Forest Ecology and Management 432 (2019) 54–63

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

The influence of seed supply and seedbed on seedling recruitment in shelterwood-treated jarrah (*Eucalyptus marginata*) forest

Jeffry Cargill, Eddie J.B. van Etten*, William D. Stock

Centre for Ecosystem Management, School of Science, Edith Cowan University, 270 Joondalup Drive, Joondalup, WA 6027, Australia

ARTICLE INFO

Keywords:
Seedling recruitment
Forest regeneration
Seedbed
Shelterwood
Sustainable forest management
Jarrah forest
Eucalyptus marginata

ABSTRACT

Successful and adequate recruitment of seedlings is an essential ecological process in forest ecosystem dynamics and is a key principle underpinning sustainable timber harvesting. This is particularly so with the shelterwood silvicultural system used in the jarrah (*Eucalyptus marginata*) forest of south-west Australia where partial cuts of overstorey are made followed by prescribed burning to stimulate seed fall and seedling establishment. There have been concerns over the lack of seedling recruitment in some shelterwood-treated areas of the jarrah forest, and hence this study was implemented to explore the roles of seed supply and seedbed conditions in limiting recruitment of jarrah seedlings. Low seedling densities were recorded across all six burnt study sites and were strongly correlated (at both broad and fine scales) with both canopy seed store and seed fall. Ample levels of post-burn seed fall only resulted in low seedling numbers suggesting that adequate seed supply did not coincide with seedbed conditions suitable for mass seedling regeneration. Conditions favourable for seedling recruitment were highly variable within sites, since both seed supply and seedbed conditions were spatially heterogeneous. Fine-scale areas burnt to mineral soil showed an additive influence to the overwhelmingly dominant factor of seed supply on seedling recruitment. However, the capacity of low intensity burns to produce these seedbed conditions at a broad scale appears to be limited. Results suggest that successful stocking of shelterwood-treated jarrah forest is not always feasible following a single silvicultural event, such as post-harvest burning under mild conditions. The chances of ample seed supply coinciding with broad-scale seedbed conditions favourable for mass germination, emergence and establishment appear to be low. Successful stocking of shelterwood-treated jarrah forest is more likely to be a longer term outcome achieved through episodic recruitment, especially when favourable environmental conditions coincide with optimal seedbed conditions. Such episodic recruitment strategies may be common in resource-limited systems such as jarrah forest and other dry eucalypt forest systems, where conditions controlling the regeneration niche are often variable and unpredictable.

1. Introduction

Ensuring adequate recruitment of dominant canopy tree species is a key requirement for the long-term management of forests, particularly those in which sustainable timber production is a primary objective (Florence, 2004; Bailey et al., 2012; Rivett et al., 2016). Obtaining adequate regeneration following timber harvesting is generally an essential pre-requisite for sustainable forestry, however, despite this, there are many reports of regeneration failure following logging reflecting many known or putative causes, including unfavourable post-harvest site conditions (e.g. persistent allelopathic effects, exposure, competition from remaining or other regenerating species), herbivory, lack of seed availability (due to lack of seed supply, high predation, or loss of viability) or inadequate seed germination (Timoney and Peterson, 1996; Dignan et al., 1998; Legras et al., 2010; Badano et al., 2015; Bradshaw and Waller, 2016; de Carvalho et al., 2017; Rhodes et al., 2017). Furthermore, global environmental change (e.g. drier and/or warmer climate, nitrogen deposition, invasive species, loss of biodiversity) is likely increase regeneration failure in many forests (Farwig and Berens, 2012; BassiriRad et al., 2015; Enright et al., 2015; Johnstone et al., 2016).

Within eucalypt forests, recruitment limitation of canopy *Eucalyptus* species has been attributed to a variety of factors that make up the regeneration niche (Eriksson and Ehrlen, 1992; Bailey et al., 2012) including: inadequate seed supply (Yates et al., 1996; Semple et al., 2007; Vesk et al., 2010); predation of seeds and seedlings (Ashton, 1979; Stoneman and Dell, 1994), pronounced seed dormancy (Battaglia, 1996); low seed viability (Orscheg et al., 2011); soil

* Corresponding author.
E-mail address: e.van_etten@ecu.edu.au (E.J.B. van Etten).

https://doi.org/10.1016/j.foreco.2018.09.008
Received 9 April 2018; Received in revised form 31 August 2018; Accepted 6 September 2018

pathogens (Florence, 2004); seedbed conditions (Gill, 1997; Bailey et al., 2012); availability of structures which trap seeds (Wilson and Gibbons, 2014), microclimatic factors (Battaglia and Reid, 1993); and availability of and competition for resources, including water and light (Facelli et al., 1999). Microsites favourable for seed germination and/or seedling emergence may not necessarily be favourable for seedling establishment. This is because the survival and growth of seedlings requires additional resources (e.g. light, nutrients, adequate moisture) which promote photosynthesis and carbohydrate reserve allocation to roots and lignotubers (Lamont et al., 1993; Walters and Bell, 2005). As such, factors affecting germination and seedling establishment may differ, and these factors will change over time with the extent of litter accumulation, shading, drought, grazing, fire, insect and fungal attack, frost, and soil disturbance being potentially different for each stage of regeneration (Facelli et al., 1999; Li et al., 2003).

Of the factors influencing regeneration, ensuring a sufficient supply of seeds and the establishment of suitable seedbed conditions have been widely identified as the two key requirements for the successful recruitment of target canopy species, particularly in the context of sustainable silvicultural practices (O'Dowd and Gill, 1984; Neyland et al., 2009; Legras et al., 2010; Vesk et al., 2010; McCaw, 2011; Pierce and Taylor, 2011; Puhlick et al., 2012; Fairman et al., 2016). Managers are able to manipulate both factors through the use of prescribed burning to facilitate both mass seed fall and the creation of suitable post-fire seedbed conditions for seedling emergence and establishment. A number of studies have shown that seed fall rates increase significantly after fire, particularly in *Eucalyptus*-dominated forests and other forests with dominant serotinous species (Loneragan, 1979; O'Dowd and Gill, 1984; Hancock et al., 2009; Pierce and Taylor, 2011). Releasing canopy seed crops through prescribed burning increases the amount of seed falling to the forest floor and thus increases the chance of an individual seed finding a suitable microsite for both germination and subsequent establishment.

The production of favourable post-fire seedbed conditions, particularly ash beds, has been shown to have a positive effect on *Eucalyptus* seedling emergence and growth, with seedling establishment rare in undisturbed seedbeds (Yates et al., 1996; Bailey et al., 2012). This positive effect could arise from a number of environmental modifications, including increased nutrient and moisture availability, more growing space and light, and soil sterilisation (Neary et al., 1999; Adams et al., 2003; Butler et al., 2017). Positive influences of ash beds in promoting favourable conditions for seedling emergence and/or growth has been shown across a number of *Eucalyptus* species including: *E. regnans* (Chambers and Attiwill, 1994; van der Meer et al., 1999; Turner et al., 2009); *E. obliqua* (Neyland et al., 2009; Turner et al., 2009); *E. wandoo* (Burrows et al., 1990); *E. salmonophloia* (Yates et al., 1996); *E. delegatensis* (Bowman and Kirkpatrick, 1986); *E. marginata* (Abbott et al., 1989); *E. gomphocephala* (Ruthrof et al., 2013); and *E. diversicolor* (Loneragan, 1979). Although many positive effects of post-fire seedbeds have been identified, Reyes and Casal (1998) found that when studied under laboratory conditions, ash showed no positive effect on the germination of *Pinus pinaster*, *P. radiata* or *Eucalyptus globulus*. Since the biophysical and chemical conditions of the forest floor are highly variable (Battaglia and Reid, 1993), there is fine-scale variability in fire behaviour, which can lead to the production of heterogeneous seedbeds (Neyland, 2004). The production of heterogeneous seedbed conditions at a fine scale provides a greater diversity of microsite conditions and thus regeneration niches.

The jarrah (*Eucalyptus marginata* Sm.) forest covers some 2.1 million ha of south-west Western Australia and is currently managed for multiple values including, but not limited to, water production, mineral extraction, conservation of biodiversity, soil and water quality, recreation and timber production (CCWA, 2013). The capacity of jarrah to regenerate following fire, the persistent nature of the species (particularly its lignotuberous habit and epicormic resprouting) and durability of its timber has led to widespread timber harvesting throughout the jarrah forest from the late 1800s to the present (Bradshaw, 1999; McCaw et al., 2011). A range of silvicultural methods have been applied in jarrah forest: thinning to promote growth of retained trees; gap release to allow development of ground coppice into mature trees; and shelterwood to promote seedlings under retained trees (Abbott and Williams, 2011; McCaw et al., 2011; CCWA, 2013).

Effective long-term realisation of these silvicultural goals for this forest relies on an understanding of factors that have the potential to limit successful outcomes. One such area requiring further work is identifying the key limiting factors for the successful recruitment of *E. marginata* seedlings in shelterwood-treated jarrah forest (Whitford et al., 2004; McCaw, 2011). The shelterwood system is used in the jarrah forest at sites which lack sufficient advance growth (which mostly comprises jarrah ground coppice, but also jarrah seedlings and saplings with well-developed lignotubers) to establish seedlings which are then encouraged to develop into advance growth to be released by gap creation at a later stage. Shelterwood is achieved by cutting to reduce tree cover and basal area, followed by burning to stimulate seed fall from retained trees and promote conditions for seedling recruitment (Abbott and Williams, 2011). Therefore initial seedling recruitment is an essential requirement for the success of shelterwood in the jarrah forest.

Despite the widespread and progressive implementation of the shelterwood method (applied to over 40% of total harvested area), its application in jarrah forest has had varied success (Whitford et al., 2004). For example, monitoring by the government agency responsible for forest management showed that over half the shelterwood-treated jarrah forest sites sampled did not meet specified standards for regeneration stocking, ten years after treatment (Abbott and Williams, 2011). The reasons for this variability have not been clearly identified (Whitford et al., 2004; McCaw, 2011).

Viability of *Eucalyptus* seed is not considered to be a significant limiting factor for recruitment, although high within-species variability in seed viability has been observed (Boland et al., 1980; Florence, 2004). In jarrah, seed viability is generally very high (over ninety per cent) and is not reduced by ground exposure (Abbott and Loneragan, 1986). Despite this, germination rates can vary considerably, ranging from twenty per cent to over eighty per cent, with the germination of large seeds shown to be higher than that of small seeds (Abbott and Loneragan, 1986; Bell, 1994). Conditions that influence field germination rates of *Eucalyptus* seeds include soil water potential, atmospheric humidity, soil temperature, soil surface characteristics, shading, pathogens and allelopathy (Battaglia and Reid, 1993; Stoneman, 1992; Tozer and Bradstock, 1997; Facelli et al., 1999; van der Meer et al., 1999; Li et al., 2003; Orscheg et al.. 2011; Bailey et al., 2012). Seed germination and emergence of jarrah under field conditions in south-west Western Australia is restricted to the winter season, where optimum moisture and temperature conditions (15–18 °C) exist in this Mediterranean-type climate region (Stoneman, 1992; Bell, 1994).

Mortality of eucalypt seedlings and factors affecting mortality are closely related to seasonal climatic conditions (van der Meer et al., 1999), with most *Eucalyptus* seedlings dying prior to, or during, the first summer (Stoneman, 1992; Fernandes et al., 2017). In addition, fine-scale (microsite) conditions can also affect seedling mortality, with losses occurring through high insolation, soil drying, frost, pathogenic fungi, and competition for light and soil moisture (Battaglia and Reid, 1993; Stoneman et al., 1994; Facelli et al., 1999; Bailey et al., 2012; Wilson and Gibbons, 2014). Survival beyond the first year is improved markedly when individual seedlings develop lignotubers, which occur in all but a few species of eucalypt (Florence, 2004). Abbott et al. (1989) reported that lignotubers of jarrah seedlings developed more quickly in the presence of ash beds. Once formed, seedlings can readily resprout from lignotubers following fire, grazing or other disturbance.

Detailed *ex situ* studies of factors influencing the germination of jarrah seeds and the growth and mortality of jarrah seedlings have been well documented and as such are not covered in the current study