Forest Ecology and Management 402 (2017) 63–75

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Fire recurrence and emergency post-fire management influence seedling recruitment and growth by altering plant interactions in fire-prone ecosystems

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ARTICLE INFO

Article history:
Received 15 May 2017
Received in revised form 23 June 2017
Accepted 18 July 2017

Keywords:
Competition
Facilitation
Large fires
Natural regeneration
Pinus pinaster
Post-fire restoration

ABSTRACT

Projections of future wildfire regimes forecast an increased frequency of large high-severity fires that create very harsh environmental conditions and constitute a challenge to post-fire ecosystem regeneration. Under these new circumstances, better knowledge of the plant interaction mechanisms underlying post-fire seedling establishment success would aid restoration management to achieve the intended targets. We evaluated the combined effect of recurrent large stand-replacing fires and conventional post-fire restoration activities (salvage logging after a single large fire, and direct seeding and linear subsoiling plus seedling planting after two subsequent large fires) on tree seedling recruitment and performance (development, annual growth, and biomass) in the early stages of succession in fire-prone maritime pine (*Pinus pinaster* Ait.) ecosystems. We quantified plant facilitative/competitive interactions between naturally recruited pine seedlings, neighbouring seedlings and potential nurse shrubs with different post-fire regeneration strategies (obligate seeders *vs* resprouters), by computing the relative interaction index (RII). The results evidenced that fire recurrence altered plant species composition and conditioned initial pine seedling recruitment and establishment, prevailing over the expected negative impact of salvage logging and positive impact of seeding. Seedling recruitment was sufficient to ensure natural tree regeneration after a single fire event and undermined by repeated fires. Both delaying burned timber removal during salvage logging operations and retaining immature dead trees without commercial value onsite in subsoiled stands enhanced seedling recruitment via facilitative interactions. Higher seedling growth and height under shrubs than in open ground resulted in lower aerial and root biomass, indicating elongation in response to shade, and net competition for resources. Inter-specific competition between naturally regenerated seedlings and shrubs was aggravated by intra-specific competition with neighbouring seedlings and by mechanical site preparation in subsoiled stands. All in all, post-burn increased soil fertility most likely counterbalanced the environmental stress created by fire, shifting the net outcome of plant interactions from positive (facilitation) to negative (competition). We recommend alternative post-fire management actions that decrease plant competition and take advantage of facilitation by residual burned wood, to ultimately accelerate ecosystem recovery after large stand-replacing fires.

1. Introduction

Positive interactions (i.e., facilitation) between neighbouring plants are common in harsh physical environments, such as arid/semi-arid areas, playing a key role in species distribution and in community dynamics and composition (e.g., Callaway et al., 2002; Maestre et al., 2003; Tewksbury and Lloyd, 2001; but see Maestre and Cortina, 2004; Maestre et al., 2005). Benefactor plants improve recruitment and performance of beneficiary ones, through numerous processes like nutrient accumulation, microclimate amelioration, and herbivory protection (Gómez-Aparicio et al., 2005, 2008; Maestre et al., 2003). Facilitation generally prevails under high abiotic stress or disturbance (Bertness and Callaway, 1994); but the net outcome of facilitative/competitive interactions acting simultaneously is the result of multiple factors (reviewed by Maestre et al., 2009), including the identity and life-strategies of the interacting species (Gavinet et al., 2016; Gómez-Aparicio,

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http://dx.doi.org/10.1016/j.foreco.2017.07.029
0378-1127/

2009; Gómez-Aparicio et al., 2008; Prévosto et al., 2012; Schöb et al., 2013) and the nature and degree of the environmental stress (Maestre et al., 2003; Pugnaire and Luque, 2001).

In extremely degraded and highly disturbed environments like fire-prone ecosystems, plant facilitation mechanisms can act as the essential basis of restoration techniques to accelerate vegetation recovery and achieve the intended targets (Brooker et al., 2008; Gómez-Aparicio, 2009; Padilla and Pugnaire, 2006). To date, much research (mostly experimental studies) has demonstrated the facilitative effects of naturally-occurring nurse plants (shrubs, in particular; Gómez-Aparicio, 2009; Gómez-Aparicio et al., 2005; Siles et al., 2008, 2010) and inanimate objects (e.g., dead logs and branches; Beghin et al., 2010; Castro et al., 2011; Marañón-Jiménez et al., 2013) in ecosystem regeneration after a single fire event (see reviews by Brooker et al., 2008; Padilla and Pugnaire, 2006). Yet, conventional post-fire management operations like salvage logging (i.e., the removal of burned trees and remaining woody debris) and mechanical site preparation with heavy machinery prior to seeding or planting of seedlings are widely implemented by forest administrations (see e.g., Beghin et al., 2010; Castro et al., 2011; Espelta et al., 2003; Leverkus et al., 2012), overlooking the advantages of alternative facilitation-based restoration practices.

Predictions of future fire regimes forecast an increase in the recurrence and severity of wildfires under a warmer and drier climate (Doblas-Miranda et al., 2014; Moreira et al., 2011; Pausas and Vallejo, 1999; Pausas et al., 2008), specifically in areas with high productivity (Pausas and Paula, 2012), together with an increase in the number of large fires that burn thousands of hectares (Moreira et al., 2011; see also Pausas and Fernández-Muñoz, 2012) and have more adverse ecological effects (Moreira et al., 2011; Pausas et al., 2008; and references therein). Ecosystem restoration after such large stand-replacing fires constitutes a new challenge for forest managers, as these fires (1) create very severe environmental conditions (e.g., high soil erosion and solar radiation), (2) entail the extensive destruction of the vegetation and, therefore, the loss of potential nurse plants, and (3) often cause major shifts in plant dominance and community structure and composition (Pausas et al., 2008; Puerta-Piñero et al., 2012; Rodrigo et al., 2004; Torres et al., 2016). Frequent large high-severity fires further result in limited or failed natural tree regeneration (Pausas et al., 2008; Tapias et al., 2001) and in the medium-term massive proliferation of pioneer shrubs (Baeza et al., 2007; Retana et al., 2002) generating homogeneous landscapes with high fuel load accumulation (Loepfe et al., 2010; Moreira et al., 2011; Pausas and Fernández-Muñoz, 2012). Whether these new circumstances created by recurrent large fires alter plant facilitation mechanisms and condition the application of alternative restoration practices is presently poorly understood.

In this study, we evaluated the joint effects of recurrent large stand-replacing fires and post-fire restoration activities on tree seedling recruitment and performance (development, annual growth, and biomass), mediated by changes in the regeneration strategies of potential nurse plants after fire: (1) obligate seeder shrubs with fire-stimulated recruitment, slow post-fire recovery and low competitive abilities (Pausas and Vallejo, 1999), and (2) resprouter shrubs highly-tolerant to short between-fire intervals, capable of fast post-fire regeneration and with high competitive abilities (Calvo et al., 2012; Keeley, 1986; Pausas and Vallejo, 1999; Valdecantos et al., 2008). We intended to determine the efficiency of conventional restoration operations applied by forest managers immediately following fire (i.e., salvage logging after a single large fire, and direct seeding and linear subsoiling plus seedling planting after two subsequent large fires) in helping the natural regeneration of fire-prone ecosystems at early stages of succession (i.e., active restoration; Moreira et al., 2012; see e.g., Ammer and Mosandl, 2007; Beghin et al., 2010; Moreira et al., 2009). We selected maritime pine (*Pinus pinaster* Ait.) forests threatened by increasing wildfire frequency (Fernandes and Rigolot, 2007), like other Mediterranean serotinous pine forests (Espelta et al., 2008; Eugenio et al., 2006), as the model ecosystem. *P. pinaster* is a fire-dependent obligate seeder species that relies mostly on the aerial seed bank for post-fire recovery (Calvo et al., 2013; Fernandes and Rigolot, 2007). Solar radiation is an important environmental factor determining maritime pine seed germination, seedling survival, and early seedling development (Fernandes et al., 2017; Rodríguez et al., 2008; Rodríguez-García and Bravo, 2013; Rodríguez-García et al., 2011; Ruano et al., 2009).

We expected that (i) under the stressful conditions after a single large stand-replacing fire the regrowth of potential nurse plants (obligate seeder shrubs in particular) will protect pine seedlings against the harsh environment, resulting in net facilitation and improved seedling performance (Castro et al., 2004; Fernandes et al., 2017; Rodríguez-García et al., 2011; Ruano et al., 2009); (ii) post-fire salvage logging after a large fire will eliminate potential nurse objects (burned tree trunks, branches, logs, and snags), increase soil compaction, and damage the soil seed bank, delaying facilitative interactions (basically, between obligate seeder shrubs and pine seedlings), and lessening seedling performance (Castro et al., 2011; Marañón-Jiménez et al., 2013); (iii) the occurrence of two subsequent large high-severity fires will favour highly-adapted resprouter shrubs over obligate seeder shrubs (Calvo et al., 2012; Keeley, 1986; Pausas and Vallejo, 1999), shifting plant-plant interactions from facilitative to competitive ones, and reducing seedling performance (Gavinet et al., 2016); (iv) mechanical site preparation prior to planting of seedlings after recurrent fires will decrease soil resistance, improve water and air transport, and promote the development of a deep root system of the planted trees, reducing competition and enhancing seedling performance (Espelta et al., 2003; but see Löf et al., 2012).

2. Materials and methods

2.1. Study site and population

The study site is located in Sierra del Teleno (NW Spain; 42°15′34″N/06°12′13″W; 915–1200 m a.s.l.; 10% average slope), a mountain range where wildfires have frequently occurred [172 small (<500 ha) and 5 large (>500 ha) fires recorded in 1974–2007 that burned 14,243 ha], typically caused by dry spring-summer storms (Santamaría, 2015). From 1978 to 2014, the number of fires that occurred in the study site ranged from 1 to 4 (four fire recurrences identified from visual interpretation of 75 Landsat images and validation with official fire reports; Fernández-García et al., 2015). The climate is Mediterranean with mean annual precipitation between 650 and 900 mm, mean annual temperature of 10 °C, and 2–3 months of summer drought. Soils are Cambisols, very sandy and acidic (pH = 4.66 ± 0.25) with low organic matter content (Calvo et al., 2008). The landscape is dominated by pine forests (73% *P. pinaster*, 3% *P. nigra* Arn., 2% *P. sylvestris* L.), deciduous forests (7% *Quercus ilex* L., 5% *Q. pyrenaica* Willd.), and shrublands (10%, mainly *Erica australis* L. and *Pterospartum tridentatum* (L.) Willk., with *Halimium lasianthum* spp. *alyssoides* (Lam.) Greuter, and *Calluna vulgaris* (L.) Hull).

The study site encompasses (Fig. 1):

(1) 8221 ha affected by a single fire event: a large high-severity man-induced wildfire that burned 11,891 ha (72% covered by *P. pinaster* natural forests for timber production with a mean tree density of 906 individuals ha^{-1} and a mean basal trunk diameter of 22.31 cm, and with a shrubby understorey dominated by the resprouter shrubs *E. australis* and *P. tridentatum*) in 19–21 August 2012. The understorey was