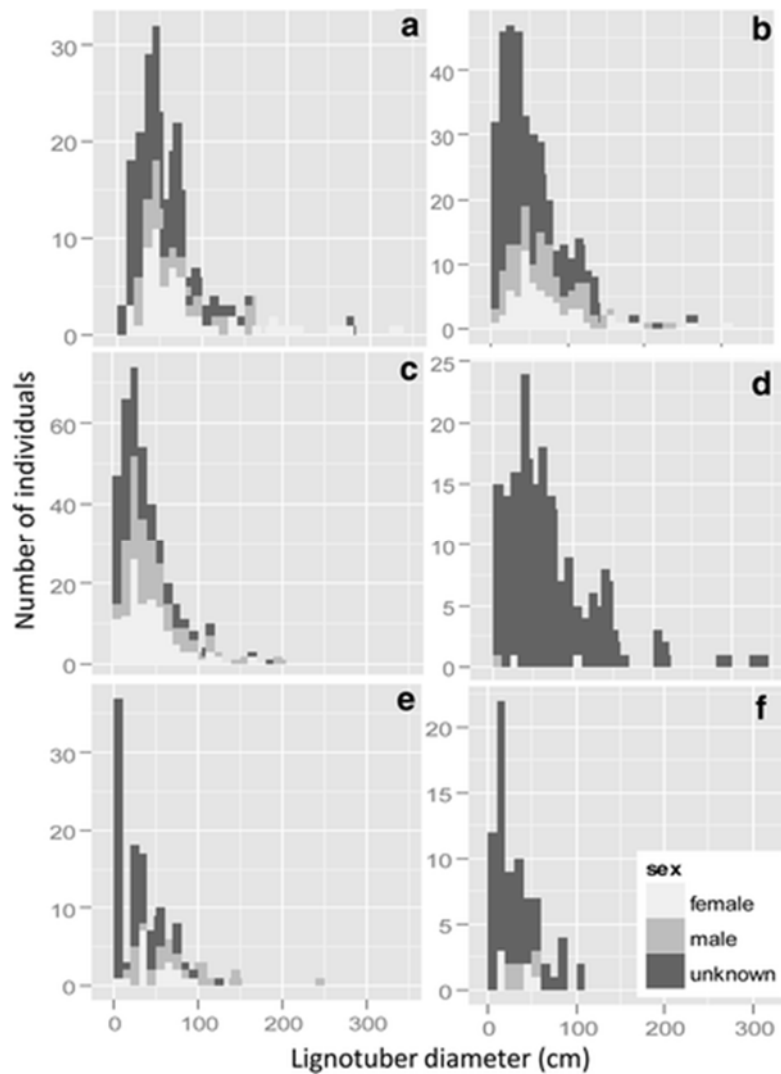
Fig. 3 Composite lignotuber size-class and gender distribution for *P. drouynianus* populations from (**a**) Nannup and (**b**) Sawyers Valley from 2012 census data
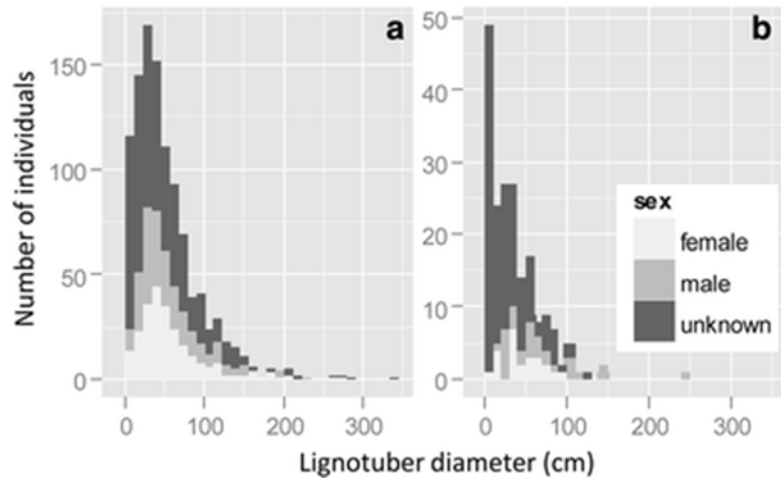
Fig. 4 Mean lignotuber diameter (cm) for reproductive *P. drouynianus* individuals sampled from different populations within Nannup and Sawyers Valley, southwestern Australia. *Black circles* indicate mean values and *open circles* outlier values, *bars* are standard errors of the mean
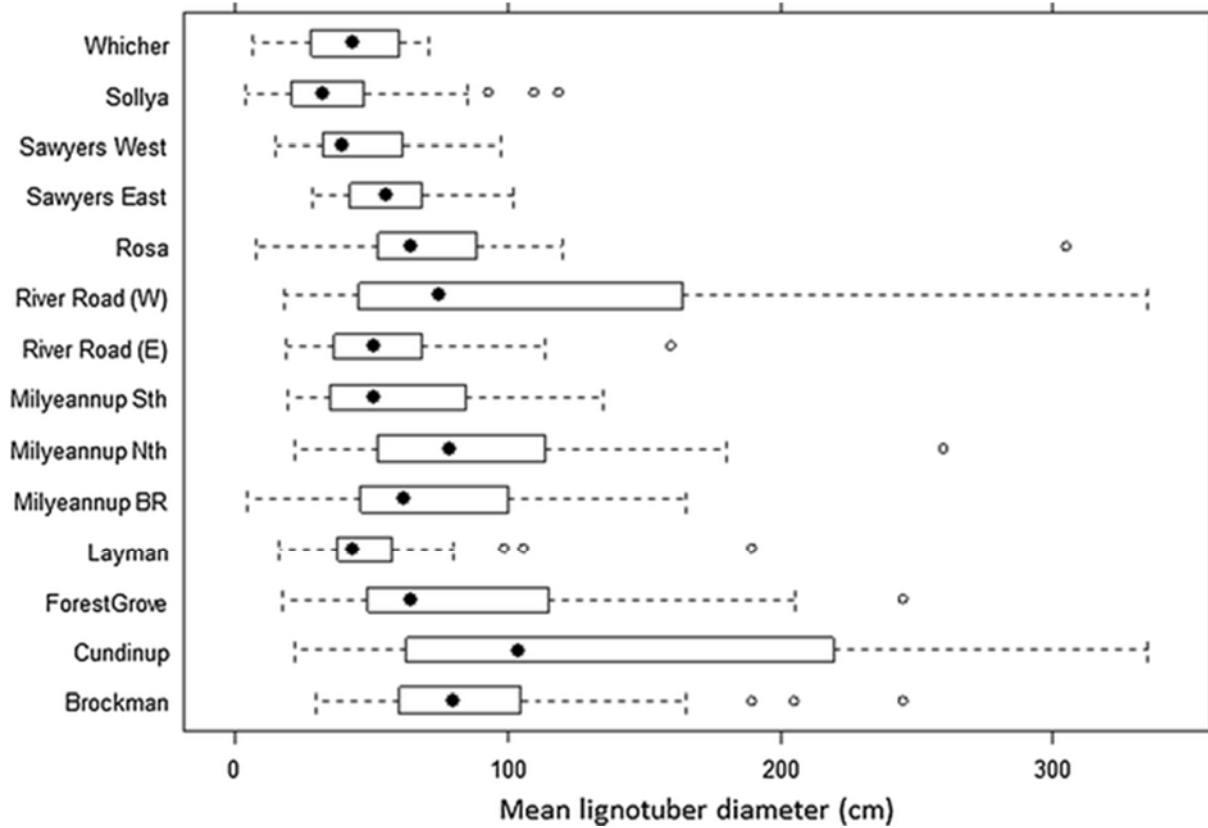
Fig. 5 Proportion of individuals producing sporophylls relative to time since fire (months) for *P. drouynianus* in populations at Sawyers Valley and Nannup, Western Australia. *Black circles* indicate mean values, *bars* are standard errors of the mean

Fig. 6 Seed production relative to time since fire (months) for *P. drouynianus* in populations at Sawyers Valley and Nannup, Western Australia. *Black circle* indicate mean values, *bars* are standard errors of the mean
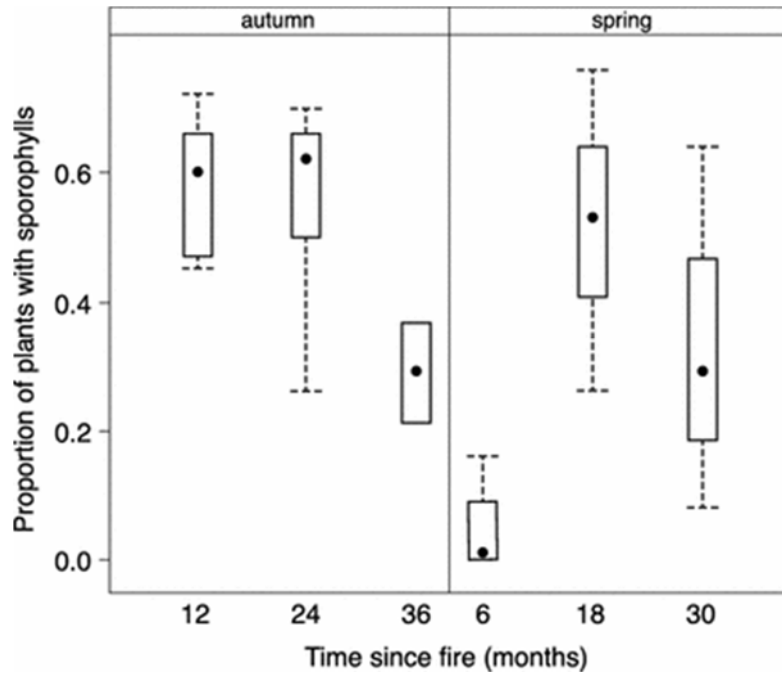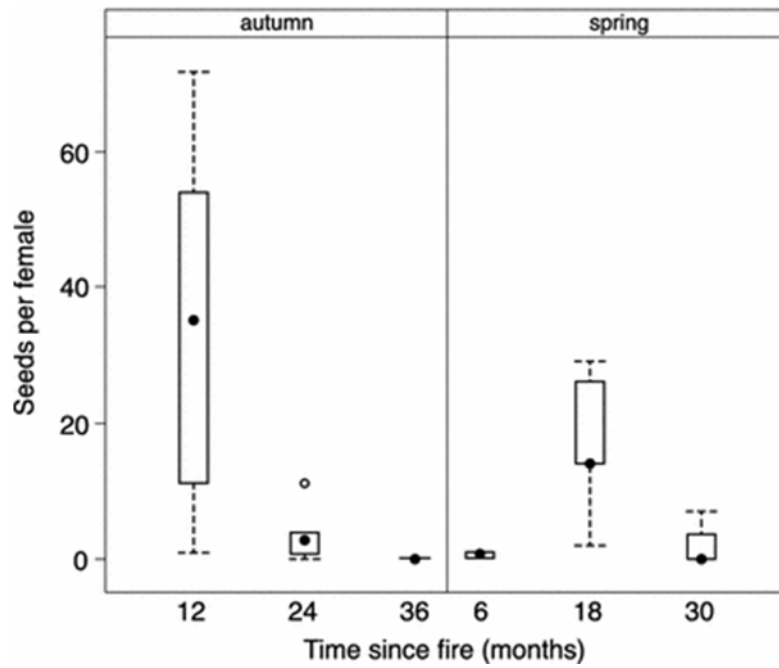
Table 1 Site name, location, season and year of prescribed fire for *P. drouynianus* monitoring plots near Nannup in the South–West region, Western Australia

Site	Location	Year	Burn season	Time since last fire
River Road (W)	34°1′12″S, 115°22′12″E	2010	Autumn	24, 36 months
River Road (E)	34°1′12″S, 115°22′12″E	2010	Autumn	24, 36 months
Layman	34°3′36″S, 115°25′12″E	2010	Spring	18, 30 months
Rosa	34°0′36″S, 115°23′24″E	2010	Spring	18, 30 months
Milyeannup Nth	34°10′48″S, 116°37′48″E	2010	Spring	18, 30 months
Whicher	33°45′36″S, 115°31′48″E	2011	Autumn	12, 24 months
Sollya	34°4′48″S, 115°36′36″E	2011	Autumn	12, 24 months
Milyeannup BR	34°7′12″S, 115°33′E	2011	Autumn	12, 24 months
Cundinup	33°33′S, 115°27′E	2011	Spring	6, 18 months
Brockman	33°35′24″S, 115°28′12″E	2011	Spring	6, 18 months
Milyeannup Sth*	34°10′48″S, 115°37′48″E	2011	Spring	18 months
Forest Grove*	NA—Random Walk	2011	Autumn	24 months
Burnham*	NA—Random Walk	2012	Autumn	12 months
Denny Rd—Sth*	34°4′12″S, 115°17′24″E	NA	NA	>10 years
Great South Rd*	34°3′36″S, 115°41′24″E	NA	NA	>10 years
Red Gully*	34°4′48″S, 115°36′36″E	NA	NA	>10 years

Plots marked with '*' were installed during the 2013 census. Time-since-fire refers to the period from ignition to census dates

Table 2 Generalised linear mixed model fitted via penalised quasi-likelihood (PQL) parameters for the impact of site, burn season, year of burn, time-since-fire and mean lignotuber width on *P. drouynianus* seed production in sample plots at Nannup and Sawyers Valley, southwestern Australia

	Effect on seed production (SE)	*t* **value**
(Intercept)	4.96 (0.79)	**6.25**
Burn season		
Spring	−0.06 (0.55)	−0.10
Year of burn		
2011	0.15 (0.64)	0.23
Site		
Sawyers Valley	0.19 (0.77)	0.24
Time-since-fire	−0.18 (0.02)	**−7.26**
Mean lignotuber width	0.01 (0.001)	**4.71**

A positive parameter value implies that the individual factor has a positive (increased) impact on seed production, however only bolded *t* values represent model parameters with a significant effect ($P < 0.05$)

Model parameters: number of seeds per plant approximate burn season + year of burn + site + time-since-fire + mean lignotuber width (1/monitoring plot)