Forest Ecology and Management 429 (2018) 300–307

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Relative size to resprouters determines post-fire recruitment of non-serotinous pines

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ARTICLE INFO

Keywords:
Plant-plant interactions
Competition
Water limitation
Mixed Mediterranean forest
Pinus nigra
Quercus

ABSTRACT

The persistence of non-serotinous pines in Mediterranean forests can be threatened by climate-mediated changes in fire regimes that may favor the dominance of resprouters or other fire-adapted species. Recovery of non-serotinous pines after large wildfires is often determined by their ability to grow under the canopy of promptly established resprouters. Mechanisms of facilitation or competition between resprouters and pines will thus have a profound effect on forest dynamics. We examined here the effect of neighboring oak resprouts on *Pinus nigra* Arn. ssp. *salzmannii* saplings 18 years after a wildfire. We determined the net outcome of interactions between oaks and pines and how they vary with the life stage and size of the interacting plants or the environmental conditions. We did not find any net facilitative effects of oaks on pine sapling growth. The sensitivity of pines to neighbors varied markedly with pine size, and to a lesser extent, with water availability during the growing season. Our findings suggest a self-reinforcing hierarchical process by which early-dispersed seedlings growing in low-competitive microsites can grow faster, mitigating neighboring competition in the later stage of canopy closure. These results entail a potentially critical role of management practices to promote post-fire recovery of non-serotinous pines under expected changing conditions of disturbance regimes.

1. Introduction

Wildfires are considered the most important natural disturbance in Mediterranean forests, driving vegetation successional processes and structuring heterogeneous landscapes (Lloret et al., 2002; Pausas, 2015; Trabaud, 1994). Many tree species in Mediterranean ecosystems present adaptive traits that allow them to persist in areas burned with high intensity and take advantage of favorable early post-fire conditions (such as the reduced competition for resources) to develop and grow (Buhk et al., 2006; Paula et al., 2009; Sánchez-Pinillos et al., 2016). This is the case of many species that are able to resprout quickly from surviving parental tissues (persistence of individuals) or that present persistent seed banks (e.g. serotinous pines) (Pausas and Keeley, 2014). In contrast, some obligate seeder species lack efficient mechanisms to rapidly regenerate after fire (Buhk et al., 2006; Lloret, 1998; Retana et al., 2002). In such cases, post-fire regeneration is subject to the resistance of species to fire or to their ability to disperse from distant surviving seed sources (Christopoulou et al., 2014).

In mixed stands composed of resprouting species and non-serotinous seeders, the former usually recruit immediately or shortly after the fire, while seeders arrive later if the aforementioned favorable conditions are met. Thus, seeder persistence will ultimately depend on the species' ability to co-exist with or replace the first established species (Gracia et al., 2002; Ordónez et al., 2004; Ordóñez et al., 2006). Once seeder species arrive at a site where resprouter and/or serotinous species are already present, post-disturbance forest dynamics strongly depend on the interactions among individuals growing close to each other. Positive and negative interactions may occur simultaneously between two neighbor plants. The net outcome of unbalanced interactions determines mechanisms of facilitation or competition (Armas and Pugnaire, 2005; Holmgren et al., 1997), and may vary with the life stage and size of the interacting plants or the environmental conditions (Callaway and Lawrence, 1997). In harsh environments such as semi-arid or Mediterranean sites, positive effects often prevail in first stages of plant development (seedling survival and initial growth) (Castro and Zamora, 2004; Gómez-Aparicio et al., 2004; Padilla and Pugnaire, 2006). However, the large size reached by resprouters for being rapidly established after fire may work against the performance of late-

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https://doi.org/10.1016/j.foreco.2018.07.009
Received 2 May 2018; Received in revised form 28 June 2018; Accepted 2 July 2018

established seeders if asymmetric competition occurs. That is when large individuals compete for resources disproportionally with smaller neighbors (Weiner and Thomas, 1986). Furthermore, extremely severe conditions may exacerbate the competitive effects of resprouters (i.e. their ability to suppress the growth of their neighbors) when resources are limited (Maestre et al., 2009; Michalet et al., 2006). Therefore, depending on the sensitivity of seeders to competition (i.e. their competitive response), one could expect that certain species acting as nurse plants during the establishment process might turn into competitors and determine forest dynamics in advanced stages (Schupp, 1995; Sthultz et al., 2007) or during stress periods (Kitzberger et al., 2000; O'Brien et al., 2017).

Mixed pine-oak forests are common forest types in Mediterranean basin, usually conformed by a pine-dominated overstory, and an understory composed of oaks and other resprouting species. While most Mediterranean pines are considered fire-prone species that shortly colonize open areas after disturbances, Spanish black pine (*Pinus nigra* Arn. ssp. *salzmannii*) lacks serotinous cones and only forms transient soil seed banks that are unable to resist the harsh environmental conditions resulted from the wildfire. In contrast, coexisting oaks usually resprout vigorously and become the dominant species immediately after fire (Retana et al., 2002). Consequently, pine recruitment after fire, and therefore the maintenance of the pine-oak mixture, is conditioned to the presence in the landscape of unburned pine forest patches that act as seed sources (Christopoulou et al., 2014; Martín-Alcón et al., 2015) and to the ability of pines to establish and grow under the net interacting effects of the resprouting oaks.

Given the increased drought and heatwaves predicted for the coming decades and the associated increase in fire risk, the persistence of these mixed forests (and particularly of some pine populations) could be compromised (Retana et al., 2002; Rodrigo et al., 2004; Vilà-Cabrera et al., 2012), leading to monospecific communities with lower ability to respond to drought or multiple disturbances (Niinemets and Valladares, 2006; Sánchez-Pinillos et al., 2016). Therefore, understanding interspecific interactions between these two functional groups at different tree life stages is crucial to guide prompt management practices focused on fostering forest resilience.

In this study, we assess the factors affecting the performance of saplings (height between 0.5 and 2.5 m) of black pine (*P. nigra*) growing under oak resprouts 18 years after a wildfire occurred in Central Catalonia (Spain). The main goal of this study is to assess the effect of neighboring trees on pine sapling growth in order to get useful insights into the coexistence mechanisms of post-fire pine-oak communities. Specifically, we address the following questions: (i) What is the net effect (facilitative or competitive) of neighboring resprouting oaks on the growth of black pine saplings and how does this effect change with oak size and distance to target pines? (ii) Is the effect of neighboring oaks mediated by the size of pines? (iii) Is the effect of neighboring oaks mediated by water availability during the growing season?

We hypothesized that the net effect of neighboring oaks would be more negative for large than for small pines, which could be favored by the shadow of larger neighbors. We also expected that competitive effects would be particularly important in dry years under conditions of limited water availability.

2. Material and methods

2.1. Study area

The study was carried out in a central zone of Catalonia (Northeast Spain) (41°52′ N; 1°36′ E) affected by a large wildfire that burned 27,000 ha (two thirds of which woodlands) in 1998 (Fig. 1). The study area locates at low slope areas and altitudes ranging from 575 to 860 m a.s.l. The climate in this zone varies from dry-subhumid to subhumid Mediterranean (according to Thornthwaite index), with a mean annual precipitation of 589.9 mm and a mean annual temperature of 13.6 °C.

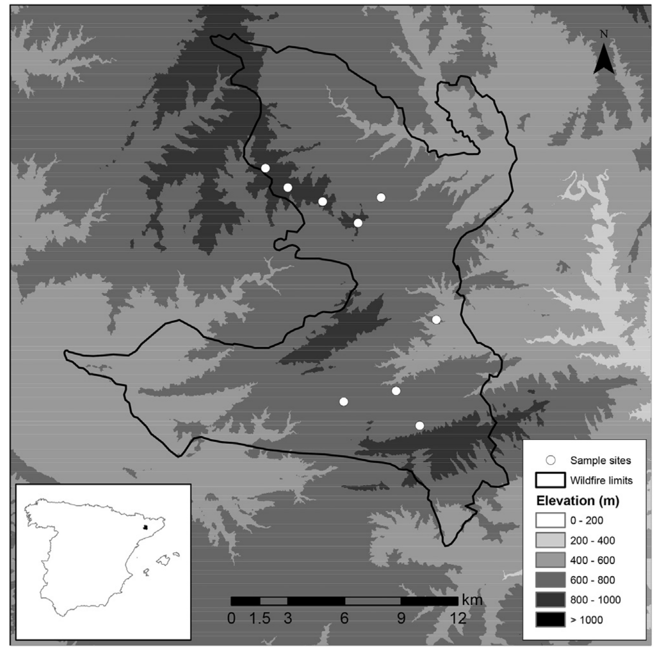

Fig. 1. Location of study sites within the perimeter of a fire occurred in central Catalonia (Northeast Spain).

Previous to the wildfire, this region was mainly occupied by Spanish black pine in pure natural stands or dominating the overstory of two-layered stands, with resprouting species (mostly deciduous sub-Mediterranean oaks) growing in the understory (Gracia et al., 2000). The wildfire triggered a wide resprout of hardwood species that are now dominant in most of the affected area, with some disperse individuals of black pine that regenerated from close unburned patches (Martín-Alcón et al., 2015; Puerta-Piñero et al., 2012). The most abundant hardwood species are *Quercus pubescens* Willd., *Quercus faginea* Lam., and the hybrid *Quercus subpyrenaica* E.H. del Villar (*Q. faginea* × *Q. pubescens*), whereas some individuals of holm oak (*Quercus ilex* L. ssp. *ballota*) can also be found. Common box (*Buxus sempervirens* L.), Kermes oak (*Quercus coccifera* L.), and blackberries (*Rubus* sp.) can be found in the understory of oak forests.

2.2. Field sampling

During spring 2016, we selected nine sites, separated between each other by at least 1.5 km to cover different environmental conditions within the 1998 wildfire perimeter (Fig. 1). Stands were selected for being currently dominated by resprouting tree species close to unburned patches of black pine (within 50–100 m), avoiding sites where salvage logging and tree plantings were carried out. We selected 183 target pine saplings with basal diameters ranging between 1 cm and 6 cm and total height between 0.70 and 2.40 m (Appendices Table A1). For each target pine, we considered as neighbors all trees growing closer than 3 m, and we also sampled neighbors between 3 and 4 m from the target whenever they presented a diameter at breast height (*DBH*) greater than 7.5 cm. For each tree (targets and neighbors), we measured its basal diameter (*BD*) and total height (H_t). We also measured the horizontal distance between trunk bases of each target pine and its neighboring trees (*dist*).

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.foreco.2018.07.009.

We measured primary and secondary growth of all targets for the last five years (2012–16). Primary growth (i.e. height growth) was obtained by measuring inter-shoot separations, whereas secondary growth (radial growth) was measured from basal disks after harvesting the target pines in autumn 2016. We defined radial growth of target