

An investigation of critical life stages to estimate optimum fire interval of the short-range, endemic, non-resprouter *Hakea victoria*



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*I declare that this Research Project is my own account of my research and contains as its main content, work which has not previously been submitted for a degree at any tertiary education institution.*

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10<sup>th</sup> June 2024

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## Thesis Structure

The structure of this thesis blends elements of a conventional thesis with those of a scholarly journal article. Chapter 1 consists of a comprehensive literature review, aiming to offer readers a deeper understanding of the research project than a typical article introduction would provide. Following this, Chapter 2 adopts the format of a journal article, complete with an abstract and extended methods and results sections. Information from the literature review is repeated in the journal article introduction where relevant, with the intent that the journal article can be read with or without the literature review chapter. References cited in both chapters are consolidated at the end of Chapter 2 for ease of access. The journal article within this thesis adheres to the style guidelines of the Australian Journal of Botany as is intended as a draft for submission, although slightly deviating from what is expected of a formal article submission. This structured approach aims to uphold the standards of professional writing expected within the Science discipline and reflect the high standards of scholarly publishing while also fulfilling the requirements of the academic program.

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## Chapter 1 – Literature Review

### Introduction

Fire serves as a significant ecological disturbance that has shaped the diversity and traits of flora in many fire-prone landscapes by influencing ecosystem structure and composition (Pausas and Ribeiro 2013; Buma *et al.* 2013; Enright *et al.* 2014; Groom and Lamont 2015; Harvey *et al.* 2017; Tangney *et al.* 2018; Archibald *et al.* 2018; Lamont *et al.* 2020; Kelly *et al.* 2020). In seasonally dry Mediterranean-type ecosystems like south-western Australia, fire is recurrent and widespread (Enright *et al.* 1998a, b; Tangney *et al.* 2018; Gosper *et al.* 2022). Essential reproductive and regenerative processes influenced by fire include heat-stimulated seed release, resprouting from protected buds above or below ground, seed release from serotinous cones, heat and smoke-cued germination and fire stimulated flowering and seed production (Gill 1981; Enright *et al.* 1998a, b; Hanley and Lamont 2000; Groom and Lamont 2015; Tangney *et al.* 2018). These common biological responses increase the probability of survival or recruitment of fire-adapted flora following fire disturbance (Gill 1981; Enright *et al.* 1998a, b; Groom and Lamont 2015).

The south-west of Australia, located within the South West Australia Floristic Region (SWAFR) boasts remarkably high plant diversity and species richness. It is typically dominated by serotinous non-resprouter species, particularly those belonging to the Proteaceae family such as *Banksia* and *Hakea* (Gosper *et al.* 2010, 2012, 2022; Crawford *et al.* 2011; Yates *et al.* 2021). Serotinous species, also known as non-resprouters, retain seeds on the plant within woody fruits for an extended period of time (a phenomenon called serotiny), with seed dispersal often triggered by fire (Enright and Lamont 1989b; Groom and Lamont 1997; Buma *et al.* 2013). In south-western Australia most strongly serotinous Proteaceae retain their seed for an average of five or more years (Lamont *et al.* 1991; Lamont and Groom 1998, Groom and Lamont 2015), progressively accumulating seed with successive reproductive events, and cued for release following fire (Lamont and Groom 1998; Enright and Goldblum 1999; Groom and Lamont 2015).



Given the close relationship between fire and biological processes in fire-prone landscapes, alterations in fire regimes and the impacts of climate change, and disease pose significant threats to plant species in the SWAFR (Yates et al. 2021). Altering the natural fire-regime through prescribed burning can impact population persistence and potentially lead to extinction and modify ecosystem structure and integrity (van Wilgen 1981; Haidinger and Keeley 1993; Morrison *et al.* 1995; Lloret *et al.* 2003; Kraaji *et al.* 2013; Enright *et al.* 2015; Tangney *et al.* 2018; Gosper *et al.* 2022;). Therefore, the management of fire regimes in fire-prone landscapes holds paramount importance in conserving and preserving the high biodiversity values of the south-west (Fontaine et al., 2012; Groom & Lamont, 2015).

## Fire as an ecosystem process

Fire is a natural environmental component that has shaped the diversity of life and of which many global landscapes are seemingly adapted (Buma *et al.* 2013; Groom and Lamont 2015; Harvey *et al.* 2017; Tangney *et al.* 2018; Lamont *et al.* 2020; Kelly *et al.* 2020). From a physiochemical perspective, fire is the rapid expulsion of energy that occurs when typically carbon rich chemical compounds oxidise (Bowman *et al.* 2012). Together, oxygen (O<sub>2</sub>), fuel and sufficient heat for ignition are the three key factors that influence this reaction (Bowman *et al.* 2012; He and Lamont, 2018). Fuel, comprising combustible material, is of central importance for natural environments because it is the flammable, dead and living vegetation that is consumed by flames (Sullivan *et al.* 2012). Not only is fire a physiochemical process but also a fundamental geochemical process (Bowman *et al.* 2009) linking biomass with the atmosphere by releasing heat, water vapour, CO<sub>2</sub>, and influencing climate as well as releasing nutrients and forming deposits of recalcitrant black carbon within the geosphere (Bowman *et al.* 2012).

Fire is estimated to have first appeared approximately 420 million years ago, coinciding with abundant terrestrial biomass and oxygen levels in the atmosphere (Bowman *et al.* 2012; He and Lamont 2018). It is likely that over the past 420 million years, changes in the fire-proneness of vegetation have been influenced by historical fire activity on Earth (He & Lamont, 2018). Increased wildfire activity during the early to mid-Cretaceous coincided with major changes in flora and the rise of angiosperms (i.e. plants that bear their seeds in fruit) as a dominant species (He & Lamont, 2018). During the Miocene, Mediterranean-type and monsoonal-type climatic conditions characterised by a long dry season, and considerable rain during the wet season, initiated highly fire-prone ecosystems by increasing the abundance of combustible fuel loads (He & Lamont, 2018). The emergence of woody forests and seasonally dry woodlands provided sufficient fuel for large forest fires over broad spatial scales, for significant periods and at regular intervals favourable for the evolution of fire-tolerant species (He & Lamont, 2018). The interconnectedness between fire and life raises questions about their potential co-evolutionary relationship (Bowman *et al.* 2012). Despite extensive research on plant adaptations to fire-prone environments, scepticism remains regarding the role of fire in plant

evolution, with ongoing debates about whether plants actively promote fire or simply tolerate it (Bowman *et al.* 2012; He and Lamont 2018).

Mutch (1970) was the first to voice the idea that fire may have co-evolved with plants. Furthermore, Gill and Ingwersen (1976) were first to demonstrate the relationship between smoke and flower of grass trees (*Xanthorrhoea*) (Bowman *et al.* 2012) and research has highlighted the important role of smoke in interrupting seed dormancy (Dixon *et al.* 1995; Bowman *et al.* 2012). The idea that plants evolved to display flammable characteristics that promote fire, thus fire-prone environments are more flammable than non-fire-prone environments (Mutch 1970) is flawed according to Bowman *et al.* (2012). It is believed that flammability of vegetation is not necessarily a direct selection to promote fire and is therefore a circular argument to claim flammable vegetation evolved to burn (Bowman and Wilson 1988; Bradshaw *et al.* 2011; Bowman *et al.* 2012). Secondly, flammable traits may arise as a response to other selective forces such as drought, nutrient impoverished soils or herbivory (Bradshaw *et al.* 2011; Bowman *et al.* 2012). Thirdly, it is essential to establish clear evidence demonstrating that plant fitness is improved with increased flammability (Bowman *et al.* 2012). Additionally, it is crucial to determine whether these traits contribute to improved plant fitness in the presence of fire and if these traits coincide with the onset of fire throughout evolution (Bowman *et al.* 2012; He and Lamont 2018). Given the diversity of plant life forms, regenerative traits and strategies, Keely *et al.* (2011) believes that the key to understanding the evolutionary relationship between plants and fire is the nexus between fire regime and plants traits.

Plants are believed to have evolved specialized traits to survive fire and/or promote burning. For example, many trees have developed thick insulating bark and regenerative tissues, with resprouting from burnt stems being a common trait in fire-prone environments (Bowman *et al.* 2012).

Additionally, for some plants, fire acts as a trigger for reproductive cycles, such as fire-stimulated flowering and smoke- and heat-induced germination (Bell *et al.* 1993; Dixon *et al.* 1995; Bowman *et al.* 2012). Similarly, open canopy architecture enables trees to coexist with a flammable understory, while oil-rich leaves and bark in some species enhance fire activity (Bowman *et al.* 2012). The ability to chart the process of how plants adapt to fire is limited due to the lack of a good fossil record

(Bowman *et al.* 2012). No definitive plant features have been identified that undeniably suggest fire-related adaptations rather than 'exaptations' - features that evolved for one purpose but later adapted for a different function or in this case, a different fire regime (Bradshaw *et al.* 2011).

## Fire as a driver of flora traits

Recent studies confirm the importance of fire as a disturbance shaping traits of the World's flora with fire, in many fire-prone landscapes, influencing ecosystem structure and composition (Pausas and Ribeiro 2013; Enright *et al.* 2014; Archibald *et al.* 2018; He and Lamont 2018; He *et al.* 2019).

Mediterranean-type climatic regions are characterised as having strong seasonality and are characterised by hot dry summers and cold wet winters (Enright *et al.* 1998a, b). Plant communities within this climate region are susceptible to disturbance by fire, however, rather than having an entirely destructive influence, its ability to trigger and facilitate fire-stimulated flowering, successful germination, and seeding establishment make the positive effects of fire, vital (Hanley and Lamont 2000).

The post-fire environment provides ideal conditions for vegetative recovery and recruitment as competition between plants/species is reduced and resources are more readily available (Groom and Lamont 2015). Key reproductive and regenerative processes influenced by fire include heat-stimulated seed release, resprouting from protected buds above or below ground, seed release from serotinous cones, heat and smoke-cued germination and fire stimulated flowering and seed production (Gill 1981; Enright *et al.* 1998a, b; Hanley and Lamont 2000; Groom and Lamont 2015; Tangney *et al.* 2018). These common biological responses increase the probability of survival or recruitment of fire-adapted flora following disturbance by fire (Gill 1981; Enright *et al.* 1998a, b; Groom and Lamont 2015).

Fundamental to successful plant population regeneration in fire-prone landscapes is the presence of seeds (in situ, canopy-held or soil-stored) that are able to survive fire and germinate at an appropriate time for seedling establishment or the presence of protected buds within above or below ground stems to allow for regeneration post fire (Enright *et al.* 1998a, b; Enright and Goldblum 1999; Jenkins *et al.* 2005; Bowman *et al.* 2012; Tangney *et al.* 2018; Lamont *et al.* 2020). The ability of plants and importantly seeds to tolerate and survive the high temperatures associated with fire in fire-prone Mediterranean-type landscapes across Europe, Western Australia, South Africa and California has been well documented (Hanley & Lamont, 2000; Tangney *et al.*, 2018). For example, *Daviesia*

*cordata* seeds (native to south-west Western Australia) stored in the soil will germinate after 10 minutes of exposure to 100°C (Bell and Williams 1998) while *Hakea trifurcata* seeds, that are typically stored in the canopy (i.e. serotiny), can survive 10 minutes out of their protective cones exposed to temperatures of 100°C (Hanley & Lamont, 2000).

## **Fire and serotiny**

Serotiny is a widespread mechanism for fire resilience and is common to species from families prominent within their natural environment, including Proteaceae, Myrtaceae, Cupressaceae and Casuarinaceae (Australia), Proteaceae and Bruniaaceae (South Africa), and Pinaceae (North America) (Buma *et al.* 2013; Lamont *et al.* 2020). Selected seed traits linked to serotiny include tolerance of high pH (ash) allowing for successful regeneration in the post-fire environment, heat-induced germination, soil/litter and burial (Lamont *et al.* 2020). It is hypothesised that serotiny is a fire promoting reproductive strategy, as is the retention of dead foliage to increase combustion (He *et al.* 2011; Buma *et al.* 2013). However, Lamont *et al.* (2020) believes that traits of serotiny are multifunctional, with thicker and denser tissue woody-fruits required for protection from granivores, which for many species may be an exaptation, having first evolved for fire resistance. The adaptive advantages of serotiny among woody plants vary, but generally they include maximising seed availability, ensuring seed release coincides with presence of favourable conditions (i.e. post-fire microsites) and minimising post-dispersal granivory (Groom & Lamont, 1997; Lamont *et al.* 2020).

The “degree of serotiny” varies between species and describes the rate at which the seed is released from fruits (Lamont 1985; Enright *et al.* 1998a; Enright and Goldblum 1999). Degree of serotiny is represented along a spectrum, with highly serotinous species (seeds held on the plant for many years) at one extreme and weakly serotinous species (fast maturing seeds in fruit offering little protection and spontaneously releasing seed) at the other (Enright *et al.* 1996; Lamont and Groom 1998; Enright *et al.* 1998a). However, it is possible for varying degrees of serotiny to be encountered within the same species (Cowling *et al.* 1987; Enright and Lamont 1989a, b; Enright *et al.* 1998a; Buma *et al.* 2013). Adaptive changes in the degree of serotiny may be expected when a) a species attempts to colonise an area with a different fire interval to its own or b) the fire regime for a species native habitat change (Ne’eman *et al.* 2004; Lamont *et al.* 2013; Lamont *et al.* 2020). Lamont *et al.* (2020) intuitively stated it may be the case that high fire frequency induces the non-storage of seeds (non-serotiny) given there is little benefit in the accumulation of seed.

The prolonged storage trait of strongly serotinous species is promoted because, should a fire occur, the annual seed production would be insufficient for plant replacement, recruitment conditions are only optimal post fire and inter-fire recruitment is an inadequate means to maintain population persistence (Lamont *et al.* 1991; Enright *et al.* 1998a; Enright *et al.* 1998b; Lamont *et al.* 2020). In addition, allowing the canopy seed bank to accumulate over a longer period may support higher seed quantity and quality (nutrient content), which has value for successful recruitment in seasonally dry, nutrient poor soils (Lamont and Groom 2013; Lamont *et al.* 2020). For strong serotiny to be effective it is required to protect seeds from environmental factors over time (years) within fruits and maintain the viability of the protected seed in the absence of fire (Lamont *et al.* 2020). However, fruits consistently remain closed for longer than seeds remain viable (Lamont *et al.* 2020). For example, 85% of seeds from the one-year-old fruits of *Banksia cuneata* remain viable in comparison to <35% of seeds in 10 to 12-year fruits even though the fruits remain intact (Lamont *et al.* 1991). Loss of seeds contained within fruit can be due to predation and consumption by insect larvae, pathogenic fungi or bacteria, desiccation, granivorous birds, gradual senescence or waterlogging (Lamont *et al.* 2020). To counter seed loss plants, have, in part, developed traits to reduce the impacts of predation including dense persistent florets to conceal fruits on some banksias and supportive woody features over the weakest part of the fruit on hakeas to deter granivores and insect larvae from reaching the seed (Midgley *et al.* 1991; Groom and Lamont 2015; Lamont *et al.* 2020).

In south-western Australia most strongly serotinous Proteaceae retain their seed for an average of five or more years (Lamont *et al.* 1991; Lamont and Groom 1998, Groom and Lamont 2015), progressively accumulating seed with successive reproductive events, and cued for release following fire (Lamont and Groom 1998; Enright and Goldblum 1999; Groom and Lamont 2015). However, there are mechanisms other than fire by which fruits may open, including drought, spontaneous opening of old fruits, branch or plant death in the inter-fire period and wetting and drying cycles (Lamont 1985; Cowling and Lamont 1985; Lamont 1991; Enright *et al.* 1996; Lamont and Groom 1998; Enright and Goldblum 1999; Groom and Lamont 2015). Although recruitment and plant survival are low in the absence of fire-cued release (Enright *et al.* 1996).



## The flora of fire-prone, south-west Australia

### *The climate and floristic character of south-west Australia*

Speciation of south-west Australian flora began at the end of the Cretaceous period (65.5 Ma) and continued rapidly during the Miocene and Pleistocene periods - a time of great climatic change, including severe aridification (Groom and Lamont 2015). The Miocene (23-5 Ma) was a crucial period in the evolution of flora in the southwest as climate became drier and more seasonal, with the proliferation of species traits including serotiny or non-serotiny, greatest during this period (He *et al.* 2011; Groom and Lamont 2015). The transformation during the Miocene and Pliocene periods from a predominantly rainforest flora to temperate woodlands and shrublands was due to increasing aridity (Byrne *et al.* 2011), which subsequently resulted in the appearance of morphological and physiological traits more suitable for the seasonally dry Mediterranean-type climate (Groom and Lamont 2015). There is direct evidence to suggest the presence of fire during the Pliocene in the south-west, although it is likely that disturbance by fire occurred substantially earlier (Gosper *et al.* 2022). Many southwest genera diversified during the Miocene and now contain both fire-sensitive and fire-tolerant species, supporting the importance of fire as an evolutionary force in the functional diversity of flora in the region (Groom and Lamont 2015).

Land plants began appearing almost 500 million years ago (Ma) with the family Proteaceae arising at 115 Ma, before separating into subfamilies Grevilleoideae and Proteoideae around 94 Ma (Groom & Lamont, 2015). Proteoideae speciated strongly in the fire-prone environment of the Cretaceous, giving rise to many major sclerophyll shrub genera including *Petrophile* (49 Ma) and *Conospermum/Synaphea* (36 Ma) while Grevilleoideae fire-adapted lineages arose much slower, with major sclerophyll shrub/tree genera including *Banksia* (61 Ma), *Hakea* (18 Ma) and *Grevillea* (11 Ma) (Groom & Lamont, 2015). Between 61 and 62 Ma, key taxa retaining highly flammable leaves and seed storage began emerging, including *Banksia*, and are considered ancestral among Proteaceae today (He *et al.* 2011; Groom and Lamont 2015).

Flora of contemporary south-west Australia, located within the Southwest Australia Floristic Region (SWAFR) are highly diverse, with dominant genera developing distinct traits to compete and survive in a climatically varied environment characterised as having nutrient impoverished soils, fire-proneness, high and low temperatures and seasonal aridity (Mucina *et al.* 2014; Groom and Lamont 2015; Gosper *et al.* 2022). The SWAFR is globally renowned for its species richness, exceptional plant diversity and is dominated by serotinous non-resprouter species including those of *Banksia*, *Hakea* and *Eucalyptus* (Gosper *et al.* 2010, 2012, 2022; Crawford *et al.* 2011; Yates *et al.* 2021). These species occur at times in excess of 50% total vegetation cover and strongly represent the threatened flora within the region (Gosper *et al.* 2022). Within this region plant species generally have a smaller geographic range and include many more endemics species than in other areas throughout Australia (Yates *et al.* 2021). Changes in fire-regimes, climate change, and disease and all significant threats to plant species within the SWAFR of south-west Australia (Yates *et al.* 2021).

#### *The role of fire*

As previously mentioned, fire in seasonally dry ecosystems including south-western Australia, is a recurrent and widespread disturbance (Tangney *et al.* 2018; Gosper *et al.* 2022). Fire significantly influences various plant population processes, such as germination, dispersal, and mortality (Burrows *et al.* 2008; Gosper *et al.* 2022). Attributes of fire regimes, including fire interval (the number of years between fires), seasonality, and severity, play particularly influential roles in shaping these processes (Burrows *et al.* 2008; Gosper *et al.* 2022). Prescribed burning is defined as the deliberate application of fire to the landscape (Fernandes and Botelho 2003; Penman *et al.* 2011). The practice of prescribed burning aims to minimise the risks and mitigate the negative consequences of high intensity wildfires and reduce the risk to human life and assets by reducing fuel loads and fire hazards in the landscape (Fernandes and Botelho 2003; Penman *et al.* 2011; Tangney *et al.* 2018). In some cases, prescribed burning is used to control invasive species, stimulate soil seed banks and promote heterogeneity, and more recently, ecological goals have been incorporated into burning programs (Fernandes and Botelho 2003; Kenny *et al.* 2004; Penman *et al.* 2011). It is believed that though prescribed burning does not prevent the occurrence of wildfires entirely it can significantly reduce the impacts (Burrows

*et al.* 2008). However, while this is commonly stated as fact, there is often debate regarding the efficacy and protective advantages of prescribed burning (Fernandes and Botelho 2003; Penman *et al.* 2011). The intimate relationship between biological processes and fire in fire-prone landscapes means that altering natural fire regimes may be damaging to ecosystems and plant communities (Tangney *et al.* 2018). For example, prescribing fires in intervals that are longer or shorter than the natural fire regime (Enright *et al.* 2014) may impact population persistence, lead to extinction, modify ecosystem structure and integrity, and affect floristic composition (van Wilgen 1981; Haidinger and Keeley 1993; Morrison *et al.* 1995; Lloret *et al.* 2003; Kraaji *et al.* 2013; Enright *et al.* 2015; Tangney *et al.* 2018; Gosper *et al.* 2022;).

The frequency of fire and its relationship with life cycle timings can be an important factor for some plant species (Brown and Whelan 1999). For instance, non-resprouters face a greater risk of population decline when the inter-fire period is shorter than the time required to build up a sufficient seed bank for post-fire recruitment or for plants to reach reproductive maturity. This vulnerability makes them more susceptible to increased fire frequency. (Morrison *et al.* 1995; Enright *et al.* 1996; Knox and Morrison 2005; Kraaij *et al.* 2013; Harvey, *et al.* 2017; Gosper *et al.* 2022).

#### *Management of south-west flora*

With fire so intimately tied to the persistence of flora, the management of fire regimes through prescribed burning in fire-prone landscapes such as south-west Australia is of ecological importance (Fontaine *et al.* 2012; Groom and Lamont 2015). With a changing climate, the risk of more intense wildfires is increasing due to warmer and drier conditions, lengthening fire seasons and increasing annual extreme weather events (Buma *et al.* 2013; Enright *et al.* 2014; Enright *et al.* 2015). The solution to these effects will likely be to undertake prescribed burning over shorter fire intervals for hazard reduction (Enright *et al.* 2015) causing species loss, invasion and potential extinction (Enright *et al.* 2014). Malcolm *et al.* (2006) identified south-western Australia as one of the most vulnerable global biodiversity hotspots in the face of global climate change, with the potential to lose more than 2000 species within the next century. As such, conserving and preserving the high biodiversity values of the south-west and the high number of endemic species found within it are now the priority for

some conservation groups and Local and Federal Government agencies. Given the importance of serotinous species in south-west Australia including *Banksia* and *Hakea*, it is vital to understand ecosystem processes and plant reproductive traits when planning fire management (Buma *et al.* 2013; Kelly *et al.* 2020). Current fire management practices in south-west Australia aim to manage fire intervals within an acceptable range that maximises the probability of population persistence of all species within an ecosystem, however, this ‘one size fits all’ approach may not be suitable for maintaining population persistence of individual species such as *Hakea victoria*.

## **Royal Hakea (*Hakea victoria*): A monarch of the fire-prone landscape**

Commonly known as Royal Hakea, *Hakea victoria* was first sighted in the Fitzgerald River National Park Colonial Botanist James Drummond in 1847, where he was taken aback by the species' splendour and bestowed the name Royal Hakea (*Hakea victoria*) after her Majesty the Queen (Zemunik, 2019). The plant is a short range, serotinous non-resprouter that is endemic to the Southwest Australian Floristic Region (SWAFR) and found across a linear coastal band of approximately 110kms from Hopetoun on the eastern edge of the Fitzgerald River National Park, and west near Bremer Bay (Florabase, March 2022; Atlas of Living Australia, March 2022). Described as a sparsely branched shrub, *H. victoria* can grow up to four metres tall and two and half metres wide, preferring sandy soils over granite or laterite or rocky slopes among quartzite (Florabase, December 2024). This charismatic species attracts locals and tourists alike due to its unusual appearance and ombre of brightly coloured red, orange and yellow leaves. Flowers are a cream to white colour, growing during autumn, winter and spring (April-October) and once pollinated develop into woody fruits.

Populations of *H. victoria* are killed during fire, with germination occurring in the post-fire environment, however the occurrence of too frequent fires has created changes in population structure. Relatively little is published on *H. victoria*, which reduces the likelihood that current land management including the use of fire, is appropriate for the species and therefore it is of great importance to study the critical life stages (i.e., age of reproductive maturity, seed bank size and seed viability over time) to assist in conservation management of the species.

# An investigation of critical life stages to estimate the optimum fire interval of the short-range, endemic, non-resprouter *Hakea victoria*

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**Context** Prescribed burning for hazard reduction is increasing in frequency due to increasing drought and dryness of available fuels, leading to more frequent and intense summer wildfires that threaten human life and ecosystems. Non-resprouters such as *Hakea victoria* are at particularly high risk of population decline when the inter-fire period is shorter than the time it takes to accumulate an adequate seed bank for post-fire recruitment or for plants to reach reproductive maturity, putting populations at risk with increased fire frequency. **Aims** To estimate the optimum fire interval for *H. victoria* we investigated critical life stages of plants from different times since last fire (TSLF) including, time to reproductive maturity, and seed production, viability and predation over time to determine at what age *H. victoria* has maximum viable seed bank size. **Methods** To test predictions, demographic characteristics of 113 individual plants from different TSLF were recorded. Of those 113 plants, 63 had fruit removed and seeds underwent a germination trial. Quadrats were used at 14 of the 18 sites with soil samples taken at each to determine soil characteristics. **Key results** *H. victoria* reached reproductive maturity at five years old with fruit production generally increasing from 13 to over 101 years of age. The presence of young plants between 0-0.99 m in height at sites 33 and over 101 years of age indicated inter-fire recruitment occurs during the inter-fire period. *Hakea victoria* reaches maximum viable seed bank size at 24 years. **Conclusions** The optimum fire interval for *H. victoria* is approximately 20-26 years.

**Keywords:** optimum fire interval, *Hakea victoria*, non-resprouter, seed bank

## Introduction

It is well known that fire is a natural component of the environment and has influenced the diversity of life globally by shaping traits of the world's flora (Bond and Scott 2010; Crisp *et al.* 2011; He *et al.* 2012; Lamont and He 2012; Lamont *et al.* 2013; Groom and Lamont 2015; Lamont *et al.* 2019; Gosper *et al.* 2022). In many fire-prone landscapes, fire influences the structure and composition of several ecosystems (Pausas and Ribeiro 2013; Enright *et al.* 2014; He and Lamont 2018; Archibald *et al.* 2018; He *et al.* 2019), with the post-fire environment providing ideal conditions for vegetative recovery and recruitment (Groom and Lamont 2015). Key reproductive processes such as heat-stimulated seed release, resprouting from protected buds, heat and smoke-cued germination, fire stimulated flowering, seed release from serotinous cones and seed production are all influenced by fire (Gill 1981; Enright *et al.* 1998, Hanley and Lamont 2000; Groom and Lamont 2015; Tangney *et al.* 2018). These biological traits are commonly found in plants that inhabit fire-prone landscapes and increase the probability of seed/plant survival or recruitment following disturbance by fire (Gill 1981; Enright *et al.* 1998; Groom and Lamont 2015). Fundamental to the natural regeneration of plant species within fire-prone

landscapes is the presence of seeds - in situ, canopy-held (serotiny) or soil stored - that are able to survive fire or the presence of protected buds that allow for regeneration post fire (Enright *et al.* 1998a; Enright *et al.* 1998b; Enright and Goldblum 1999; Jenkins *et al.* 2005; Bowman *et al.* 2012; Lamont *et al.* 2020).

Serotinous species (non-resprouters or obligate seeders) have the ability to retain their mature woody fruits on the plant for an extended period of time, with seed dispersal triggered by fire-induced fruit opening, while non-serotinous species (resprouters) are able to regenerate after fire from protected buds within branches or in the soil (Enright and Lamont 1989b; Groom and Lamont 1997; Buma *et al.* 2013). The 'degree of serotiny' varies between species and describes the rate at which seed is released from fruits held on the plant (Lamont 1985; Enright *et al.* 1998a; Enright and Goldblum 1999). Degree of serotiny is typically represented along a spectrum from highly serotinous (seeds held on the plant for many years) to weakly serotinous (fast maturing seeds and spontaneous seed release), however, it is possible for varying degrees of serotiny to be encountered within the same species (Cowling *et al.* 1987; Enright and Lamont 1989a, b; Enright *et al.* 1998; Buma *et al.* 2013). Typically, Proteaceae reach

reproductive maturity between 4 and 9 years of age (Van der Moezel *et al.* 1987; Muir 1987; Cowling *et al.* 1987; Lamont *et al.* 1991; Enright *et al.* 1996, 1998; Bell 2001; Bradstock and Kenny 2003; Burrows *et al.* 2008; Jenkins *et al.* 2010; Kraaji *et al.* 2013) and on average most serotinous Proteaceae retain their seed for five or more years (Lamont *et al.* 1991; Lamont and Groom 1998; Groom and Lamont 2015), progressively accumulating seed with successive reproductive events, cued for release following fire (Lamont and Groom 1998; Enright and Goldblum 1999; Groom and Lamont 2015).

Fire in seasonally dry ecosystems like the Mediterranean-type climatic regions characterised by hot dry summers and cold wet winters, is a widespread and recurrent disturbance that affects the germination, dispersal and mortality of plant populations (Enright *et al.* 1998a; Tangney *et al.* 2018, Gosper *et al.* 2022). As such, attributes of fire regimes, including fire interval (the number of years between fires), seasonality, and severity, play significant roles in shaping these processes making fire a particularly influential disturbance (Burrows *et al.* 2008; Gosper *et al.* 2022). Current hazard reduction and conservation management practices in fire-prone areas include the practice of prescribed burning – a deliberate application of fire to reduce fuel loads and fire hazards in the landscape (Fernandes and Botelho 2003; Penman *et al.* 2011; Tangney *et al.* 2018). Prescribed burning aims to minimise the risks and mitigate the negative consequences of high intensity wildfires and reduce the risk to human life and assets and more recently, to meet conservation goals (Fernandes and Botelho 2003; Kenny *et al.* 2004; Penman *et al.* 2011; Tangney *et al.* 2018). However, the intimate relationship between biological processes and fire in fire-prone landscapes means that altering natural fire regimes may be damaging to ecosystems and plant communities (Enright *et al.* 2014; Tangney *et al.* 2018). For example, prescribing fires in intervals that are longer or shorter than the natural fire regime (Enright *et al.* 2014) may impact population persistence, lead to extinction of some species, modify ecosystem structure and integrity, and affect floristic composition (van Wilgen 1981; Haidinger and Keeley 1993; Morrison *et al.* 1995; Lloret *et al.* 2003; Kraaji *et al.* 2013; Enright *et al.* 2015; Tangney *et al.* 2018; Gosper *et al.* 2022). Non- resprouters are at particularly high risk of population decline when the inter-fire period is shorter than the time required to build up a sufficient seed bank for post-fire recruitment or for plants to reach reproductive maturity. This vulnerability makes them more susceptible to increased fire frequency (Morrison *et al.* 1995; Enright *et al.* 1996; Knox and Morrison 2005; Kraaij *et al.* 2013; Harvey *et al.* 2017; Gosper *et al.* 2022).

With fire so intimately tied to the persistence of flora, the management of fire regimes through prescribed burning in fire-prone landscapes such as south-west Australia is of ecological importance (Fontaine *et al.* 2012; Groom and Lamont 2015). With a changing climate, the risk of more intense wildfires is increasing due to warmer and drier conditions, lengthening fire seasons and increasing annual extreme weather events (Buma *et al.* 2013; Enright *et al.* 2014; Enright *et al.* 2015). The solution to these effects will likely be to undertake prescribed burning over shorter fire intervals for hazard reduction (Enright *et al.* 2015) causing species loss, invasion and potential extinction (Enright *et al.* 2014). Malcolm *et al.* (2006) identified south-western Australia as one of the most vulnerable global biodiversity hotspots in the face of global climate change, with the potential to lose more than 2000 species within the next century. As such, conserving and preserving the high biodiversity values of the south-west and the high number of endemic species found within it are now the priority for some conservation groups and Local and Federal Government agencies. Given the importance of serotinous species in south-west Australia including *Banksia* and *Hakea*, it is vital to understand ecosystem processes and plant reproductive traits when planning fire management (Buma *et al.* 2013; Kelly *et al.* 2020). Current fire management practices in south-west Australia aim to manage fire intervals within an acceptable range that maximises the probability of population persistence of all species within an ecosystem, however, this ‘one size fits all’ approach may not be suitable for maintaining population persistence of individual species such *Hakea victoria*.

*Hakea victoria* (Proteaceae) is a short range, serotinous non-resprouter endemic to the Southwest Australian Floristic Region and has seen changes in population structure due to too frequent fires. Relatively little is published on *H. victoria*, which reduces the likelihood that current land management including the use of fire, will be appropriate for the species and could put it at risk, therefore it is vital to study the critical life stage (i.e., age of reproductive maturity, seed bank size and seed viability over time) to assist in responsible conservation management of the species.

Accordingly, this study aimed to investigate the critical life stages of *H. victoria* to enable the estimation of the optimum fire interval for the species: that time when the canopy seed bank is maximised. To achieve this goal the study was driven by the following research questions:

- 1) At what age is reproductive maturity reached?
- 2) How does fruit and seed production change over time?
- 3) How does seed age and predation effect seed viability over time?
- 4) How does inter-fire recruitment and plant mortality effect stand density with time since fire?
- 5) In what age range do we see maximum viable seed bank size?

These five questions were designed to address the overarching inquiry: what fire interval range is optimal for ensuring the persistence of *Hakea victoria* in a fire-prone ecosystem?

## Methods and materials

### *Study location and species*

*Hakea victoria* (Royal Hakea; Fig. 1) is endemic to the Esperance plains bioregion of the Southwest Australian Floristic Region (SWAFR), a global biodiversity hotspot with exceptional plant diversity (Gosper *et al.* 2022). *H. victoria* is a typically sparsely branched serotinous shrub, that when mature can reach up to 4 metres tall (Florabase, 10th June 2022). This charismatic species attracts tourists due to its unusual appearance and ombre of brightly coloured leaves; likened to a sunset. *H. victoria* plants are killed during fire, with germination occurring in the post-fire environment. Flowers are a cream to white colour, growing during autumn, winter and spring (April-October) and once pollinated develop into woody fruits.

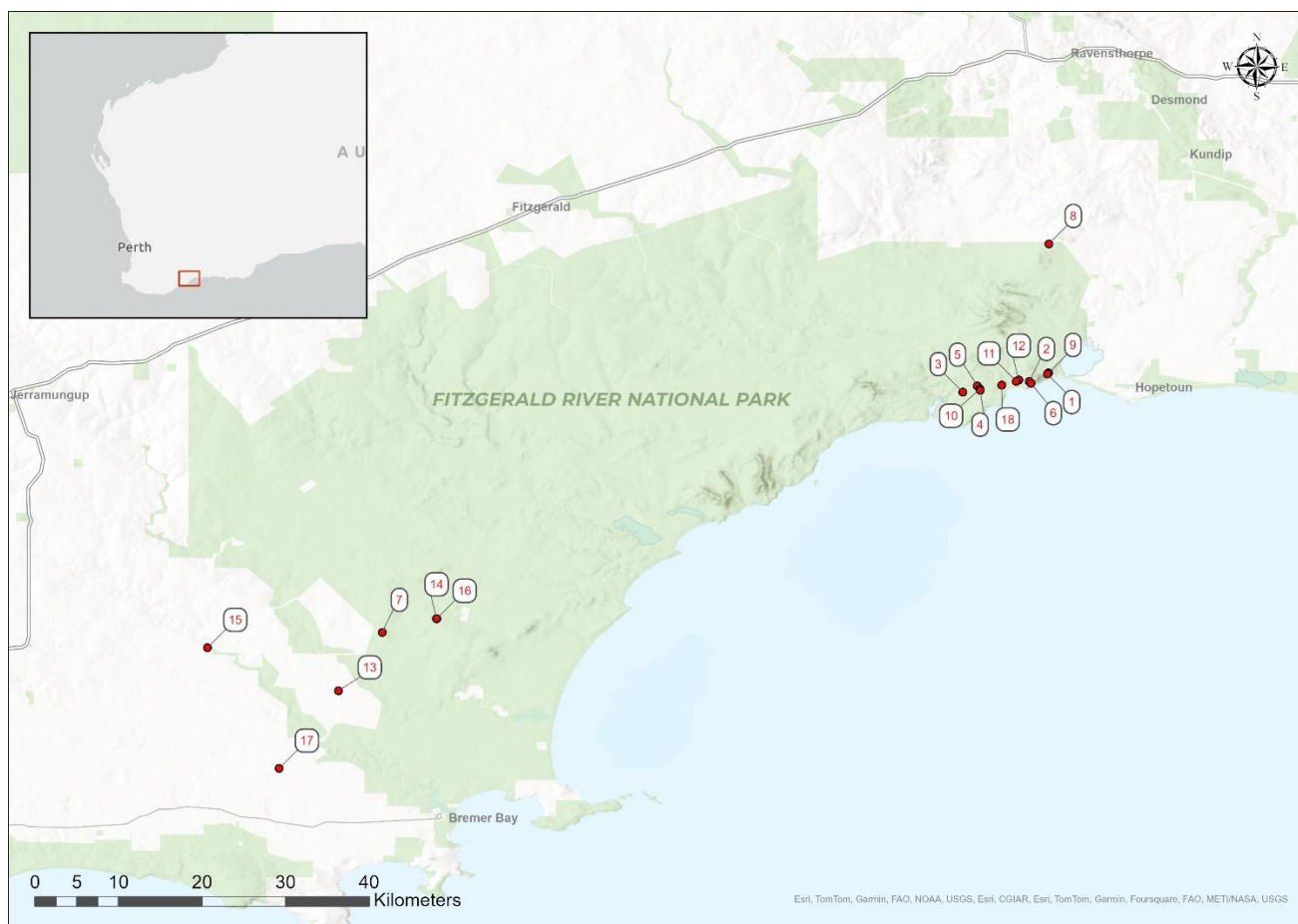
*H. victoria* is found across a linear coastal band of approximately 110kms from Hopetoun on the eastern edge of the Fitzgerald River National Park (FRNP), and west near Bremer Bay (Florabase, March 2022; Atlas of Living Australia, March 2022). The climate of the region is typically Mediterranean characterised by warm to hot summers with sporadic rainfall and cool, damp winters

(Everaardt 2003; Cochrane 2018; Vincent *et al.* 2019). The climate is moderated by the proximity to the Southern Ocean with the 100-year average annual maximum and minimum temperatures ranging between 21.8 - 22.8°C and 9.3°C - 11.5°C respectively, and the average total annual rainfall ranging between 386.7mm to 481.5mm (Bureau of Meteorology, 8<sup>th</sup> March 2024). The FRNP supports a range of ecosystems from high open shrublands and coastal heath to semi-arid woodlands (Aplin and Newbey 1990; Gosper *et al.* 2022). Stands of *H. victoria* grow in mosaic patches on white or grey sand over granite or laterite, or on rocky slopes among quartzite within areas of coastal heath, open shrublands, valleys, and mountain sides amongst *Eucalyptus sepulcralis*, *Eucalyptus pleurocarpa*, *Eucalyptus sinuosa*, *Banksia spinulosa*, and *Banksia speciosa*. While *H. victoria* is currently 'not threatened' (Western Australian Herbarium, 1998-), its restricted distribution increases the risk of extinction.



**Fig. 1.** A branching adult *Hakea victoria* plant with clear annual growth increments ranging in colour from yellow to dark orange. Plant located near East Mount Barren on the eastern side of the Fitzgerald River National Park.





**Fig. 2.** Location of the 18 sites used in this study, spanning across approximately 110km of coast from Hopetoun and west to Bremer Bay, including the Fitzgerald River National Park. Sites are indicated by red circles with the site number indicated in the connecting bubbles. Sites 14 and 16 were delineated by a fire break created during the February 2022 wildfire.

### Study design

A space for time approach (the observation of plant behaviour over multiple temporal and spatial scales) (Estes, et al. 2018) was used to investigate the differences in *H. victoria* population density, seed viability and seedbank size at different plant ages. Given that *H. victoria* is killed by fire, it was assumed that time since last fire could be used as a surrogate for plant age, therefore sites with differing times since last fire and stands of *H. victoria* were identified.

Fire history data collated by the Department of Biodiversity, Conservation and Attractions (DBCA) from 1922 to 2022 (dataWA, 2022) was mapped (ArcMap, ArcGIS 2021 v.10.9.1, Esri) alongside distribution data for *H. victoria* (Florabase and Atlas of Living Australia) to identify potential field sites. The legitimacy and accuracy of the DBCA data was confirmed by experienced locals including Shire employees, DBCA rangers, the Friends of the Fitzgerald River National Park and farming community neighbouring the FRNP. In total 18 sites were identified with stands of *H. victoria* and varying time since last fire: 1, 13, 16, 19, 24, 33 and over (the exact year could not

be confirmed) 101 years (Fig. 2; Table 1). Sites were selected based on their time since last fire, the recorded presence of *H. victoria* and their proximity to roads and tracks. Soil characteristics were quantified for a representative sample of the field sites (i.e. 2, 3, 4, 5, 7, 8, 9, 10, 11, 12, 13, 14, 15, and 16; Table 1). At each site, four soil samples dug to a depth of 10 cm were collected, bulked and later analysed to determine nutrient levels (CSBP, Bibra Lake, Western Australia).

All field work was undertaken between April 2022 to September 2023. This included, validating a method for estimating plant age. To confirm using TSLF was an accurate means to age plants, Lamont's (1985) ageing method was used to estimate age of *H. victoria* plants in different areas of time since last fire. As this method was time consuming to apply, plant height was also recorded to assess if it could be used as a surrogate for plant age. Individual plants were assessed for several demographic characteristics and fruits were harvested for seed viability testing. Germination trials to test for seed viability were undertaken between May 2023 to December 2023 at the Western Australian Herbarium, Kensington.

### *Estimating plant age*

The most accurate method for determining age, growth rate, reproductive rate and survival is to follow a cohort of plants over time and through different life stages (Jenkins *et al.* 2005), however for perennial species, this requires extensive time investment. As a result, we adopted a space-for-time approach to mitigate temporal constraints. Being an obligate seeder *H. victoria* is killed by fire and thus time since last fire is a reliable estimate of plant age, assuming seeds germinate during the first winter post-fire. However, in this study being able to estimate plant, fruit and seed age independent of time since last fire was important: to determine if *H. victoria* shows inter-fire recruitment, the length of the juvenile period, and how seed viability changes with seed age. For this reason, Lamont's (1985) method that relies on counting nodes between adjacent annual growth increments was applied to *H. victoria*.

Plant age was estimated by combining a count of annual growth increments (nodes) from the tallest apex of the plant with the estimated average growth rate in height for any uncounted sections from the ground to the lowest 'confidently identified' node. While this aging technique proved sufficiently accurate for *H. victoria*, it had limitations, with age determination restricted to approximately 30 years (see Results). Challenges arose when identifying older nodes due to secondary thickening and leaf loss, impeding the identification of nodes and internodes necessary for aging the stem from the terminal apical meristem. Node counting proved to be a time-consuming process and consequently, we investigated the feasibility of using plant height as a surrogate for age. To reinforce the aging method, we monitored 15 randomly selected plants at sites 7, 12 and 13 which displayed evidence of new growth, over 14 months, to observe the development of any new annual growth increments. Copper tags were secured underneath the newest (terminal) growth increment in July 2022 (Fig. 3).

### *Plant stand density and age structure*

Changes in stand density and age structure of *H. victoria* over time since fire was investigated using 14 sites, representing all fire histories (Table 1; Sites 2, 3, 4, 5, 7, 8, 9, 10, 11, 12, 13, 14, 15 and 16). Sites were selected based on the time since fire and the presence of *H. victoria*, and collectively included as much geomorphological and habitat diversity from across the species range as possible. The density and age structure of *H. victoria* was estimated from 14, 400-800 m<sup>2</sup> survey quadrats. Quadrats were positioned at each site a minimum of 10 meters from a track or road to avoid edge effects and were adjusted in size and/or shape to accommodate plant-stand shape and/or density.

Within each quadrat *H. victoria* (dead and alive) were measured for height (an indicator of age; see Results),

number of branches and branch characteristics: dead/alive and reproductive/ non-reproductive (i.e. branches that have reach reproductive maturity and have developed flowers and/or fruit). The level of detail recorded of branch characteristics varied between plants due to: challenges of time constraints and plant size (e.g. only total number of branches was recorded for site 15 due to the large size of the plants); site characteristics (e.g. plants at site 16 had no branches due to being young seedlings following a recent fire); and early on in the project the method was extended in response to new insights.

### *Plant size and complexity and fruit production*

A total of 113 plants from 15 sites representing all fire histories were selected to age and collect data on fruit production. The height of each plant and height from the base of the stem to the nearest confidently aged annual growth increment was recorded to allow plant age to be estimated (see Estimating plant age). To understand current and potential future reproductive output and seedbank size, the number of reproductive branches, open fruit and closed fruit, were recorded for each plant. Plants were selected if their size and form was representative of the surrounding population and also on the ability to accurately age each annual growth increment (e.g., plants with a broken stem at the apex were excluded). Three plants from over 101 years since last fire had a subsample of fruit collected due the large size of the plant, while all branches were counted to allow for extrapolation of number of fruit and viable seed on each plant.

### *Seed production, viability and predation*

As *H. victoria* is a serotinous non-resprouter that accumulates seeds over multiple reproductive events it was crucial to evaluate the number of fruits produced, viable seed and predated seed per plant over time. This assessment was necessary to estimate maximum viable seed bank size.

From 63 of the 113 plants, closed fruits that each contained two winged seeds, were collected for viability testing. Fruit collection was completed between July 2022 and September 2023 from plants with differing time since fire (16, 19, 24, 33 and 101 years) and bagged according to the age of the growth increment they were from (i.e., age-specific cohort). In instances where growth increments could not be defined, fruit was bulked for the whole plant. And where some of the plant could be aged and other areas could not, fruit from the identifiable growth increments were collected separately and all remaining fruit bulked.

Collected fruits were stored in a drying room set at 15% relative humidity and 15°C at the Western Australian Herbarium for 1-6 months prior to germination. Fruits

and seeds for each plant and growth increment were counted and assessed for condition (i.e. either full or predated and/or rotten) before seeds were stored for a further 7-28 days in a drying room.

While the preferred germination temperatures for *Banksia* and other *Hakea* species are generally known (i.e. between 13°C and 16°C; Cochrane et al, 2014) a trial was used to verify the optimum germination temperature and the time to peak germination for *H. victoria*. Germination of commercially acquired seed (Tranen Revegetation Systems, Western Australia) was examined at five constant temperatures (7, 12, 15, 18, and 23°C) and one alternating (18/7°C) on both agar and filter paper over moistened synthetic sponge. The most successful combination of temperature and medium, with 98% of seeds germinating was 15°C and agar. Germination peaked between two to four weeks while no germination occurred at 23°C.

All field collected seeds, irrespective of whether it had evidence of predation, mould or other imperfections were plated on 90 mm diameter plastic petri dishes containing 7.5g/L agar, with a maximum of 26 seeds per petri dish. Seeds of the same plant were plated on the same day and collectively all seeds were plated at weekly intervals over 12 weeks. Petri dishes were held in airtight plastic containers to minimise water loss and containers were kept in a growth room at 15°C.

Germination of seeds was assessed weekly until three consecutive weeks of zero germination had occurred or once eight weeks had passed. Germination was deemed successful when the radical had emerged to at least 3 mm in length. In some instances, monitoring continued past five weeks and ungerminated seeds were sterilised in a custom 10% plant preservative solution (containing 0.1350% 5-Chloro-2-methyl-3(2H)-isothiazolone and 0.0412% 2-Methyl-3(2H)-isothiazolone), for 15 minutes to minimise additional growth of mould, fungus and bacteria. Treated seeds were re-plated on new petri dishes containing 7.5g/L agar. After peak germination

had occurred remaining ungerminated seeds were subject to a cut test. Seeds were cut open and defined as one of the following: (1) dead – seed intact and discoloured, (2) full – seed hard and intact with a white/cream colour and (3) predated – seed casing empty, no seed present inside or evidence of predation (small entry hole). Seed viability was scored based on successful germination or the presence of a full seed during the cut test. Predation of seeds was determined pre-plating and later confirmed during the cut test.

#### *Statistical analysis*

Data were assessed for normality, skewness, kurtosis and homogeneity of variances prior to testing using a one-way ANOVA. As data did not meet the assumptions for parametric analysis the non-parametric Kruskal-Wallis test was used (with significant values adjusted by the Bonferroni correction) and followed by pair-wise comparisons using Dunn's test. All analyses were completed using SPSS (Statistical Package for the Social Sciences, v29.0.0.0 (421), IBM).

Total viable seed bank size ( $S_v$ ) for each time since last fire was estimated for *H. victoria* as the product of three individual measures (see details below): number of plants per hectare ( $P_H$ ), total viable seed ( $V_s$ ) and number of plants sampled ( $P_s$ ).

$$S_v = (V_s \div P_s) \times P_H$$

Number of plants per hectare ( $P_H$ ) was calculated using the total number of plants in each quadrat at sites 2, 7, 8, 9, 10, 13, 14, and 15 (Table 1) and total quadrat size (m<sup>2</sup>).

**Table 1. Descriptions of the 18 sites used, including: time since last fire (TSLF), number of quadrats surveys and their relative area, relative vegetation density and critical soil nutrients concentrations. Location, age, nutrient levels, density and topography for each of the 18 sites used.** The sites described as 101 years since last fire are an undefined period older than 101 years, because the fire history data used only contained records from 1922 (dataWA, March 2022).

TSLF (years)	Site	Location	Latitude	Longitude	# Quadrats	Quadrat size (m <sup>2</sup> )	Vegetation density	Aspect, slope	NH <sub>3</sub> (mg/kg)	P (mg/kg)	K (mg/kg)	C (%)	S (mg/kg)
1	16	Pabelup Dr. firebreak	-34.18262	119.37711	3	400	1	North-west, gently sloping	3	2	< 15	0.84	0.7
13	17	Tozer's Bush Camp	-34.34377	119.20742	-	-	1-2	Flat	-	-	-	-	-
16	9	DBCA (right side of hill)	-33.9184	120.03527	1	400	3	South-west, steep	6	3	117	2.79	9.1
16	1	Hamersley Dr. (southern side), uphill of DBCA	-33.91976	120.03397	-	-	2-3	South-east, moderately sloping	-	-	-	-	-
16	2	East Mt. Barren trail	-33.92776	120.01436	1	406	2	West, moderately sloping	2	< 2	31	1.19	5.5
16	12	West of East Mt. Barren	-33.92605	120.0031	1	400	2	WSW, gently sloping	7	< 2	41	2.32	1.5
16	11	East Miley Beach (north side of Hamersley Rd)	-33.92752	120.00059	1	400	2	SSW, moderately sloping	4	< 2	29	1.27	1.6
16	18	Miley's Beach Road	-33.93166	119.98472	-	-	1	South-east, gently sloping	2	< 2	15	0.71	1.7
19	8	No Tree Hill	-33.7797	120.03563	4	362 - 453	1-2	North-east, gently sloping	3 - 4	< 2 - 6	22 - 45	1.03 - 1.31	1.4 - 2.7
24	7	Mount Maxwell	-34.19755	119.31822	3	417 - 419	2-3	South, gently sloping	2 - 4	< 2 - 2	< 15 - 29	1.42 - 2.03	2.6 - 3.3
33	3	Hamersley Inlet Rd.	-33.93901	119.94283	1	2070	2	North-west, moderately sloping	-	-	-	-	-
33	5	Corner of Hamersley Dr and Hamersley Inlet Rd.	-33.93258	119.95868	1	1100	1-2	Flat	-	-	-	-	-
33	6	Hamersley Dr between East Miley Beach carpark and Barrens lookout	-33.92971	120.01648	-	-	2	South-east, moderately sloping	-	-	-	-	-
33	10	Hamersley Dr (eastern side before gravel)	-33.93574	119.96136	1	426	1-3	Flat	2	< 2	16	1.06	2.3
33	4	Hamersley Dr (western side before gravel)	-33.93724	119.96155	1	400	2	Flat	-	-	-	-	-
101	13	Murray Road	-34.26012	119.27131	1	625	2	Flat	3	< 2	37	0.77	2
101	14	Pabelup Dr. firebreak	-34.18262	119.37688	1	400	2-3	North-west, gently sloping	4	< 2	15	1.01	1.4
101	15	Devil's Creek Road	-34.21388	119.1303	1	780	1-2	Flat	3	< 2	28	0.77	1.1

\*Relative density of vegetation given as one of three categories; (1) Vegetation surrounding whole plant 0.5m high or less, (2) Surrounding vegetation covers 50% of entire plant or (3) Surrounding vegetation covers 50% or more of entire plant.

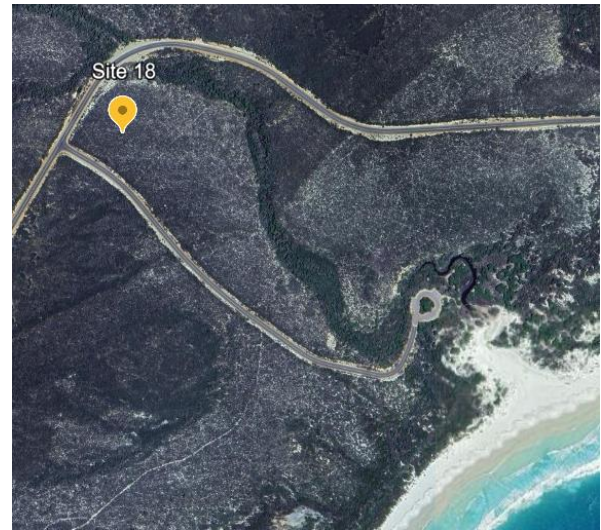
## Results

### Estimating plant age

Plant age was important for determining seed bank size, seed viability and population dynamics over time. Repeated annual growth increments can be seen along the stem of *H. victoria* between adjacent nodes, with wider leaves at the base of the increment and reducing in width towards the top (Fig. 3). Of the 15 plants monitored for apical growth, 60% ( $n=9$ ) produced a single new growth increment, as predicted. Of the 6 plants that did not produce an annual growth increment, three were from Site 18 where the site dealt with ‘tougher’ conditions including sloping topography towards the south, low vegetation density, low levels of ammonium nitrate (2 mg/kg), phosphorus (< 2 mg/kg), potassium (15 mg/kg), organic carbon (0.71 %) and sulfur (1.7 mg/kg) (Table 1). In addition, Site 18 was open to the impacts of close coastal proximity (i.e., wind and possibly salt aerosol; Fig 4).

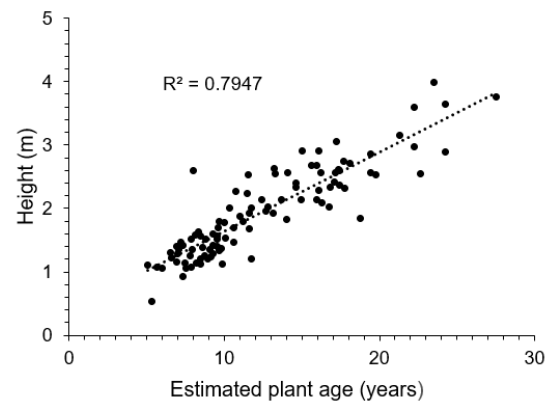


**Fig. 3.** *H. victoria* plant displaying annual growth increments, with a copper tagged attached at the base of the second growth increment.

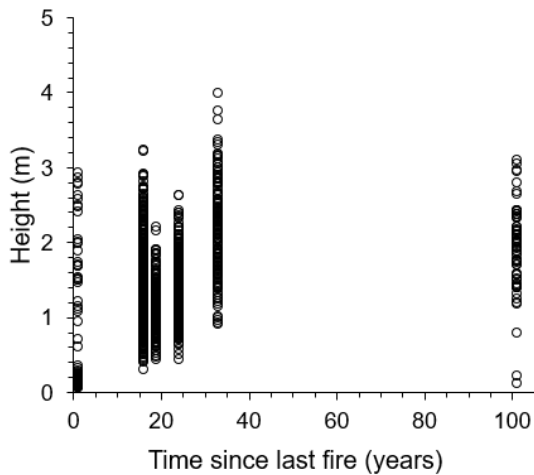


**Fig. 4.** Aerial view of Site 18 (orange icon) in relation to the coast. Distance from coast is approximately 700 m.

There was a strong positive linear correlation between estimated plant age and height, confirming height as a good predictor of plant age ( $r^2=0.7947$ , Fig. 5). While this relationship supports the estimation of plant age from height, it is limited up to approximately the first 30 years of life. This is because the range of estimated plant ages only extends to 27 years, and beyond 33 years old, plant growth in height appears to plateau and growth is focused on branching outwards (Fig. 6; Fig. 9).



**Fig. 5.** Relationship between total plant height and estimated plant age for *H. victoria*. Plant age was estimated from the number of confident increments, average growth rate and height to the nearest confident increment.



**Fig. 6.** Relationship between total plant height and time since last fire for *H. victoria* showing that plant height plateaus after 33 years since fire where plants begin to focus on branch growth.

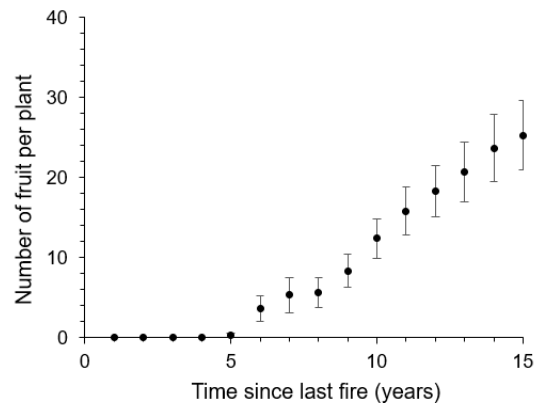
#### *Juvenile period and fruit production*

Since sites aged between 1 and 13 years were unavailable, we utilised growth increment data to extrapolate the fruit production per plant over time. This allowed us to ascertain the age at which *H. victoria* reaches reproductive maturity (Fig. 7). This was accomplished by staggering the growth increment data for individual plants according to time since last fire. (i.e., the first annual growth increment observed on a 33-year-old plant represents the plant at 33 years old, while the first annual growth increment on a 16-year-old plant represents the plant at 16 years old). Plants first produced fruits at an age of five years, after which fruit production continued at a steady linear rate. Fruit production was sustained from 5 years to over 101 years, with the rate incrementally increasing as plants grow older (Fig. 7 and 8).

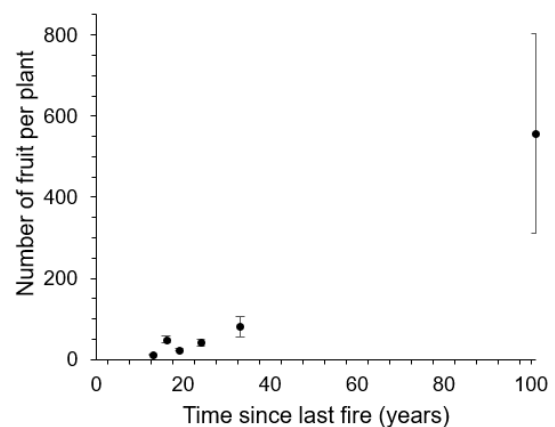
Fruit production generally increased continuously on plants from 13 years ( $11.64 \pm 2.14$  fruits per plant) to over 101 years ( $557.10 \pm 246.41$ ) with a significant difference in the number of fruits per plant across sites with different time since last fire ( $p < 0.001$ , Kruskal-Wallis; Fig. 8). The average fruit per plant was higher than expected for plants of 16 years since fire and this appears to correlate with topographical and nutrient differences at Site 9 (Table 1). Of the five 16-year-old sites, Site 9 was notably wetter in a steep gully and had higher concentrations of ammonium nitrate, potassium, sulfur, organic carbon and phosphorus and density of the surrounding vegetation was high (Table 1). The unexpected effect of Site 9 can be seen in the pairwise comparisons where there is a significant difference between the number of fruits per plant between 13 and 16 years ( $p < 0.001$ , Dunn's test) and 16 and 19 years ( $p = 0.004$ ), however there is no significant difference in

the number of fruits per plant between 13 and 19 years ( $p = 0.84$ ). From this it can be assumed that without the differences of Site 9 fruit production would consistently increase with plant age.

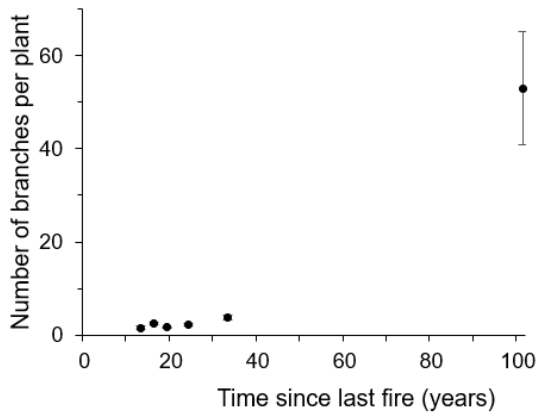
The largest increase in the number of fruits per plant ( $476.16 \pm 221.74$ ) was between 33 to 101 years after fire, although this increase was not significant ( $p = 0.079$ , Dunn's Test; Fig. 8). This correlates with the large increase in the average number of branches per plant ( $49.27 \pm 11.63$ ); if a p-value of 0.06 is accepted as the cut-off to reject the null hypothesis ( $p = 0.060$ ; Fig. 9).



**Fig. 7.** Average accumulative fruit per plant ( $\pm$ SE) for *H. victoria* over time since last fire. Fruit number prior to 13 years TSLF has been extrapolated from the increment data to determine the juvenile period for *H. victoria*.



**Fig. 8.** Average number ( $\pm$ SE) of fruit per plant for *H. victoria* over time since last fire ( $n = 11, 28, 28, 18, 18$  and  $10$  for each time since last fire, respectively). Plants for each time since last fire were surveyed from 17 sites.

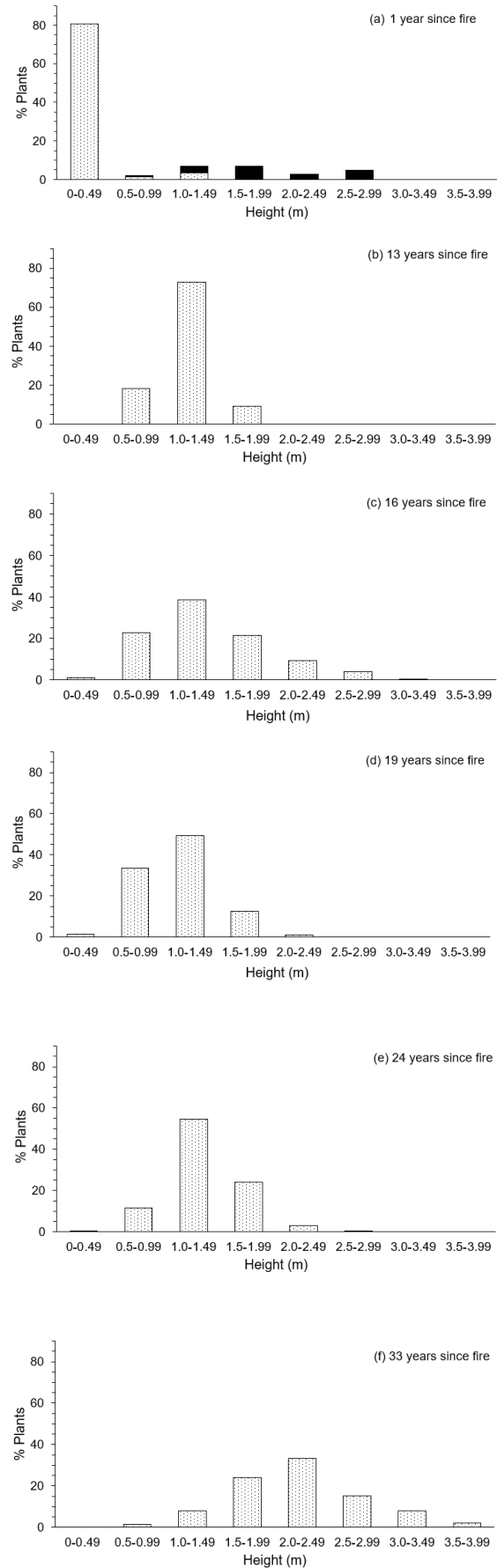


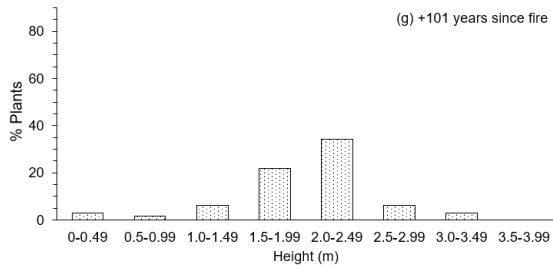
**Fig. 9.** Average number ( $\pm$ SE) of reproductive branches per plant for *H. victoria* over time since last fire ( $n=11, 28, 20, 18$  and  $10$  for each time since last fire, respectively). Plants for each time since last fire were surveyed from 17 sites.

#### Stand age-structure and inter-fire recruitment

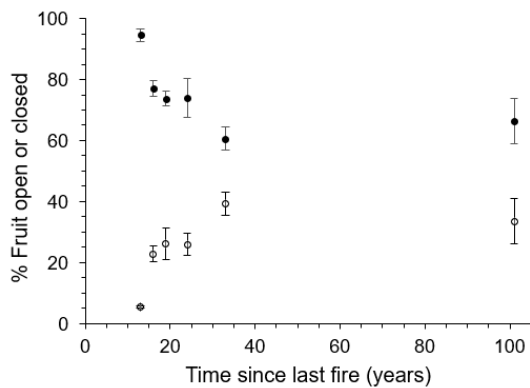
To test whether inter-fire recruitment occurs in *H. victoria* plant height (as a surrogate for age) was measured at site of each time since last fire. As predicted, plant height generally increased with time since last fire. In older plant stands (33 and 101 years) height ranges were greater than those of younger stands of *H. victoria* (Fig. 10a-g). Considering that one-year post-fire, 81% of the living stand comprises young plants within the 0-0.49 m height range, averaging  $0.14 \text{ m} \pm 0.01$ , it can be assumed that finding plants of similar heights at older sites indicates inter-fire recruitment within stands of *H. victoria*. Inter-fire recruitment is particularly evident with the presence of young plants between 0-0.99 m in height at sites 33 years and over 101 years since fire (Fig. 10a-g). Although inter-fire recruitment does occur, recruits always represent a small portion (<5 %) of the population and likely do not have a significant impact on plant density.

The presence of young plants tends to coincide with the pattern of fruit opening. There was a significant difference in the number of open fruits across sites with different time since last fire ( $p < 0.001$ , Kruskal Wallis; Fig. 12). Between 13-16, 16-19 and 24-33 years since fire there is a significant difference in the average percentage of open fruits ( $p < 0.001$ ,  $p = 0.018$  and  $p = 0.011$  respectively; pairwise comparisons, Dunn's test). After 33 years the number of open fruits plateaus, showing no significant difference with the number of open fruits for plants over 101 years since fire ( $p = 0.702$ ). Although the number of open fruits remains constant after 33 years the percentage of dead *H. victoria* plants continues to increase over time in a strong linear fashion (Fig 11).

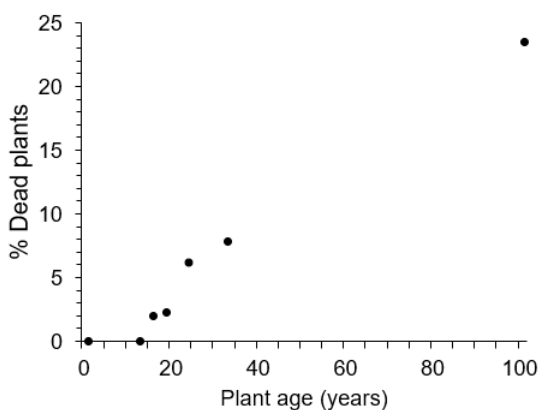




**Fig 10.** Frequency (%) distributions of alive plant height (a surrogate for age between 0-27 years; see Fig. 5) for stands of *H. victoria* at different times since last fire; (a) 1 ( $n=149$ ), (b) 13 ( $n=11$ ), (c) 16 ( $n=551$ ), (d) 19 ( $n=217$ ), (e) 24 ( $n=645$ ), (f) 33 ( $n=153$ ) and (g) +101 ( $n=64$ ) years. Dead burnt plants that formed the pre-fire stand are shown in the 1-year-post-fire survey in solid black. Plants were surveyed from 14 sites with varying time since last fire.



**Fig. 11.** Average percentage ( $\pm$ SE) of open and closed fruit per plant ( $n=73$ ) for *H. victoria* over time since last fire. Plants for each time since last fire were surveyed from 17 sites. Open symbols represent open fruit; solid symbols represent closed fruit.



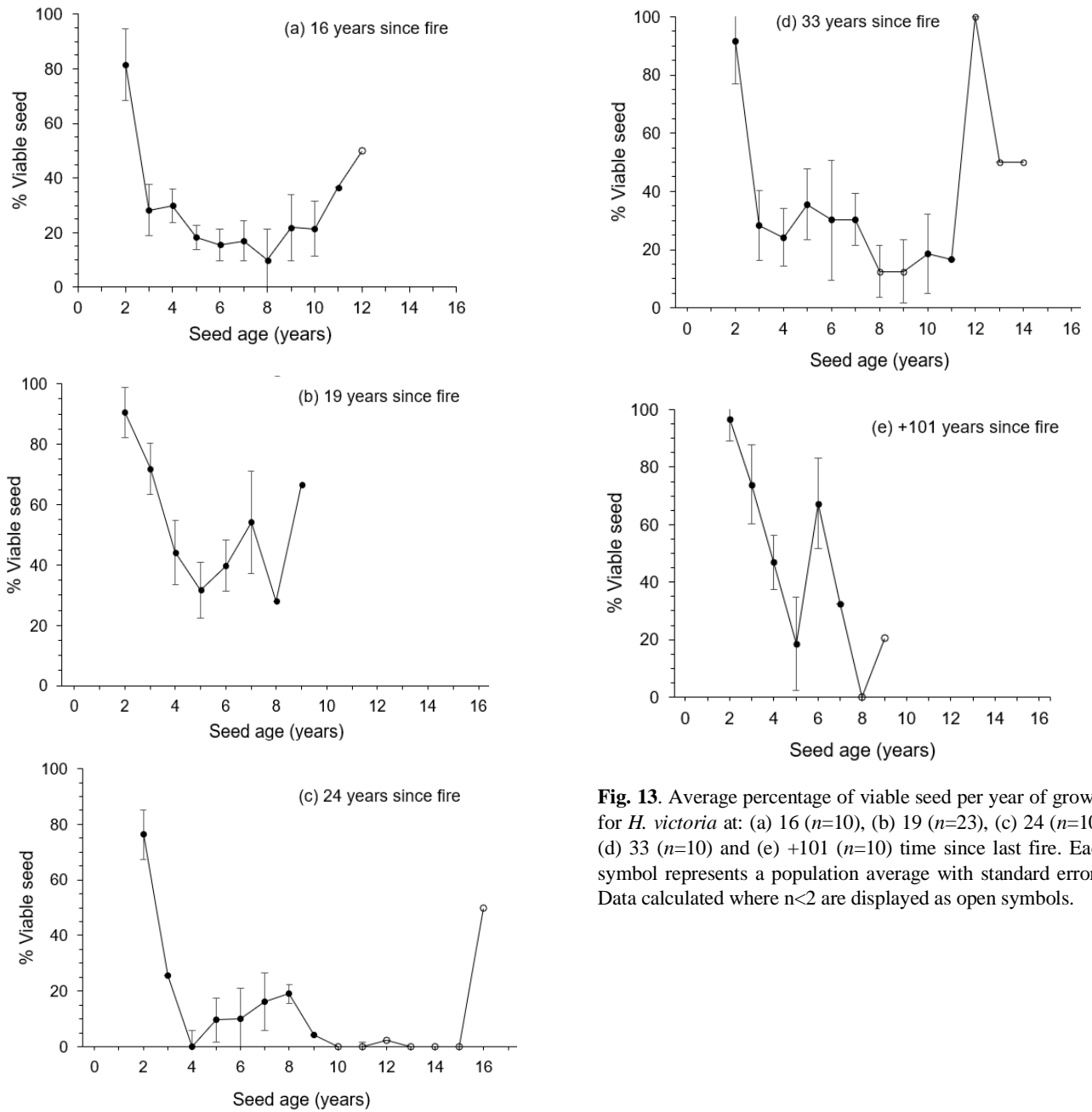
**Fig. 12.** Percentage of plant death following fire (i.e., not killed by fire) for *H. victoria* over time (1 ( $n=0$ , all alive), 13 ( $n=0$ , all alive), 16 ( $n=11$ ), 19 ( $n=5$ ), 24 ( $n=40$ ), 33 ( $n=12$ ), +101 ( $n=15$ )).

### Seed viability and predation

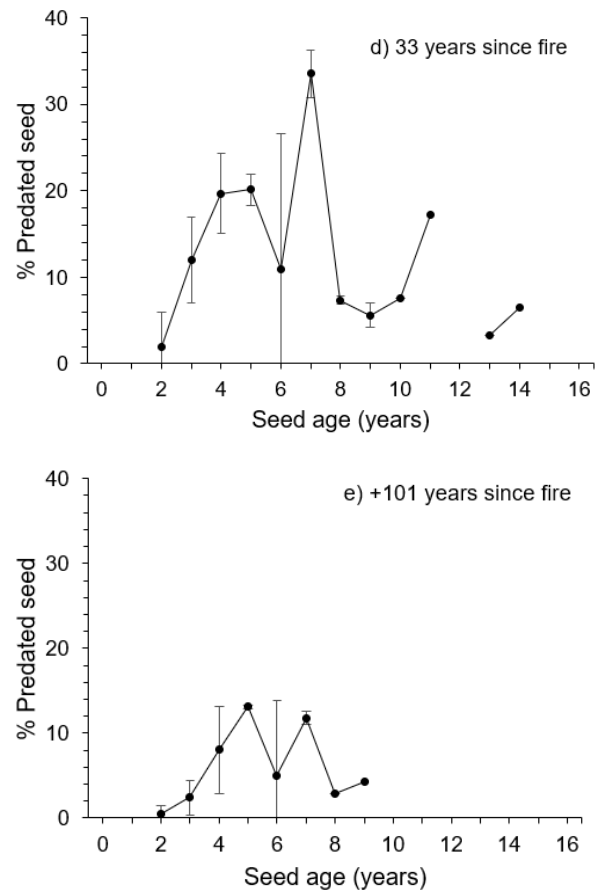
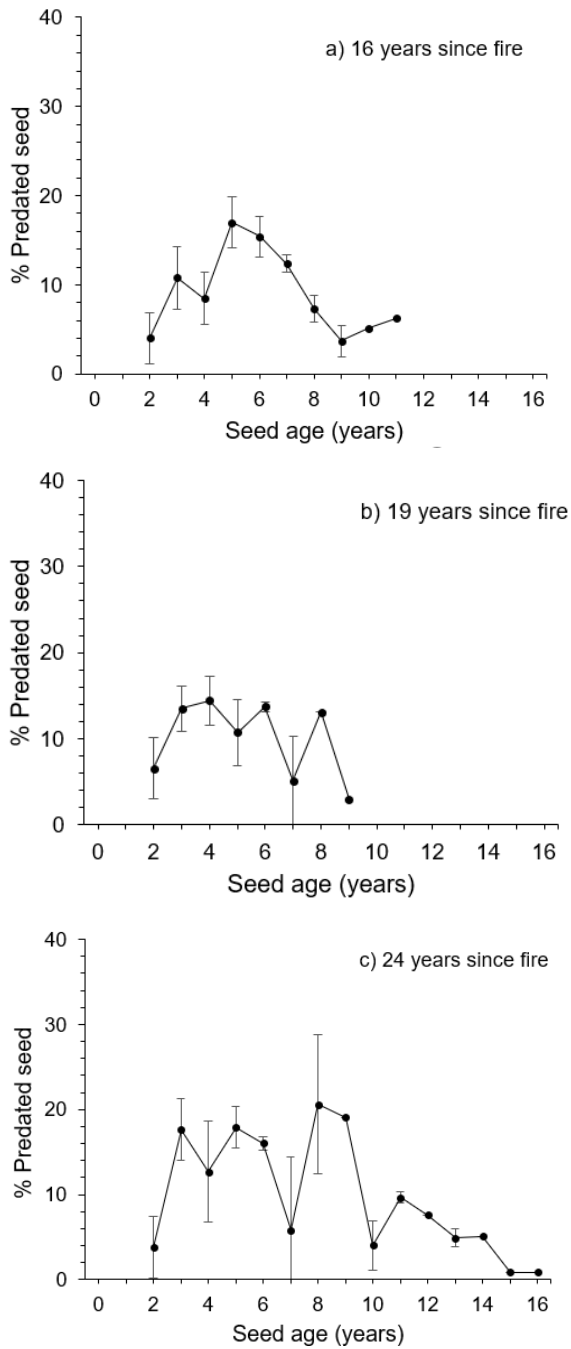
Seed viability and seed predation were identified during the germination process, and viability was compared for plants from sites of different time since fire and between seeds of different ages, i.e. from different seed cohorts associated with different annual growth increments. A clear trend can be seen across the plants from all times since last fire, with two-year-old seeds showing the highest viability of any age cohort (Fig. 13a-e). However, there was no significant difference in the number of viable seeds between ages 2 and 3 across different time since last fire ( $p=0.821$ , Dunn's test; Table 2). Furthermore, there was a significant difference in number of viable seeds per plant with different times since last fire ( $p<0.001$ ; Kruskal-Wallis, Table 2). As expected, 16 years since fire had a higher average number of viable seeds per plant ( $24.1 \pm 9.9$ ) due to the effect of Site 9. Between 19 and 33 years the average number of viable seeds remained constant before increasing significantly ( $p<0.021$ , Dunn's test) between 33 and 101 years since fire ( $12.5 \pm 2.9$  and  $98.6 \pm 23.3$  seeds per plant, respectively), which correlates with the increase in average number of branches per plant (Fig. 9). The reduction in the number of viable seeds over time since last fire is consistent with the pattern of predation.

Seed predation follows a similar, but inverse pattern to that of seed viability (Fig. 14a-e). Loss of seeds through predation is low for seeds aged two years across all age cohorts ( $5 \pm 2.1$  average predated seed per plant, Table 3) before peaking when seeds reach four years of age ( $11.8 \pm 3.3$ ; Fig 14a-e; Table 3). Between the ages of 5 and 8 the average number of predated seeds per plant remained relatively constant ( $8.5 \pm 1.9$  to  $10.7 \pm 1.7$ ), before fluctuating between 9 and 14 years of age ( $4.6 \pm 1.4$  to  $11.5 \pm 5.3$ ) (Fig 14a-e; Table 3). Despite these trends there was no significant difference in the number of predated seeds per plant between any growth increment for each age cohort ( $p=0.641$ ; Table 3).





**Fig. 13.** Average percentage of viable seed per year of growth for *H. victoria* at: (a) 16 ( $n=10$ ), (b) 19 ( $n=23$ ), (c) 24 ( $n=10$ ), (d) 33 ( $n=10$ ) and (e) +101 ( $n=10$ ) time since last fire. Each symbol represents a population average with standard errors. Data calculated where  $n < 2$  are displayed as open symbols.



**Fig. 14.** Average percentage of predated seed per year of growth for *H. victoria* at: (a) 16 ( $n=10$ ), (b) 19 ( $n=23$ ), (c) 24 ( $n=10$ ), (d) 33 ( $n=10$ ) and (e) +101 ( $n=10$ ) time since last fire. Each symbol represents a population average with standard errors.

**Table 2. The effect of seed age and plant age on the number of viable seeds of *H. victoria*. Data are the average number of viable seeds ( $\pm$ standard error and n in parentheses) from each age cohort (annual growth increment) of plants across 11 sites with differing time since last fire (TSLF). No seed indicates that no sample was taken for that increment; 0 indicates there were no viable seeds in the sample, only non-viable seeds. Only green fruit were present in increment one and were not removed from the plant for testing due to their immaturity.**

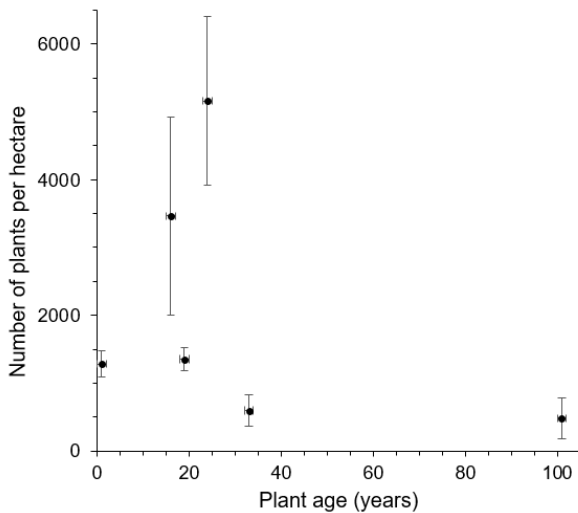
Seed age (years)	TSLF (years)					Average number of viable seeds per age cohort
	16	19	24	33	+101	
1	No seed	No seed	No seed	No seed	No seed	No seed
2	19.6 $\pm$ 4.4 (3)	3.1 $\pm$ 0.5 (8)	5.2 $\pm$ 1.8 (7)	6.6 $\pm$ 1.9 (3)	48 $\pm$ 22.8 (4)	13.3 $\pm$ 4.9 (25)
3	3.2 $\pm$ 0.8 (4)	6.9 $\pm$ 1.6 (11)	7 $\pm$ 2.5 (4)	2.3 $\pm$ 0.2 (3)	26.3 $\pm$ 8.9 (3)	8.1 $\pm$ 1.9 (25)
4	5.5 $\pm$ 2.6 (7)	5.7 $\pm$ 0.9 (10)	0	4.7 $\pm$ 2.6 (4)	5.8 $\pm$ 1.4 (5)	5.5 $\pm$ 0.9 (26)
5	6.5 $\pm$ 3.1 (7)	9.1 $\pm$ 1.8 (6)	6.5 $\pm$ 3.1 (2)	6.5 $\pm$ 1.5 (6)	5.6 $\pm$ 1.9 (3)	7 $\pm$ 1.1 (24)
6	6 $\pm$ 2.2 (8)	8 $\pm$ 1.4 (6)	7.5 $\pm$ 4.5 (2)	3.4 $\pm$ 0.6 (5)	19 $\pm$ 2.1 (3)	7.7 $\pm$ 1.3 (24)
7	7.8 $\pm$ 2.7 (5)	5 $\pm$ 1.4 (3)	4.5 $\pm$ 0.3 (2)	3.5 $\pm$ 0.35 (2)	4.5 $\pm$ 0.3 (2)	5.6 $\pm$ 1.2 (14)
8	1.6 $\pm$ 0.5 (3)	5 $\pm$ 2.1 (3)	4 $\pm$ 0.7 (2)	1 (1)	0	3.2 $\pm$ 0.9 (9)
9	5 $\pm$ 2.8 (3)	4 (1)	2 (1)	1 (1)	6 (1)	4 $\pm$ 1.3 (7)
10	3.5 $\pm$ 1 (2)	No seed	0	2 $\pm$ 0.4 (3)	No seed	2.6 $\pm$ 0.6 (5)
11	8.3 $\pm$ 3.3 (3)	No seed	0	3 (1)	No seed	7 $\pm$ 2.7 (4)
12	1 (1)	No seed	1 (1)	2 (1)	No seed	1.3 $\pm$ 0.2 (3)
13	No seed	No seed	0	1 (1)	No seed	1 (1)
14	No seed	No seed	0	2 (1)	No seed	2 (1)
15	No seed	No seed	0	No seed	No seed	No seed
16	No seed	No seed	2 (1)	No seed	No seed	2 (1)
Average number of viable seeds per plant	24.1 $\pm$ 9.9 (10)	12.4 $\pm$ 3.1 (23)	11.5 $\pm$ 5.1 (10)	12.5 $\pm$ 2.9 (10)	98.6 $\pm$ 23.3 (10)	

**Table 3. The effect of seed age and plant age on the number of predated seeds of *H. victoria*. Data are the average number of predated seeds ( $\pm$ standard error and n in parentheses) from each age cohort (annual growth increment) of plants across 11 sites with differing time since last fire (TSLF). No seed indicates that no sample was taken for that increment; 0 indicates there were no predated seeds in the sample, only viable seeds. Only green fruit were present in increment one and were not removed from the plant for testing due to their immaturity.**

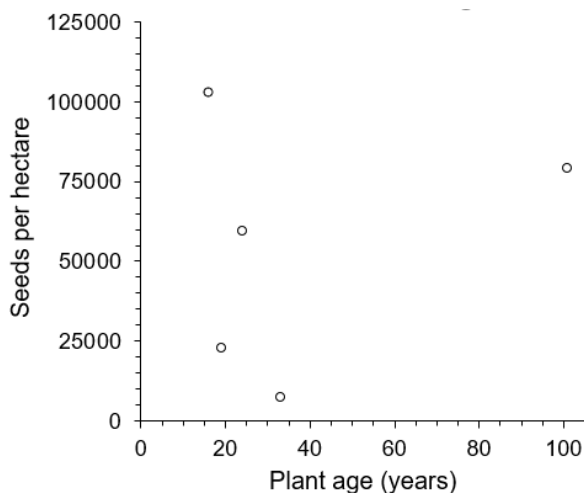
Seed age (years)	Plant age (years)					Combined average number of predated seeds per cohort
	16	19	24	33	+101	
1	No seed	No seed	No seed	No seed	No seed	No seed
2	16 (1)	6 (1)	2 $\pm$ 0.7 (2)	3 (1)	1 (1)	5 $\pm$ 2.1 (6)
3	13.2 $\pm$ 6.8 (5)	5.7 $\pm$ 2.1 (7)	7.1 $\pm$ 1.8 (6)	5.2 $\pm$ 0.6 (5)	7 $\pm$ 2.6 (3)	7.5 $\pm$ 1.6 (26)
4	17.7 $\pm$ 11.9 (8)	5.6 $\pm$ 1 (11)	7.1 $\pm$ 2.1 (6)	18 $\pm$ 8.1 (5)	16.2 $\pm$ 5.1 (4)	11.8 $\pm$ 3.3 (34)
5	17.3 $\pm$ 2.9 (9)	3.2 $\pm$ 0.5 (9)	7 $\pm$ 1 (7)	10.4 $\pm$ 2.2 (7)	12.2 $\pm$ 5.9 (5)	9.9 $\pm$ 1.4 (37)
6	16.2 $\pm$ 4 (10)	5.7 $\pm$ 2 (8)	10.3 $\pm$ 2.6 (6)	7.5 $\pm$ 2.6 (7)	16 $\pm$ 4.2 (2)	10.7 $\pm$ 1.7 (33)
7	14.7 $\pm$ 3.9 (7)	3 $\pm$ 0.7 (2)	5 $\pm$ 2.6 (5)	8.6 $\pm$ 2.8 (3)	3.3 $\pm$ 1.5 (3)	8.5 $\pm$ 1.9 (20)
8	9 $\pm$ 2.6 (6)	4.7 $\pm$ 1.3 (4)	10.7 $\pm$ 2.9 (4)	9.5 $\pm$ 5.3 (2)	11.5 $\pm$ 5.3 (2)	8.7 $\pm$ 1.5 (18)
9	4.2 $\pm$ 1.1 (4)	2 (1)	10 $\pm$ 0.9 (3)	3 $\pm$ 0.7 (2)	20 (1)	6.8 $\pm$ 1.6 (11)
10	7.3 $\pm$ 2.1 (3)	No seed	4 (1)	3.6 $\pm$ 0.9 (6)	No seed	4.8 $\pm$ 1 (10)
11	7.3 $\pm$ 1.6 (3)	No seed	9.6 $\pm$ 5.4 (3)	10 (1)	No seed	8.7 $\pm$ 2.4 (7)
12	0	No seed	11.5 $\pm$ 5.3 (2)	0	No seed	11.5 $\pm$ 5.3 (2)
13	No seed	No seed	11 (1)	1 (1)	No seed	6 $\pm$ 3.5 (2)
14	No seed	No seed	6 $\pm$ 1.4 (2)	2 (1)	No seed	4.6 $\pm$ 1.4 (3)
15	No seed	No seed	2 (1)	No seed	No seed	2 (1)
16	No seed	No seed	2 (1)	No seed	No seed	2 (1)
Combined average number of predated seeds per plant	76 $\pm$ 22.6 (10)	10.4 $\pm$ 2.1 (23)	38.2 $\pm$ 13.9 (10)	33.1 $\pm$ 12.2 (10)	73.7 $\pm$ 17 (10)	

### Viable seed production with time since fire

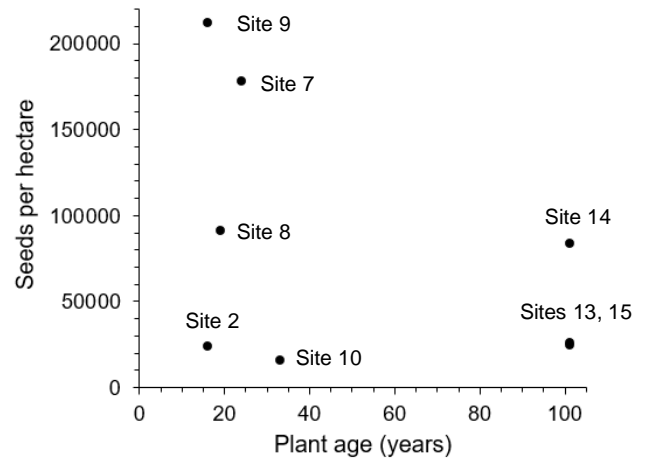
The estimated average number of plants per hectare generally increased between the ages of 1 and 24 (3880  $\pm$  24) before greatly reducing between 24 and 33 years of age (Fig 15). Figure 17 shows an increase in estimated total viable seeds per hectare between the ages of 16 and 24 (when excluding Site 9) before reducing between the ages of 24 and 33. Site 7 (24 years since last fire) has the highest estimated viable seed bank with a total of 178,135 viable seeds per hectare (Fig 17). As expected, the average number of plants per hectare for Site 9 was high, although the standard error indicates the high variability of the site (Fig 15). Further, Site 9 had the highest average number of viable seeds per hectare (Fig 16), however site by site comparison clearly displays that Site 9 is vastly different from Site 2 (also 16 years since last fire) with a difference of 188,515 total estimated viable seed; Fig 17).



**Fig. 15.** Estimated average number ( $\pm$ SE) of *H. victoria* plants per hectare with different time since last fire.



**Fig. 16.** Estimated average total number ( $\pm$ SE) of *H. victoria* seeds per hectare with different time since last fire.



**Fig. 17.** Estimated total viable seed bank size for *H. victoria* per hectare with different time since last fire. Each circle represents a surveyed site (Table 1).

### Discussion

The overarching goal of this study was to investigate the optimum fire interval for *H. victoria* and was driven by five questions designed to reveal an understanding of the critical life stages of *H. victoria* that are relevant to the species survival in a fire-prone environment. This understanding is significant to the management *H. victoria* in the FRNP.

#### Juvenile period

*H. victoria* reaches reproductive maturity and begins producing fruit at approximately five years old (Fig. 7). This time to reproductive maturity is similar for several other serotinous, non-resprouter species (Enright *et al.* 1996, 1998). Various studies have found that typically Proteaceae species have a juvenile period ranging from 4 to 9 years comparable to Proteaceae species found in southeast and southwest Australia (Cowling *et al.* 1987; Lamont *et al.* 1991; Enright *et al.* 1996, 1998; Bell 2001; Bradstock and Kenny 2003; Jenkins *et al.* 2010; Kraaji *et al.* 2013).

Species with longer juvenile periods (> 4 years) were found to be mostly obligate seeders occurring in areas of low rainfall (Muir 1987; Van der Moezel *et al.* 1987; Burrows *et al.* 2008), suggesting that annual rainfall can influence the length of the juvenile period of non-resprouters (Burrows *et al.* 2008). Intra-species variation in the juvenile period can occur in areas with different average annual rainfall for example, with low rainfall (750 mm per annum) *Hakea amplexicaulis* reaches reproductive maturity at 30 months of age in comparison to 18 months with high rainfall (1000-1350 mm per annum) (Burrows *et al.* 2008). *H. victoria* inhabits an area of low to moderate rainfall with an average total annual rainfall ranging between 386.7mm to 481.5mm (Bureau of Meteorology, 8<sup>th</sup> March 2024). More recently

Gosper *et al.* (2022) predicts that anticipated future declines in precipitation in the SWAFR due to climate change will lead to an increase in length of the juvenile period (>10 years longer) for serotinous species, suggesting that decreasing rainfall is likely to impact the length of the juvenile period of *H. victoria*.

#### *Fruit and seed production*

The rate at which fruit is produced over time is critical when determining at what age maximum seed bank size is reached. Furthermore, measuring fruit production across different spatial extents within the same time year since last fire enables the assessment of the influence of other environmental factors on fruit production. Fruit production increased steadily between the ages of 5 and over 101 with an average fruit increase of  $557.1 \pm 246.41$  per plant over 96 years (Fig. 8). The average fruit production per plant was higher than expected at Site 9 ( $49.09 \pm 8.49$ ).

Typical Mediterranean plant communities are dominated by sclerophyllous woody plants that are associated with old, poor-quality soils that are often limited in the availability of nutrients and water, particularly in the SWAFR (Sardans and Penuelas 2013). The capacity of soil to hold nutrients and water has been shown to have an outstanding role in the structure and distribution of plant communities and plant growth, with water content, nitrogen and phosphorus all named as limiting factors (Sardans and Penuelas 2013). The average number of fruit production per plant was higher than expected at Site 9 ( $49.09 \pm 8.49$ ; Fig. 8). Higher levels of phosphorus, ammonium nitrogen, sulfur and organic carbon (Table 1) at Site 9 can therefore account for the higher level of fruit production and plant growth.

Site 9 was in a steep, south-west facing gully, mostly blocked from prevailing southern winds by East Mount Barren and surrounded by dense vegetation where water retention and organic matter were likely higher than the other 17 sites. As well as the higher levels of nutrients, it can be speculated that the high productivity of Site 9 is also attributed to the topography and thus the higher water content in the soil. This infers that with higher rainfall and thus high-water content in the soil, plant growth may occur at a faster rate and fruits and seeds are more abundant. In contrast, persistent low rainfall could mean that plant growth and fruit and seed production occur at a slower rate, creating a smaller seedbank than would be typically expected.

#### *Seed bank size, seed viability and predation*

For *H. victoria* the canopy seed bank is critical for replacing a stand lost to fire and its size varies with seed viability over time. Seed viability peaked at two years of age across all age cohorts of *H. victoria*. For any given

plant, the seedbank is likely maximised when the annual production of fruit and seed per plant is at its highest, which correlates with the number of reproductive branches (potential fruit production) per plant. However, the data indicates that the canopy seedbank has its limitation in accumulation, as seeds lose viability over time. Therefore, the ‘benefit’ of new seeds is offset by the declining viability of older seeds. Although the largest plants, aged over 101 years, surprisingly exhibit the highest productivity, their occurrence is sufficiently low, suggesting that the maximum seedbank is likely reached earlier. Additionally, larger plants may exhibit higher productivity and average viable seed per hectare (Fig. 16), however due to low occurrence of plants the estimated total viable seedbank is comparable in size to that of a 19-year-old plant (Sites 14 and 18; Fig. 17). Figure 17 illustrates that the maximum seed bank is present at 24 years since last fire, when removing the effect of Site 9.

Seed predation increases significantly after the second year of fruit production, likely due to the weakening of the fruit’s outer casing, which allows predators to access the seed (Fig. 14). However, the decrease in predation observed in older age cohorts (>10 years) is likely due to small seed sample sizes (Fig. 14, Table 3). While on ground seed predation is one factor contributing to seed loss, seeds held within plant canopies are also vulnerable to predation. Fruit morphology, such as larger seeds with greater food supplies, likely plays a key role in food choice for granivores (Midgley *et al.* 1991; Groom and Lamont 1997). This is true for *H. victoria*, where abundant fruit supply appears attractive to granivores, typically insects. If serotiny is high, fruits (and seeds) are exposed for longer periods, increasing their risk of predation (Groom and Lamont 1997).

#### *Stand age-structure, serotiny and inter-fire recruitment*

Given the anticipated strong level of serotiny of *H. victoria* fruit, we were surprised to find up to 39% of fruits on plants aged 33 years to be open (Fig. 11). Even more so, that 22-26% of fruit on plants between 16 and 24 years old were open (Fig. 11). According to Lamont *et al.* (1991) and Groom and Lamont (1996) most species of *Hakea* are serotinous, and seed release is cued to fire, however, this is not the only mechanism in which fruits may open. The physical weathering of fruits over time, drought stress, branch death, collapse due to the excessive weight of fruit on aged branches or plant death may all result in the spontaneous release of seed from plants in the absence of fire (Enright *et al.* 1996; Groom and Lamont 1996; Enright and Goldblum 1999). These opportunities for inter-fire recruitment are seen in stands of *H. victoria* that remain unburnt for longer than 24 years (or in some cases like Site 9) where the number of open fruit increases (Fig. 10a-g; Fig. 11).

Examination of the age structure of *Hakea victoria* stands over time shows a pattern of mixed-age plants (including smaller inter-fire recruits) that are particularly evident at 33 and over 101 years since fire, with evidence of seedlings progressing into the taller height (age) classes (Fig. 10a-g), indicating that mixed-age stands of *H. victoria* can develop and populations may on occasion be able to maintain themselves in the absence of fire. However, the proportion of the stand consisting of *H. victoria* plants younger than the original cohort (inter-fire recruits 0-0.99 m in height) is minimal, with percentages of 0.15%, 1.3% and 4.68% for stands aged 24, 33 and over 101 years, respectively. This recruitment of seedlings with time is also offset by increasing plant mortality over time (Fig. 12). The low quantity of young seedlings (plants 0-0.99 m) found in the upper ages (33 to over 101) of *H. victoria* stands may be explained by the extremely low probability of seedling survival due to environmental factors (i.e., seed released at different times of the year, low water availability, seed predation) and competition with parent plants and surrounding established vegetation (Enright *et al.* 1996).

The presence of many younger *H. victoria* plants at Site 9 may be explained by the fact that commonly in arid and semi-arid systems, plants are found to be more abundant beneath the canopy of other shrubs, or in this case older *H. victoria* plants, due to the favourable establishment conditions (i.e., accumulation of organic matter, reduced water stress from lower temperatures, higher nutrient availability and soil water retention) (Holland and Steyn 1975; Facelli and Temby 2002). This, however, is unlikely to be the case at sites that have lower surrounding vegetation density, soil water content and low nutrients.

#### *Optimum fire interval*

To determine the optimum fire interval to support the return of an obligate seeder species, the dynamics of seed production, storage, viability and loss need to be determined (Enright *et al.* 1996). If fire occurs prior to reproductive maturity or before a sufficient seed bank is accumulated, then a population may be at risk of extinction (Enright *et al.* 1996). For *H. victoria* short fire intervals greatly increase the risk of extinction given that fruit production begins at five years of age and even then, additional years are required to build a suitable sized seed bank, and the rate of seed accumulation is relatively slow when plants are young because of their simple structure and few reproductive apices.

Estimates of appropriate fire intervals are typically based on age to reproductive maturity and seed production over time (Kraaji *et al.* 2013). According to Gill and Nicholls (1989), Bell (2001), and Kraaji *et al.* (2013), fire intervals should equate to at least double the primary

juvenile period of a species to allow for adequate seed production prior to the next fire. Furthermore, Enright *et al.* (1998) state the optimum fire interval for *Banksia hookeriana* (a non-resprouter of the Proteaceae family) was estimated at 15-18 years even though the species began flowering at 3-4 years of age (Kraaji *et al.* 2013), while Gill (1981) estimates that the mean natural fire interval for Mediterranean shrublands in eastern Australia is 5-15 years.

By the time *H. victoria* plants reached 33 years of age the impacts of granivory, spontaneous seed release and plant death resulted in little additional accumulation of viable seed (Fig. 14d; Fig. 11, Fig 12 and Fig, 16, respectively). This suggests that over 33 years of age is too long a gap between regular fire intervals for populations of *H. victoria*. Having infrequent fires may result in the complete loss of the seed bank due to plant death before the next fire. While seed released from desiccating fruits of dead plants may contribute to new recruits, the probability of establishment appears low. And for those recruits that do establish in the inter-fire period they may not have time to develop a suitably sized seed bank or even reach reproductive maturity before fire (Enright *et al.* 1998).

#### *Aging method*

The intended use of Lamont's (1985) ageing method was to give an informed estimate of plant age rather than definitive and although there was some variability in the method, we found it to be fairly accurate. Therefore, there is cause to use this method for determining age of patches of *H. victoria* that are of an unknown age up until they reach approximately 30 years, after which height appears to plateau and plants begin to prioritise branching outwards. Despite the moderate success of the method (Wills 2003; Jenkins *et al.* 2005), there are limitations, such as some plants do not produce a new annual growth increment during a single year and the loss of nodes towards the base of the trunk where they become indistinct and difficult to count over time. Both limitations can cause an underestimation of plant age (Jenkins *et al.* 2005).

#### **Conclusion**

Although currently 'not threatened' the endemic nature and lack of published knowledge of *Hakea victoria* puts the species at risk of extinction. The application of short fire intervals put *H. victoria* at risk by not allowing the development of a sufficient seed bank, while long fire intervals may also act disadvantageously for the species, particularly for small stands. Impacts of fire intervals (wildfire or previous prescribed burning) should be considered prior to undertaking any prescribed burning in areas where *H. victoria* is present. This research has determined that the optimum fire interval for *H. victoria*

is between 20 and 26 years when seed bank size is at its maximum viability. Future research opportunities may include study of the implications of increased or decreased rainfall on fruit and seed production and time to reproductive maturity.

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