Forest Ecology and Management 408 (2018) 129–136

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Frequent fires control tree spatial pattern, mortality and regeneration in Argentine open woodlands

Martin Svátek*, Martin Rejžek, Jakub Kvasnica, Radomír Řepka, Radim Matula

Department of Forest Botany, Dendrology and Geobiocoenology, Faculty of Forestry and Wood Technology, Mendel University in Brno, Zemědělská 3, 613 00 Brno, Czech Republic

ARTICLE INFO

Keywords:
Fire
Caldenal
Tree spatial pattern
Prosopis caldenia
Sprouting

ABSTRACT

In open woodlands and savannas, fire is often the dominant disturbance that shapes and maintains their structure and dynamics. Numerous studies have explored tree-grass coexistence under different fire regimes in these ecosystems; however, there is a lack of research on the tree-tree relationship in the presence or absence of fire. In the present study, we explored the effects of fire regime on tree spatial pattern, mortality and regeneration in the Argentine Caldenal, which is one of the most endangered and least studied open woodlands in the Neotropics. While there was no significant difference in the overall tree density between frequently burned and fire-excluded regimes, we found clear divergences between fire regimes in the within-stand spacing of not only all trees, but also of large and small trees in addition to their spatial interactions. In contrast with previous results from other frequently burned open forests, trees in the Caldenal were randomly distributed in burned plots whereas both mid- and long-term fire exclusion lead to the strong short-scale aggregation of trees. In the absence of fire, both large and small trees were significantly clumped, but in the frequently burned woodlands, large and small trees had a tendency to repulsion and aggregation, respectively. Fire regime also significantly affected tree mortality and regeneration mechanisms in the Caldenal. Our mortality analysis indicated that fire suppression led to the shift from fire-induced to competition-driven mortality of trees. When analysing tree regeneration, we found a lack of seedlings in any of the fire regimes but the presence of vigorous sprouting only in frequently burned plots. The present study thus revealed the key role of frequent fires in the Caldenal open woodlands because recurrent burning not only shaped the spatial arrangement of trees, but fire-induced mortality also triggered an essential tree recruitment mechanism in these ecosystems.

1. Introduction

In many ecosystems worldwide, fire is the dominant disturbance that influences structure, composition and function (Barnes et al., 1998; Morgan et al., 2001; Perry et al., 2008). Woody vegetation is shaped and maintained by wildfires, especially in open woodlands and savannas, which are some of the most frequently burned formations in the world (Dwyer et al., 2000). Tree-grass coexistence in such fire-prone communities has developed over a long history of frequent fires, and any subsequent anthropogenic changes in fire regime may thus have a profound effect on tree dynamics in these ecosystems (Bond and Keeley, 2005; Higgins et al., 2000).

Fire frequency influences woody structure and dynamics in many savannas and open woodlands in South America (e.g., Moreira, 2000), Australia (Bowman and Panton, 1995; Russell-Smith et al., 2003), Africa (Case and Staver, 2017), and forests in North America (Knapp et al., 2017; Peterson and Reich, 2001; Scherer et al., 2016). Frequent fires have been credited to maintaining these fire-dependent ecosystems prior to European settlement (Felderhof and Gillieson, 2006; Peterson and Reich, 2001; Veldman et al., 2014), whereas reduction in fire frequency caused by agricultural expansion, landscape fragmentation and fire suppression has led to significant structural changes such as increased tree densities (Cowley et al., 2014; Faber-Langendoen and Davis, 1995; Taylor and Skinner, 2003). However, the magnitude of the effect of fire frequency on the structure of open woodlands and savannas varies substantially among continents (Lehmann et al., 2014) and the impacts of altered fire regime on some of these ecosystems remain seriously understudied.

One of the least studied, traditionally burned open woodlands that have experienced human-induced changes in fire frequency in the 20th and 21st centuries is the Caldenal in Central Argentina, situated in a semi-arid temperate region between the Pampas and Monte desert (Cabrera, 1976). Until the 1900s, the Caldenal was formed by open savanna-like woodlands with scattered large endemic caldén (*Prosopis*

* Corresponding author.
E-mail address: msvatek@centrum.cz (M. Svátek).

http://dx.doi.org/10.1016/j.foreco.2017.10.048
Received 18 July 2017; Received in revised form 20 October 2017; Accepted 23 October 2017

caldenia Burkart) trees in a grassland matrix (Dussart et al., 1998; González-Roglich et al., 2012). Following European settlement in Argentina in the early 20th century, the Caldenal has been subjected to the introduction of livestock, wood harvesting and the prolongation of the period between fires (Busso, 1997; Llorens, 1995; Morris and Ubici, 1996). As a result, many caldén woodlands have been transformed into agricultural lands, and the remaining stands have undergone drastic structural changes, such as increases in the density of young trees (Dussart et al., 1998; Sarasola et al., 2005), contrasting with a complete lack of tree regeneration in other caldén woodlands (Bogino et al., 2015). However, the underlying processes leading to these changes in Caldenal structure are poorly understood.

While deforestation affected the Caldenal mostly in the first half of the 20th century (Peinetti et al., 2007) and the intensity of large-scale logging has decreased since then (Sarasola et al., 2005), grazing and fire remain two key factors shaping the caldén vegetation. Numerous studies have explored the effects of overgrazing on caldén (e.g., Busso, 1997; de Villalobos et al., 2005; Villamil et al., 2001); however, the role of fire in tree dynamics is still not fully understood in the Caldenal (Bóo et al., 1997; Sarasola et al., 2005) or in other regions of Argentina (Rostagno et al., 2006). During the 20th century, the mean interval between fires in the Caldenal increased from approximately 5 to 10 or more years (Busso, 1997; de Villalobos et al., 2007), but because there is no official advice regarding whether to suppress or prescribe fires, some areas are being burned too frequently while fires are being completely prevented in others without knowing the consequences of fire management for caldén woodlands (Morris and Ubici, 1996). Because no area in the Caldenal has escaped continuous grazing (Fernandez et al., 2009), the differences in fire regimes may play a crucial role in controlling stand structure, tree mortality and regeneration.

One of the ways to learn how different fire regimes shape the dynamics of woody vegetation is to analyse the response of tree spatial patterns to fire (Briggs and Gibson, 1992; Holdo et al., 2009; Rebertus et al., 1989). A within-stand spatial pattern analysis may reveal how spatial interactions between trees change in response to the presence or absence of fire (Gray and He, 2009; Yu et al., 2009). Most studies on tree spatial patterns under different fire regimes come from North American open forests, in which fire exclusion is considered to be responsible for the accumulation of dense young trees, while frequent fire disturbance is thought to be essential for preserving the historic open character of the stands (Bond and Keeley, 2005; Cooper, 1961). A recent review showed that the frequent burning of these forests usually resulted in a clumped tree pattern with widely spaced large individual trees (Larson and Churchill, 2012) but also revealed that there is only a limited body of existing literature on fire-related spatial patterns. A lack of analyses exploring tree spatial patterns is even more evident in savannas and other open wooded landscapes because the majority of research in such ecosystems has focused on tree-grass coexistence rather than on the interactions among woody plants themselves (Dohn et al., 2017). Nonetheless, tree-tree interactions may be as important as tree-grass relationships in determining savanna structure (Dohn et al., 2017; Wiegand et al., 2006). Whereas frequent fires in savannas can induce inverse density-dependent mortality by preferably burning those trees which are isolated from the clumps and thence surrounded by higher amount of fine grass fuel than in the clumps, thus supporting tree clumping (Hochberg et al., 1994), under fire exclusion, self-thinning resulting from increased tree competition may be a prevalent mortality mechanism (Belay and Moe, 2012; Sea and Hanan, 2012).

In the Caldenal, despite the importance of tree spatial patterns in understanding the structural changes in originally open woodlands with once widely spaced trees, no study has yet explored the spatial distribution of caldén trees. Although the spacing of trees has been repeatedly mentioned as a main feature of original caldén woodlands (e.g., Dussart et al., 1998, González-Roglich et al., 2012, Distel, 2016), to our knowledge, only one study (Dussart et al., 1998) attempted spatial analysis of trees in the Caldenal, but its sampling design including only two young stands did not allow the performance of any detailed tree pattern analyses.

In our study, we analysed fine-scale tree spatial patterns in burned and unburned caldén woodlands to investigate how the fire regime affects their spatial arrangement and structure. To better explain the underlying causes of tree stratum processes, we also explored the mechanisms of tree mortality and regeneration, both vegetative by sprouting and generative by seeding, under different fire regimes. By studying three sets of plots, one frequently burned, one without fire for 20–30 years, and one unburned for at least the last six decades, we examined the following hypotheses. First, we expected to find significant differences in woodland structural parameters among the fire regimes. Specifically, we hypothesized that tree density would increase with the length of fire exclusion due to the lack of fire-induced thinning (Matula et al., 2014) but that the proportion of dead trees would be higher in the plots having experienced 60 years since the last fire than in those having experienced only 20–30 years of fire exclusion due to the increased competitive self-thinning (Belay and Moe, 2012) (see also the fifth hypothesis below). Second, in terms of tree regeneration, we anticipated sprouting to be triggered by fire in burned plots, whereas in the absence of fire disturbance, we expected seeding to be a prevalent tree regeneration mechanism. Third, we expected that the differences in fire regimes would generate divergence in the overall tree spatial pattern, which we anticipated to be more clumped under the frequent fire regime than under fire exclusion. Fourth, because numerous studies repeatedly mentioned the presence of large trees in the pre-20th century Caldenal but the occurrence of previously unseen dense small trees since 1900 (Dussart et al., 1998; Peinetti et al., 2007; Sarasola et al., 2005), we also explored the spatial patterns of large and small trees separately. While we predicted the overall spatial pattern of all (both large and small) trees to be aggregated in the frequently burned plots, we supposed that large trees would be more widely spaced than small trees in these plots, thus following the characteristic pattern of other frequently burned open forests (Larson and Churchill, 2012). Fifth, we expected tree mortality to be induced by size- and distance-dependent competition in fire-excluded but not in fire-frequent woodlands. Therefore, in the absence of frequent fire, we supposed that competitive self-thinning would be reflected in a positive spatial association between small dead and large live trees, while no such spatial correlation was anticipated under frequent fire.

2. Methods

2.1. Study area

The study was carried out in the La Pampa and San Luis provinces in central Argentina (Fig. 1) in the temperate semi-arid district of the Caldén in the south of the Espinal phytogeographical province (Cabrera, 1976). The mean annual temperature in the study area ranges between 15.2 and 16 °C, while the mean annual precipitation ranges from 520 to 580 mm (Cano et al., 1980). The soils are entisols and mollisols on sandy and loamy eolic plains (Cano et al., 1980).

2.2. Data collection

Within the study area, six sites with remaining caldén woodlands were chosen (Fig. 1). At each site, three square plots (2500 m^2 each) were placed in the woodlands with three different fire regimes (1 plot per fire regime). Since caldén woodlands exist today mostly in small fragments, we placed plots within those fragments large enough to ensure that the distance between the plot boundary and fragment border was at least 20 m. The plot boundaries always followed the four cardinal directions. Of the total of 18 plots, six plots were placed in stands where fires occurred frequently in recent decades, with at least two fires occurring within the last 10 years (hereafter referred to as the