Nield, A.P., Monaco, S., Birnbaum, C. and Enright, N.J. (2015) Regeneration failure threatens persistence of Persoonia elliptica (Proteaceae) in Western Australian jarrah forests. Plant Ecology, 216 (2). pp. 189-198.

Regeneration failure threatens persistence of Persoonia elliptica (Proteaceae) in Western Australian jarrah forests

Andrew P. Nield, Sophie Monaco, Christina Birnbaum and Neal J. Enright

School of Veterinary and Life Sciences, Murdoch University, Perth, Australia

Abstract

The severe disruption of herbivore relationships can result in catastrophic, demographic consequences for plant populations. We investigated the potential roles of herbivory, fire and their interaction, in the observed long-term regeneration failure of *Persoonia elliptica* R.Br. (Proteaceae), an understory tree species of fire-prone jarrah (*Eucalyptus marginata* Sm.) forests in southwestern Australia. Seed production, storage and viability were assessed, as was seedling recruitment in both the presence and absence of fire (a potential germination cue), using experimental herbivore exclosure plots. We also sought to determine the 'herbivory zone' (height) within which *P. elliptica* was susceptible to browsing. Herbivores, primarily the western grey kangaroo, preferentially consumed leaves of *P. elliptica* up to a browsing height of 1.5 m. Viability of fresh seeds was low at ca. 39 % and rapid viability loss was observed in the soil seed bank, with only ca. 5 % of seeds remaining viable for >1 year. Germination was restricted almost solely to burned areas and survival of recruits to the confines of herbivore exclosures. We suggest that an increase in the primary herbivore, combined with low viable seed supply, is the likely cause of continuing regeneration failure in this species. The slow growth of the species suggests that without intervention, seedlings and juvenile plants will be unable to escape the herbivory zone. Management actions to facilitate recruitment might best focus on the combination of managed fires to break seed dormancy, followed by fencing to protect seedlings from large herbivores.

Keywords: Fire; Herbivory; Population decline; Recruitment; Soil seed bank

Introduction

Successful establishment and persistence of plants depends on multiple biotic (e.g. plant–animal mutualisms) and abiotic factors (e.g. temperature, rainfall, light; Harper 1977). For instance, successful seed dispersal plays a pivotal role in ensuring the long-term continuation of a population (Auld et al. 2007). Recruitment from seeds directly influences plant population dynamics by replacing dead individuals, increasing local populations and establishing new individuals and populations away from parent plants (Hulme 1998). McConkey et al. (2012) suggest that there is growing evidence of a global seed dispersal crisis which has been until now masked by the long life span of many perennial plants. Some such plants, ‘the living dead’ (Janzen 1986; McConkey et al. 2012), are able to persist for decades in apparent healthy state without evidence of regeneration (Guimarães et al. 2008). Although these plants may not be on conservation priority lists yet (Janzen 1986; McConkey et al. 2012), understanding the drivers of their regeneration failure now may greatly assist in conservation action to preserve these species into the future.

Regeneration failure has long been identified on the basis of stand structure, most usually characterised as a gap in the population size/age structure for tree and shrub species, with mature individuals (and perhaps seedlings) present, but few or no plants persisting beyond the establishment stage (Jones 1945). More often than the seed dispersal crisis proposed by McConkey et al. (2012), regeneration failure may be a consequence of several mutually non-exclusive factors, including low seed set, high seed predation and poor germination, as well as high mortality of seedlings due either to biotic (e.g. herbivory, pathogens) or abiotic (e.g. low light, desiccation) factors. Some authors have suggested that disturbance and climate change may act as vectors of apparent regeneration failure (Park 1970; Bray 1971; Lusk and Ogden 1992). For instance, in New Zealand, the regeneration gap present in many conifer stands is now attributed to the natural population dynamics of these long-lived pioneer species which require light for early growth and thus episodes of major canopy disturbance for recruitment to occur (Stewart and Rose 1988). This 'episodic recruitment' strategy has been confirmed as a major cause of apparent recruitment failure in many long-lived tree species (Enright et al. 1998). On the other hand, grazing by invasive animals e.g. deer in New Zealand (Husheer et al. 2003), rabbits in Australia (Denham and Auld 2004), livestock (e.g. goats in Mongolia; Khishigjargal et al. 2013) and native animals where release from predator pressure has led to population increase (e.g. kangaroos in Australia, Koch et al. 2004; deer in North America, Anderson and Katz 1993) may limit the recruitment and survival of seedlings. This may lead to persistent recruitment failure in palatable species and potential shifts in species composition as unpalatable species increase in relative (or absolute) abundance (Tiver and Andrew 1997; Pettit and Froend 2001).

Persoonia elliptica R.Br. (Proteaceae) is a common, fire-tolerant understory tree in the jarrah (*Eucalyptus marginata* Sm.) forests of southwestern Australia which shows evidence of persistent regeneration failure, with no seedling or sapling-sized individuals present over large areas of the species range (Abbott and van Heurck 1988). Abbott and van Heurck (1988) speculated that heavy animal browsing on *P. elliptica* seedlings by kangaroos may have contributed to widespread regeneration failure in this species. Palatability of seedlings to animals such as rabbits (Lange and Graham 1983), sheep (Pigott 1983), goats (Clark and Clark 1981) and kangaroos (Koch et al. 2004) has been recognized as a cause of regeneration failure in many ecosystems (Abbott and van Heurck 1988; Aldrich et al. 2005). However, there is no direct evidence concerning the contribution of kangaroo herbivory to *P. elliptica* regeneration failure in these forests, or of other possible causal factors.

The aim of this study was to elucidate the cause of regeneration failure of *P. elliptica* in the jarrah forests of southwestern Australia, and to identify management procedures to facilitate recruitment, and long-term persistence, of the species. To fulfil these aims, we quantified population structures at two widely separated forest sites to establish that regeneration failure was widespread, expecting to find no evidence of population regeneration (seedlings and small saplings) within either site having occurred during the ~25 years since Abbott and van Heurck's (1988) assessment. We also predicted that poor soil seed bank viability in conjunction with limited seed production might explain regeneration failure, and so examined seed production and viability for mature trees, as well as size and viability of the soil seed bank beneath trees. Finally, following reports of herbivory pressure and fire limiting seedling recruitment and survival by Abbott and van Heurck (1988), we placed wire mesh exclosures within areas subjected to different experimental fire treatments beneath mature trees to exclude kangaroos (*Macropus fuliginosus*) and other mammal browsers, to test for herbivory and fire effects.

Methods

Study species

Persoonia elliptica is an understory tree to 8 m height that is widely distributed through the jarrah forests of SW Australia across a range of topography and soil types (sand, loam and laterite). Mature individuals are fire-tolerant, resprouting from epicormic buds on branches in the plant crown. A seed crop is generally produced each year in mature plants, excepting the year following fire. Seeds are dispersed by several bird and mammal species, including the emu (*Dromaius novaehollandiae*), currawong (*Strepera graculina*) and western grey kangaroo (*M. fuliginosus*) (Abbott and van Heurck 1988). Seeds that are not dispersed (or removed via predation) accumulate in a shallow soil seed bank. Flowering occurs from October to February, with seeds (a fleshy drupe ca. 1 cm length × 0.5 cm width) ripening in April–May.

Study site

Two study sites were selected—an 810 ha area in Sawyers Valley State Forest (31.54°S 116.13°E), located ca. 30 km east of Perth and a 900 ha area in Avon Valley National Park (31.34°S 116.09°E) ca. 50 km north-east of Perth. The Avon Valley lies at the northern end of the Darling Scarp on the transition between the northern extent of the jarrah (*Eucalyptus marginata*) forest and the drier wandoo forest (*Eucalyptus wandoo*). *Eucalyptus marginata* is associated with lateritic hill tops and ridges, and *E. wandoo* with the clay/loam soils of the valleys. Sawyers Valley is also a part of the northern Darling Plateau, with lateritic duricrust on ridges and upper slopes, and sands and gravels in shallow depressions. The average fuel age (an analogue of fire history) of both sites is ~10 years, and both sites have not been actively clear-felled for at least 50 years (Department of Parks and Wildlife, *pers. comm.*). However, the patchiness of fire, both prescribed and natural, results in a mosaic of fire ages. Annual rainfall at Sawyers Valley is 1200 mm and 800 mm at Avon Valley, respectively, confined to the cool, wet winter months (Australian Bureau of Meteorology; BOM 2014).

Population size structure

Eight 400 m × 400 m (16 ha) random-sited systematic plots within the 810 ha study area at Sawyers Valley were established and searched for saplings and mature individuals in February 2012. The location of the initial sampling plot was random within the study area, with following systematic placement of plots ensuring a complete ‘grid’ coverage of the region. Stem diameter at breast height (DBH), plant height and longest canopy width (and width perpendicular to this) were recorded for all *P. elliptica* individuals, and searches conducted for seedlings (<30 cm height) within a 10 m radius of each tree. At Avon Valley, the same demographic parameters were recorded for the first 100 individuals encountered along a random walk and searches conducted for *P. elliptica* seedlings within a 10 m radius of each tree >5 cm DBH. The 100 trees sampled at Avon Valley represent a subset of the 343 *P. elliptica* individuals recorded during a related study within a 900 ha area. No seedlings or saplings were located (S Krauss, *pers. comm*). While we focus on the population structure of two study sites in the northern jarrah forests of SW Australia, sampling of nine other *P. elliptica* populations throughout the range of the species by Abbott and van Heurck (1988) revealed recruitment failure in all of them.

Seed production

In December 2011, 20 branches (five per cardinal direction) on each of ten randomly selected trees were tagged, branch length measured and the number of flowers and pedicels (left after poorly developed flowers had fallen) counted (following Bauer et al. 2001). DBH, canopy width and height were recorded for each tree. In autumn 2012, the tagged shoots were remeasured and the number of mature and immature/aborted seeds was counted. In 2013, an additional 10 trees were surveyed, with the total number of seeds per tree estimated as the mean number of mature seeds counted on 50 randomly chosen shoots, multiplied by the estimated number of shoots on the tree. Generalised linear models (GLM) were used to test for effects of sampling year and stem DBH on seed production. The error distribution was taken from a quasi-Poisson distribution to account for data overdispersion. All statistical analyses were conducted in R version 2.15.2 (R Core Team 2012) using the base GLM statistics function and internal base statistic functions, and variation around the mean presented as 95 % confidence intervals.

Soil seed bank dynamics

In April 2012, 10 *P. elliptica* individuals >10 cm DBH were randomly selected for soil seed bank analysis. A 0.5 m × 0.5 m quadrat was placed on the soil surface at 0.5, 1.5 and 3.0 m from the base of each tree along transects running to the north and south. In each quadrat, the surface litter was removed along with any freshly fallen drupes from the current seed crop, and the soil was searched to a depth of 2 cm for soil-stored seeds. The same procedure was repeated in April 2013 for an additional 10 individuals to increase the overall sample size. Seeds collected in 2013 were stored in paper bags at 4 °C until viability testing was performed. A GLM was also used to analyse the impact of distance from tree, sampling year and cardinal direction sampled on soil seed bank density.

Seed viability

We collected between 10 and 20 ripe seeds (fleshy drupe fully developed contain a large, hard seed) from each of 10 individuals. The low number of seeds collected per tree reflected low seed production. Each seed was cut tested to determine potential seed viability. Seeds were considered to be potentially viable if they contained a white, fleshy embryo.

Seeds collected for the 2013 seed bank density assessment were used to determine potential seed viability of soil-stored seeds. For soil seed bank samples collected beneath five trees, 10 seeds (where possible) were randomly selected from each of the sampled distances (0.5, 1.5 and 3.0 m) for viability testing. Each seed was cut tested. A general linear mixed-effects model was used to examine the impact of seed source (i.e. seeds freshly harvested from the canopy vs. soil-stored seeds) on overall *P. elliptica* seed viability. Seed source was included in the model as a fixed effect and the sampled tree as a random effect. Linear mixed models were conducted using the ‘lme4’ linear mixed-effects model package in R (Bates and Maechler 2009).

A burial experiment was conducted to assess the potential loss of seed viability in the soil seed bank following 1 year of burial. In September 2012, three bags each containing 100 fresh *P. elliptica* seeds in a washed river sand matrix were buried 2 cm below the surface litter layer at three random locations. Each bag was made by stitching together two, ~30 cm × 30 cm of UV-stabilized polyethylene shade cloth. The bags were retrieved in September 2013 and the seeds were cut tested to assess viability.

Herbivory

A pilot herbivory experiment in 2011 showed that fresh foliage from mature trees of *P. elliptica* provided at ground level was quickly found and consumed by kangaroos and wallabies (*Macropus irma*) (Monaco 2012). In order to further investigate herbivory impacts, we compared the levels of herbivory for *P. elliptica* by assessing the canopy height to which browsing occurred. A 2.5 metre post was driven into the ground at three random locations at Sawyers Valley. Young branches (i.e. supporting up to one-year-old leaves) were cut from mature trees. The number of leaves and seeds present on each branch was recorded and branches were then attached to the posts at 0, 0.5, 1.0 and 1.5 m above ground. A minimum of 25 leaves were present at each height. Motion sensitive/infra-red cameras were installed near each post and set to record thirty second videos with a ten-second interval upon triggering. These were left in place for 7 days, after which the number of leaves remaining on each branch was counted. The identity of herbivores captured on the video cameras was recorded. We measured the height to the lowest-hanging foliage for ten randomly selected trees at each site and compared this with browsing height results from the browsing experiment.

Seedling recruitment

Exclosure plots were installed under the canopies of five mature trees in each of three areas of different burn histories (management fires for fuel reduction in autumn 2011, spring 2011 vs. unburnt) to investigate the impact of herbivory and/or fire on seedling emergence and survival. Exclosure plots were 4 m × 4 m with metal corner posts supporting rabbit proof fence mesh around the trunk of a randomly selected mature *P. elliptica* tree. The fencing wire extended from just below the ground surface to a height of 1 m to exclude the assumed primary herbivores; wallabies, kangaroos and rabbits (*Lepus curpaeums*). Five control (unfenced) plots were also established beneath trees in each of the burnt and unburnt areas. The plots were established in early winter 2011 and 2012 for the autumn 2011 and spring 2011 burnt areas, respectively. The exclosures and control plots within the unburnt areas were established in summer 2012. For the autumn 2011 burnt plots, a seedling emergence assessment was conducted in winter 2012. During spring 2012, all plots (including those burnt in spring 2011) were visited to check for the presence of germinants. Where present, each seedling was tagged and its height measured. A repeat census was conducted in autumn 2013 across all plots to obtain estimates of seedling survival and growth rates. A generalised linear mixed model was used to determine the effects of burn history and exclosure on the seedling survival (a binomial model examining the proportion of seedlings surviving within each plot treatment (exclosed vs. control) and season of burn (spring vs. autumn) included in the model as fixed factors). ‘Sample plot’ was included in the model as random effect. A seedling was considered to have survived if it was alive at the time of the final census.

Results

Population size structure

P. elliptica populations at Avon Valley and Sawyers Valley showed a unimodal peak in stem diameters between 15 and 25 cm (Fig. 1), with only one individual of sapling size (<5 cm DBH) recorded (stem DBH 4.5 cm), and few individuals in the smallest tree class (5–10 cm DBH). The largest individual recorded had a stem diameter of 45 cm.

Seed production and viability

Estimated seed production per tree ranged from 0 to >2000. There was a significant positive linear relationship between stem diameter and seed production (Fig. 2), but no difference between years of seed production assessment (Table 1a). However, variability was high, with some large individuals producing few or no seeds, and others producing many. Estimated viability of fresh seeds from the canopy was 39 (±11) % (Fig. 3a). Mature trees resumed flowering in the second year after fire.

Soil seed bank

Soil seed bank density decreased as distance from the base of the trunk increased, with only ~25 % of the number of seeds found within the soil sample at 3 m from the trunk in comparison to 0.5 and 1.5 m. Significantly fewer seeds were found in the soil seed bank from samples taken on the south side of the trees (Fig. 3b; Table 1b).

Viability of seeds in the soil seed bank was low, with only 13 (±6) % of seeds containing potentially viable embryos (Fig. 3a). When considering the source of seeds (canopy vs. soil seed bank), viability in soil-stored seeds was significantly lower relative to canopy-sourced seeds (Table 1c). Seeds buried for 1 year showed low viability, with only 5.6 (±2.6) % containing a viable embryo.

Herbivory

At two of the three locations at Sawyers Valley there was no herbivory recorded. At the third location, all *P. elliptica* leaves were consumed at the ground and 0.5 m level by the western brush wallaby and western grey kangaroo as revealed by the sensor-triggered camera footage and only 3 % of leaves remained at 1.0 m. No leaves were taken from 1.5 m. The mean *P. elliptica* height of lowest foliage was 142 (±7) cm.

Seedling recruitment

P. elliptica seedling emergence was low overall, with a total of 71 germinants recorded across the 30 4 m × 4 m plots. On average, 5 (±4) seedlings plot^{-1} emerged in exclosed and control plots in the area burnt in spring 2011, compared with two (±3) seedlings plot^{-1} in the autumn 2011 burnt area. Only one seedling emerged in exclosure plots in the unburnt area, while no seedlings were recorded in the control plots. The survival rate of seedlings was significantly higher in exclosed plots burnt in autumn 2011 (~90 %) versus those burnt in spring 2011 (~55 %). Survival of seedlings emerging in control plots was low (<5 %) (Table 1d).

The growth of *P. elliptica* seedlings was slow: pooled across the exclosure/control treatments, germinants in the autumn 2011 burnt areas increased in height by three (±3) mm from winter 2012 to autumn 2013, while those from the spring 2011 burnt areas increased by 8 (±4) mm.

Discussion

Seed production and seed viability

We established that fire and protection from herbivory are essential for successful recruitment of *P. elliptica*, with seedling recruitment restricted to the first winter following fire, and seedling persistence to protection from large herbivores. As in many other resprouting species, seed set and viability in *P. elliptica* are comparatively low (Enright et al. 1996, 1998; Bellingham and

Sparrow 2000). Our study revealed that while mature trees produce moderate numbers of potentially viable seeds, the number of viable seeds stored in the soil is low and seed longevity there is likely only 1–2 years. However, this pattern is not common to all *Persoonia* species. Some *Persoonia* sp. native to eastern Australia have very long-lived seeds that are reported to retain their viability for many years, recruiting from a soil-stored seedbank only after major disturbances, such as fire (Ayre et al. 2009).

The decline in seed viability in the soil bank in just 1 year (from ~39 to ~5 %) suggests the rapid removal of viable freshly fallen seeds by frugivores, a rapid loss in viability within the soil seed bank, or a combination of these effects. Based on results here, *P. elliptica* seems largely dependent upon the last season's seed crop to generate new recruits. High annual variability in seed production as observed for many fire-evolved species (Higgins et al. 2000), would make this a high-risk seedling recruitment strategy. However, we found no difference in seed production for successive years. We also found that mature trees resumed flowering in the second year after fire, so that there may be a relatively constant seed supply available through time. Although little is known about the breeding system of *P. elliptica*, it is possible that fertilisation may be pollen limited owing to the small size and widely spaced pattern of individuals at most sites (House 1992). With relatively poor seed production observed for some *P. elliptica* individuals across all size classes, seed bank limitation including poor viability (canopy seed viability was less than the ~75 % reported by Abbott and van Heurck (1988) is likely an impediment to regeneration, though this has not been considered a cause of recruitment failure in a previous assessment of the species (Abbott and van Heurck 1988).

Seedling recruitment

Seedling recruitment was most frequent in the first winter following fire in plots that had been burned in the previous autumn or spring, but was almost absent from plots in unburned forest. Post-fire recruitment is a commonplace strategy in perennial plant species of SW Australia, and many other fire-prone environments, with recruitment timed to coincide with maximum resources for early growth (increased light, moisture and nutrient availability), and maximum time for accumulation of a seed and/or bud bank before the next fire occurs (Enright et al. 1996). Fire has already been shown to break seed dormancy for other common and rare *Persoonia* species (Mullins et al. 2002; McKenna 2007). The absence of seedlings in the unburned areas reported here could be due to a lack of fire to break seed dormancy (a common requirement for many fire-adapted species; Dixon et al. 1995), intense herbivory pressure (Abbott and van Heurck 1988) or the combination of these two factors.

Herbivory

In fire-prone environments such as the dry sclerophyll forests described here, herbivores are attracted to recently burnt areas to graze/browse soft, young plant tissue (seedlings and new growth on resprouts) in the forest understory (Midgley et al. 2010). Although many species possess adaptations to cope with this flush of herbivory, slow growing, highly palatable species like *P. elliptica* are likely to be vulnerable to even short-term effects (Midgley et al. 2010).

The removal of foliage up to ~150 cm on adult trees indicates selective herbivory at all life stages (seedling to adult) of *P. elliptica*. The loss of foliage up to this height accords with our herbivory zone experiment, which revealed removal of foliage up to nearly this height. The slow height growth of seedlings reported here indicates that it would take many decades for seedlings to transition into height classes above the kangaroo and wallaby browse ‘kill zone’, so that they would need to escape detection by these herbivores for a very long time if they were to survive to maturity. Given that some of the experimental herbivore leaf displays were detected and removed within 7 days, long-term escape from herbivores seems unlikely.

Synthesis

The population structure of *P. elliptica* indicates regeneration failure, with no saplings or seedlings recorded in our plots, and this accords with the concept of extinction debt as identified for many species of fragmented habitats such as urban reserves (Tilman et al. 1994). Extinction debt refers to the time-delayed, but inevitable, extinction of a species where habitat change precludes recruitment, so that the population persists only as long as its longest-living extant individual (Tilman et al. 1994).

Regeneration failure in *P. elliptica* was observed by Abbott and van Heurck (1988) but they did not determine the reason. It is likely that herbivory is severe on seedlings that regenerate after fire, while few if any seedlings establish during inter-fire years. Although initially we thought it improbable that kangaroos could find all seedlings, this seems to be the case, with vulnerability to herbivory exacerbated by low seed viability and slow seedling growth, leaving seedlings and saplings exposed to herbivore pressure for a long period of time (at least several decades). Thus, we conclude that herbivore pressure has increased in the last 50–100 years, perhaps due to the decline of dingoes and Aborigines as controls on kangaroo populations. Aborigines are thought to have maintained stable kangaroo populations in many areas of Australia (Kohen 1995), and so their displacement may have led to increased herbivore abundance. There is evidence to suggest that vegetation clearing, provision of artificial watering points and control of dingo (*Canis lupus dingo*) populations to facilitate the grazing of domestic stock have improved the habitat for kangaroos in rangelands, resulting in a general population increase from pre-European times (Russell 1974; Newsome 1975; Caughley et al. 1980; Grigg 1982; Squires 1982; Letnic and Koch 2010). Available evidence does suggest that kangaroo numbers in some nature reserves in Western Australia may have increased, with a negative impact on local biodiversity (Department of Conservation and Land Management 2005). Increasing numbers of kangaroos, coupled with small-scale fires creating heavily browsed ‘regeneration hotspots’, place further limits on recruitment.

Further negative impacts of regeneration failure on current *P. elliptica* populations may arise as extant adults continue to age and senesce. The largest (and presumably oldest) individuals in our study produced almost no seeds. It is difficult to link patterns of seed production to plant size/age for resprouting species such as *P. elliptica*. Although seed production did increase significantly with stem DBH, it is not clear if larger individuals would produce an overall greater viable seed crop than smaller individuals. As long-lived resprouters age, the viability of the overall seed crop can decline (despite the production of numerous seeds) as fertilisation is increasingly geitonogamous (Enright et al. 1996; Lamont and Wiens 2003).

Conclusions

Our results suggest that recruitment failure in *P. elliptica* has been occurring for at least 50 years (and maybe 100 years) and is on-going, with extant populations destined to decline and eventually disappear unless there is successful management intervention. Long-lived plants able to regrow vegetatively after fire (or other disturbances) do not need many successful recruitment events to sustain stable populations over generational time scales. However, while it is possible that conditions for regeneration are episodic and rare, and have simply not occurred in recent decades, this seems unlikely. We confirm the hypothesis of Abbot and van Heurck (1988) that kangaroo herbivory is likely the main factor limiting recruitment, and we add fire as a critical interacting factor, with seedling emergence and survival maximised in burned, low herbivore impact (exclosed) plots, but largely absent from all other treatment combinations. While we are confident in our conclusions and their management implications, corroborative data from other forest areas within the species range is needed to confirm the generality of our findings. We propose that small management fire sizes (concentrating herbivore pressure), combined with low levels of seedling emergence and slow growth rates, result in recruitment failure, with seedlings unable to escape the herbivore browsing zone before they are found by browsing animals. Populations of *P. elliptica* in these forests are unlikely to recover without management assistance. The most likely approach to successfully support *P.elliptica* regeneration will be control of herbivore density to reduce herbivore pressure on seedlings, and burning followed by fencing to exclude kangaroos and wallabies. Fences need to remain in place until seedlings have grown through the herbivore ‘kill zone’ (i.e. to at least 1 m height). While fencing is expensive to construct and maintain, alternative approaches such as culling kangaroo populations and/or burning much larger forest blocks to dissipate herbivore pressure are also expensive options and may not be successful.

Acknowledgements

We thank two anonymous reviewers and the editor for constructive comments that significantly improved the manuscript. This study was made possible by support from an Australian Research Council Discovery project Grant (DP110101480) to NJE and a Murdoch University Strategic PhD scholarship to APN. The authors wish to thank M. Gerlach, D. Nield and V. Weber for assistance with field data collection, and the Western Australian Department of Parks and Wildlife (DPaW) for undertaking the experimental fires at the Sawyers Valley site.

References

Abbott I, van Heurck P (1988) Widespread regeneration failure of *Persoonia elliptica* (Proteaceae) in the northern Jarrah forest of Western Australia. J Roy Soc West Aust 71:15–22

Aldrich PR, Parker GR, Romero-Severson J, Michler CH (2005) Confirmation of oak recruitment failure in Indiana old-growth forest: 75 years of data. Forest science. Society of American Foresters, Bethesda, United States, pp 406–416

Anderson RC, Katz AJ (1993) Recovery of browse-sensitive tree species following release from white-tailed deer *Odocoileus virginianus zimmerman* browsing pressure. Biol Conserv 63:203–238

Auld TD, Denham AJ, Turner K (2007) Dispersal and recruitment dynamics in the fleshy-fruited *Persoonia lanceolata* (Proteaceae). J Veg Sci 18:903–910

Ayre DJ, Ottewell KM, Krauss SL, Whelan RJ (2009) Genetic structure of seedling cohorts following repeated wildfires in the fire-sensitive shrub Persoonia mollis ssp. nectens. J Ecol 97:752–760

Bates D, Maechler N (2009) Linear mixed-effects models using s4 classes. R package version 0.999375-32

Bauer LM, Johnston ME, Williams RR (2001) Rate and timing of vegetative growth, flowering and fruit development of *Persoonia virgata* (Proteaceae). Aust J Bot 49:245–251

Bellingham PJ, Sparrow AD (2000) Resprouting as a life history strategy in woody plant communities. Oikos 89:409–416

BOM (2014) Climate data online. http://www.bom.gov.au/climate/data/

Bray JR (1971) Vegetational distribution, tree growth and crop success in relation to recent climatic change. Adv Ecol Res 7:177–233

Caughley G, Grigg GC, Caughley J, Hill GJE (1980) Does dingo predation control the densities of kangaroos and emus? Wildlife Res 7:1–12

Clark DA, Clark DB (1981) Effects of seed dispersal by animals on the regeneration of *Bursera graveolens* (Burseraceae) on Santa Fe Island, Galapagos. Oecologia 49:73–75

Denham AJ, Auld TD (2004) Survival and recruitment of seedlings and suckers of trees and shrubs of the Australian arid zone following habitat management and the outbreak of Rabbit Calicivirus Disease (RCD). Austral Ecol 29:585–599

Department of Conservation and Land Management. (2005) Thompsons Lake nature reserve management plan. Perth, Western Australia

Dixon KW, Roche S, Pate JS (1995) The promotive effect of smoke derived from burnt vegetation on seed germination of western Australian plants. Oecologia 101:185–192

Enright N, Lamont BB, Marsula R (1996) Canopy seed bank dynamics and optimum fire regime for the highly serotinous shrub, *Banksia hookeriana*. J Ecol 84:9–17

Enright NJ, Marsula R, Lamont BB, Wissel C (1998) The ecological significance of canopy seed storage in fire-prone environments: a model for resprouting shrubs. J Ecol 86:960–973

Grigg G (1982) Roo harvesting. Are kangaroos really under threat? Aust Nat Hist 21:123–127

Guimarães PR Jr, Galetti M, Jordano P (2008) Seed dispersal anachronisms: rethinking the fruits extinct megafauna ate. PLoS ONE 3:e1745

Higgins SI, Bond WJ, Trollope WS (2000) Fire, resprouting and variability: a recipe for grass–tree coexistence in Savanna. J Ecol 88:213–229

House SM (1992) Population density and fruit set in three dioecious tree species in Australian tropical rain forest. J Ecol 80:57–69

Hulme PE (1998) Post-dispersal seed predation: consequences for plant demography and evolution. Perspect Plant Ecol 1:32–46

Husheer SW, Coomes DA, Robertson AW (2003) Long-term influences of introduced deer on the composition and structure of New Zealand Nothofagus forests. Forest Ecol Manag 181:99–117

Janzen DH (1986) Blurry catastrophes. Oikos 47:1–2

Jones E (1945) The structure and reproduction of the virgin forest of the north temperate zone. New Phytol 44:130–148

Khishigjargal M, Dulamsuren C, Lkhagvadorj D, Leuschner C, Hauck M (2013) Contrasting responses of seedling and sapling densities to livestock density in the Mongolian forest-steppe. Plant Ecol 214:1391–1403

Koch JM, Richardson J, Lamont BB (2004) Grazing by kangaroos limits the establishment of the grass trees *Xanthorrhoea gracilis* and *X. preissii* in restored bauxite mines in Eucalypt forest of southwestern Australia. Restor Ecol 12:297–305

Kohen JL (1995) Aboriginal environmental impacts. University of New South Wales (UNSW) Press, Sydney, Australia

Lamont B, Wiens D (2003) Are seed set and speciation rates always low among species that resprout after fire, and why? Evol Ecol 17:277–292

Lange R, Graham CR (1983) Rabbits and the failure of regeneration in Australian arid zone Acacia. Aust J Ecol 8:377–381

Letnic M, Koch F (2010) Are dingoes a trophic regulator in arid Australia? A comparison of mammal communities on either side of the dingo fence. Austral Ecol 35:167–175

Lusk C, Ogden J (1992) Age structure and dynamics of a podocarp-broadleaf forest in Tongariro National Park, New Zealand. J Ecol 80:379–393

McConkey KR, Prasad S, Corlett RT, Campos-Arceiz A, Brodie JF, Rogers H, Santamaria L (2012) Seed dispersal in changing landscapes. Biol Conserv 146:1–13

McKenna DJ (2007) Demographic and ecological indicators of rarity in a suite of obligate-seeding *Persoonia* (Proteaceae) shrubs. University of Wollongong thesis collection

Midgley JJ, Lawes MJ, Chamaillé-Jammes S (2010) Savanna woody plant dynamics: the role of fire and herbivory, separately and synergistically. Turner review No. 19. Aust J Bot 58:1–11

Monaco S (2012) Seed dispersal, herbivory and recruitment failure of *Persoonia elliptica* (Proteaceae) in Western Australian Jarrah (*Eucalyptus marginata*) forest. Honours thesis, Murdoch University

Mullins RG, Koch JM, Ward SC (2002) Practical method of germination for a key jarrah forest species: snottygobble (*Persoonia longifolia*). Ecol Managt Rest 3:97–103

Newsome A (1975) An ecological comparison of the two arid-zone kangaroos of Australia and their anomalous prosperity since the introduction of ruminant stock to their environment. Q Rev Biol 1:389–424

Park G (1970) Palaeoclimatic change in the last 1,000 years. Tuatara 18:114–123

Pettit NE, Froend RH (2001) Long-term changes in the vegetation after the cessation of livestock grazing in *Eucalyptus marginata* (jarrah) woodland remnants. Austral Ecol 26:22–31

Pigott C (1983) Regeneration of oak-birch woodland following exclusion of sheep. J Ecol 71:629–646

R Core Team (2012) R: a language and environment for statistical computing. R Foundation Statistical Computing, Vienna, Austria

Russell EM (1974) The biology of kangaroos (*Marsupialia-Macropodidae*). Mamm Rev 4:1–59

Squires V (1982) Competitive interactions in the dietery preferences of kangaroos and sheep, cattle and goats in inland Australia. J Arid Envion 5:337–345

Stewart GH, Rose AB (1988) Conifer regeneration failure in New Zealand: dynamics of montane *Libocedrus bidwillii* stands. Vegetatio 79:41–49

Tilman D, May RM, Lehman CL, Nowak MA (1994) Habitat destruction and the extinction debt. Nature 371:65–66

Tiver F, Andrew MH (1997) Relative effects of herbivory by sheep, rabbits, goats and kangaroos on recruitment and regeneration of shrubs and trees in eastern south Australia. J Appl Ecol 34:903–914

Fig. 1 Comparative stem demography of *P. elliptica* at Avon valley national park (*n* = 100) and Sawyers Valley state forest (*n* = 320)

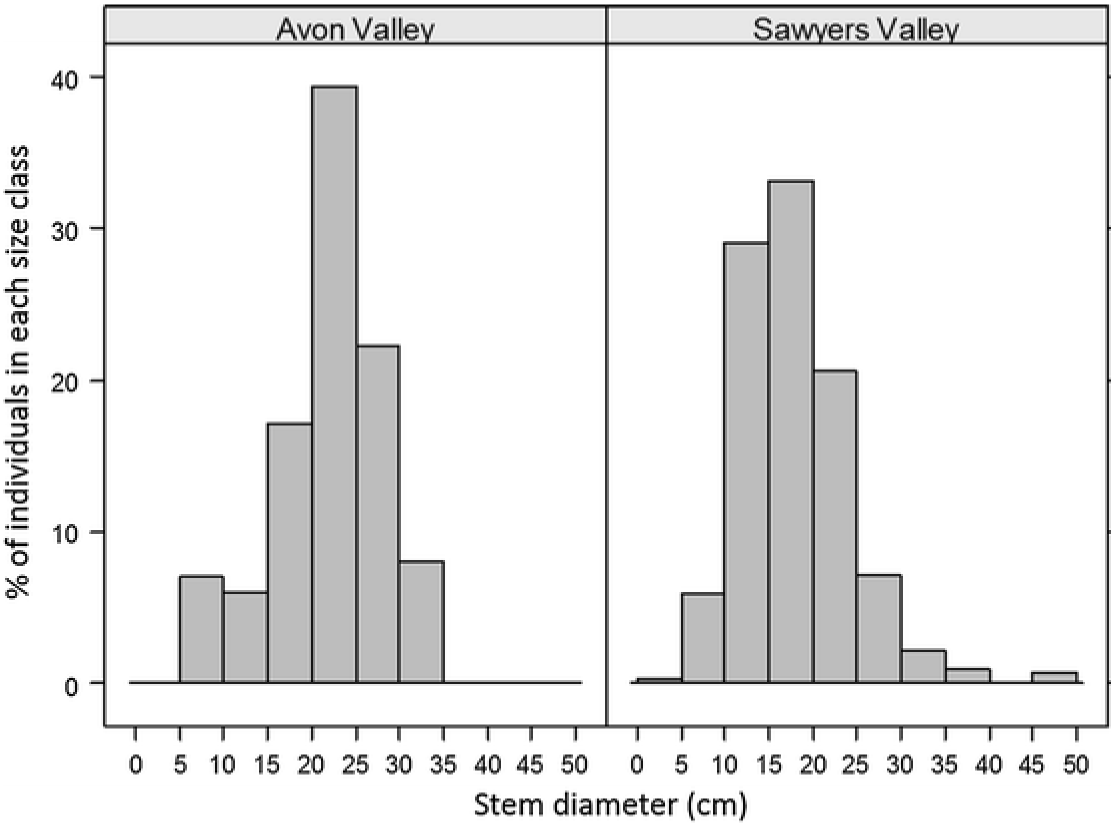

Fig. 2 The relationship between seed production (y = 60.67stem.dbh−685; df = 18, R^2 = 0.27) and stem size for *P. elliptica* at Sawyers Valley, southwestern Australia

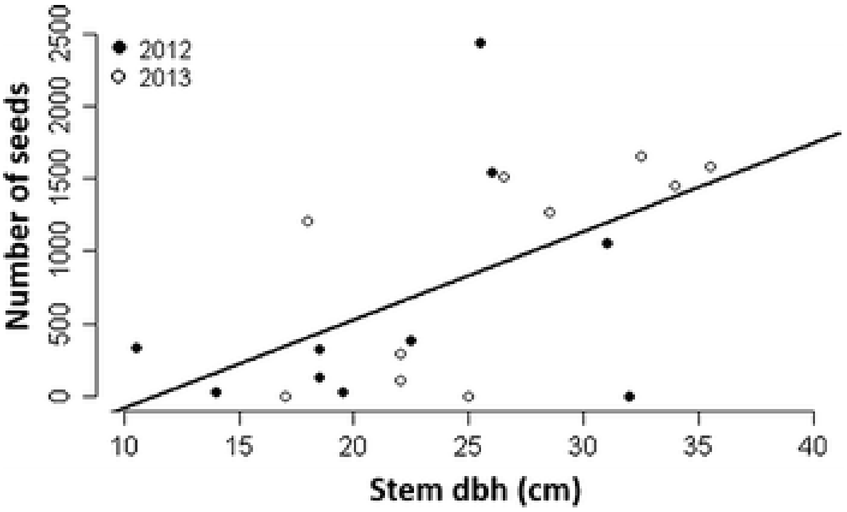

Fig. 3 a Mean proportion of potentially viable seeds (±95 % CI) of *P. elliptica* sourced from the soil seed bank and from the plant canopy and **b** mean number of seeds per soil seed bank sample (±95 % CI, calculated from the exponent of the natural log of the number of seeds) by distance from the base of the tree at Sawyers Valley, southwestern Australia

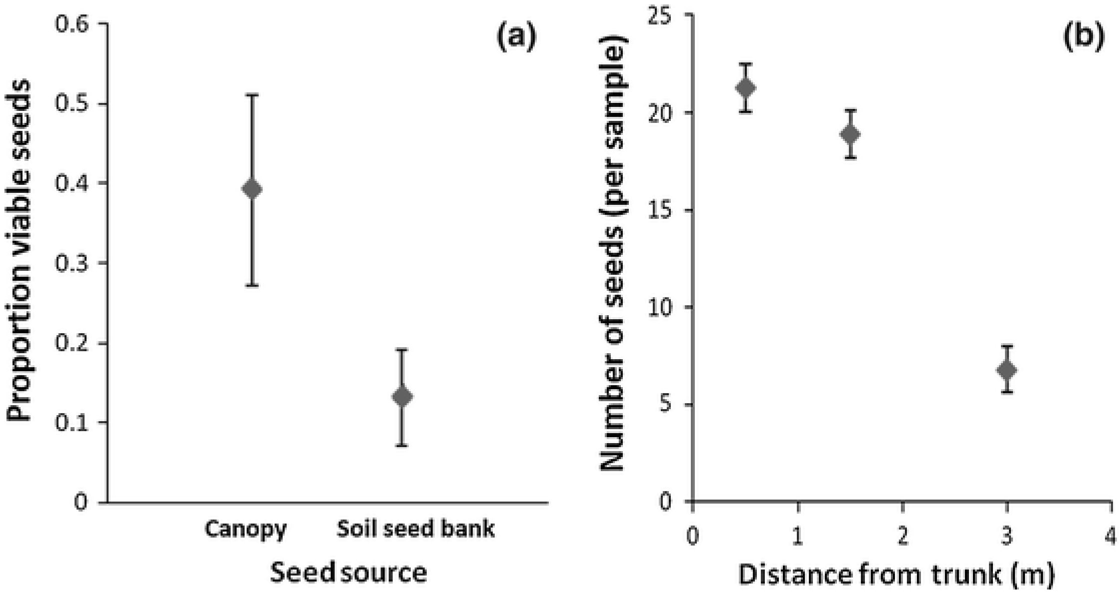

Table 1 The effect of model parameters (derived from generalised linear and linear mixed modes) on **a** *P. elliptica* seed production, **b** soil seed bank density, **c** overall seed viability (considering seed source) and **d** seedling survival

Parameters	**Effect on seed production (a)**	***t* value**
Year		
2013	0.03 (0.43)	0.07
Stem diameter	0.08 (0.03)	**2.4**
	Effect on seed bank density (b)	***t* value**
Distance from trunk (m)	−0.41 (0.16)	**−2.49**
Year		
2013	0.30 (0.31)	0.95
Direction from trunk		
South	−0.70 (0.33)	**−2.14**
	Effect on seed viability (c)	***z* value**
Source		
Soil seed bank	−0.76 (0.35)	**−2.15**
	Effect on seedling survival (d)	***z* value**
Treatment		
Exclosure	2.18 (0.72)	**2.98**
Burn history		
Spring 11	−1.83 (0.64)	**−2.84**
Unburnt	13.31 (2399)	0.006

Bolded *z* and *t* values represent model parameters significant at $p < 0.05$. A positive value of the model parameter suggests an increased/positive effect on the model outcome e.g. exclosures significantly increased seedling survival. Numbers in parentheses are the SE of the parameter estimate