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Environmental influences on growth and reproductive maturation of a keystone forest tree: Implications for obligate seeder susceptibility to frequent fire

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ABSTRACT

Anthropogenic modifications to climate and natural fire regimes are occurring globally, leading to the production of environments that may be unsuitable for some species. Fire-intolerant plant species that rely on specific fire regimes for reproduction are at risk of population decline when successive fires occur in less than the time taken to produce seed. Quantifying key fire-related life history traits in such species is therefore critical for developing models of population viability, species distributions and ecosystem persistence.

We studied the Australian mountain ash (*Eucalyptus regnans*), the world's tallest angiosperm and an ecologically and economically important keystone species. We tested whether mountain ash populations exhibit variation in susceptibility to increasing fire frequency by characterising the response of key vital rates to stand age (time since fire) under different environmental conditions.

We found that the time taken to produce seed varied geographically. Mean growth rates were greater in areas receiving higher levels of solar radiation, a trend that became stronger with tree age. Tree size and age had the strongest influence on the production of fruit capsules. Mature fruit capsules were found in trees as young as 11 years old, but stands may not contain reproductively viable seed crops until they are more than 21 years old.

Our results show that environmental factors influence the primary juvenile period of a keystone obligate seeder, in turn affecting the time taken for a population to develop a reproductively viable seed amount of seed. Reduced fire return intervals may therefore constrain the species' realised niche (and geographic distribution) to areas where it can tolerate shorter fire return intervals due to faster growth and maturation. We suggest that populations of obligate seeders that reach reproductive viability faster are thus more likely to persist when exposed to multiple fires in short succession. Intra-stand variation in seed crops suggests that selection could also act on rapidly-maturing individuals, resulting in some populations exhibiting high levels of precocious reproductive activity.

1. Introduction

Fire influences vegetation communities in multifarious ways, driving ecosystem structure (Bond and Keeley, 2005) and the evolution of plant traits (Dantas et al., 2013; Keeley et al., 2011; Pausas et al., 2006, 2004). However, anthropogenic modifications to natural fire regimes are occurring in ecosystems worldwide (Abatzoglou and Williams, 2016; Pausas and Keeley, 2014a), with important consequences for species that have strong successional preferences or traits adapted to specific fire regimes (Bowman et al., 2014; Morrison et al., 1995). Altered fire regimes can therefore lead to geographic shifts in environmental suitability for species. This can influence population viability and therefore the distribution of individual species. However, in the case of ecologically important 'foundation' or keystone species (*sensu* Tewksbury and Lloyd, 2001, Lindenmayer and Laurance, 2016) such as dominant overstorey forest trees, there are potential major implications for many other dependent species. If we are to predict the responses of plant species to changing fire regimes, we need to quantify the key life history traits that are likely to determine plant sensitivity to changing fire regimes (Enright et al., 2015).

One functional group of plants that may be impacted by modified fire regimes is the obligate seeders (Bradstock, 2008; Keith, 1996). Such species do not produce vegetative regrowth from lignotubers or epicormic buds, and thus regenerate only from seed, with adults usually being killed by crown fire (Pausas and Keeley, 2014b). For many plants, one of the key life history traits for maximising fitness is the age of

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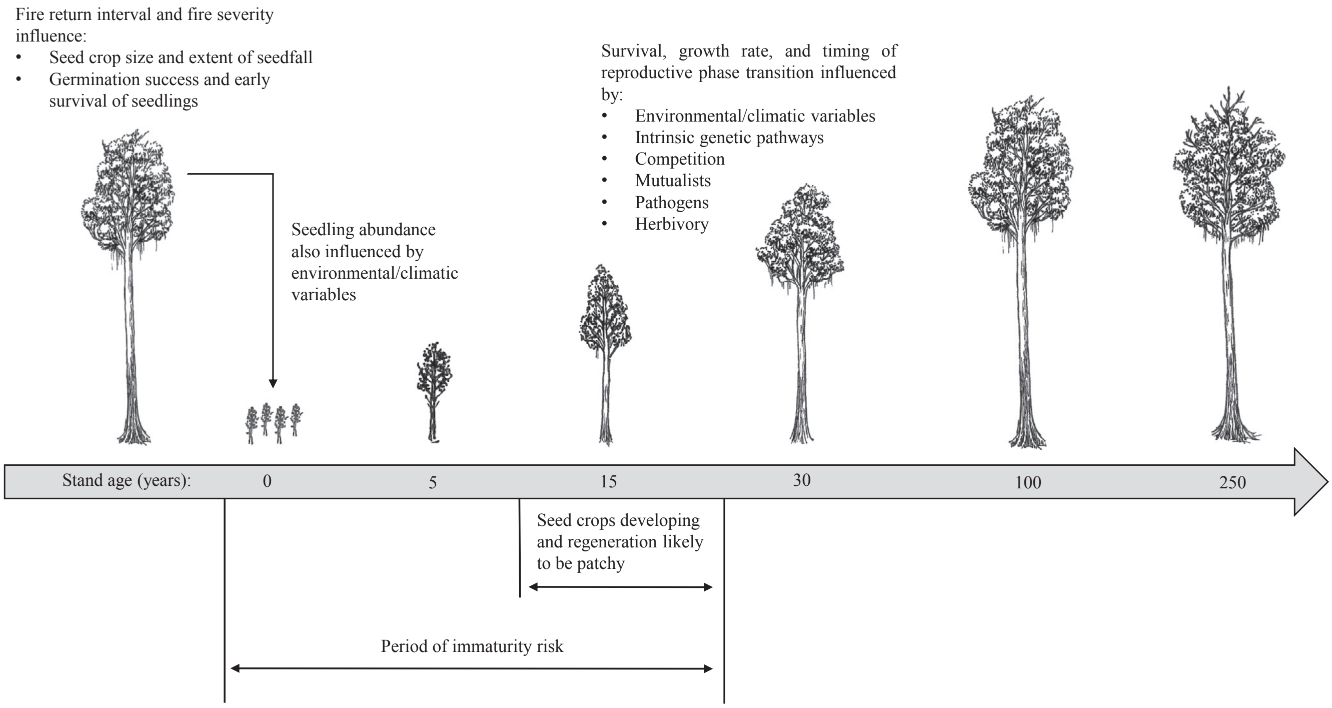

Fig. 1. Conceptual model of the lifecycle of an obligate seeder, showing some of the factors that influence vital rates. While some obligate seeders have soil-stored seed banks, others, such as the *Eucalyptus regnans* depicted here, rely solely on canopy-stored seed for reproduction. Clarification of factors influencing the length of the primary juvenile period is critical for understanding the influence of changing disturbance regimes on population viability.

reproductive activity (Amasino, 2010; Huijser and Schmid, 2011), with seed production a key component of regeneration and community assembly (Larson and Funk, 2016). But for obligate seeders, the timing of the transition (phase change) to a reproductive state is particularly relevant, as these species may be susceptible to population declines and extinctions if they depend on a particular fire regime for regeneration (Stephens et al., 2013). In some cases, increasing fire frequencies threaten population persistence, with the age of reproductive maturity placing a critical lower threshold on the interval between fires that can be tolerated by a species (Bassett et al., 2015; Bowman et al., 2014; Keeley et al., 1999; Lindenmayer et al., 2011; Syphard et al., 2006).

In the context of global changes to disturbance regimes and climate, it is critical that we are able to link plant vital rates such as growth and reproduction to environmental variables (Ehrlén et al., 2016; Enright et al., 2015), particularly for predicting how the distribution and viability of a population is likely to change. For obligate seeders, clarification of parameters relating to the age of reproductive maturity is an essential part of this process (de Gouvenain and Ansary, 2006). In particular, two parameters are critical for predicting species responses to shifting fire regimes:

- The *primary juvenile period* of an individual, defined here as the age at which the plant has first produced viable seed, ready for dissemination. This is the best definition in the context of obligate seeders, as some species do not produce flowers (thus negating references to flowering) (Trauernicht et al., 2012), and flowering species may not produce viable seed for some years after the initiation of inflorescence buds (Ashton, 1975).
- *Stand-level reproductive viability*, which we define as a state in which a population is capable of producing an equivalent population of offspring plants, without human intervention. This state is determined by a combination of factors. For example, the amount and distribution of seed available for regeneration is likely to be a critical aspect for many obligate seeders (Bassett, 2011). For serotinous species (which release seed in response to an environmental trigger), and species that rely on ash-beds or gaps in vegetation for successful regeneration, the timing and intensity of a fire event is likely to influence germination and survival (Ooi et al., 2006). For species with canopy-stored seedbanks, stand characteristics (e.g. canopy height) may also influence how much seed is available for dissemination after fire (Taylor et al., 2014).

To accurately quantify the two above parameters involves understanding the degree to which they are influenced by environmental variation (Ehrlén et al., 2016). This is because, while the primary juvenile period and time to stand-level reproductive viability define thresholds for tolerance of fire return intervals, environmentally-driven variation in these parameters may drive niche shifts in obligate seeders under increasing fire frequency, whereby some populations have increased tolerance for short fire return intervals under particular ecological conditions (Scheele et al., 2017; Swab et al., 2012).

In this study, we investigate the influence of environmental variables on individual and stand-level maturation patterns in the world's tallest flowering plant, the obligate seeder mountain ash *(Eucalyptus regnans)*. These forests are a good system to develop an understanding of the ways in which modified fire regimes can influence life history traits such as reproductive maturation, as research from the past 60 years has led to a good understanding of the ecology of the ecosystem (Ashton, 1956; Cremer, 1975; Lindenmayer, 2009a; Lindenmayer et al., 1996, 1991; Loyn, 1985; McCarthy et al., 1999; Smith et al., 2016).

In mountain ash forests, intervals between high-intensity stand-replacing fire events may be reduced from historical levels of 75–150 years (McCarthy et al., 1999) to less than the time to reproductive viability of a stand. As all seed is stored in the canopy of mature mountain ash trees, the occurrence of tree-killing fires before the production of viable canopy seedbanks could cause the widespread collapse of mountain ash forest ecosystems (Fig. 1) (Bowman et al., 2014; Gilbert, 1959; Lindenmayer, 2009b). Indeed, we have already begun to see large areas of forest dominated by obligate seeding species require artificial reseeding to maintain ecosystem persistence (Bassett et al., 2015; Fagg et al., 2013).