Forest Ecology and Management 382 (2016) 214–224

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Dynamics of competition over water in a mixed oak-pine Mediterranean forest: Spatio-temporal and physiological components

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ARTICLE INFO

Article history:
Received 19 June 2016
Received in revised form 6 October 2016
Accepted 9 October 2016
Available online 15 October 2016

Keywords:
Plant-to-plant interactions
Point patterns
Stable isotopes
Pinus halepensis
Quercus ilex
Ecohydrology

ABSTRACT

Understanding inter- and intra-specific plant interactions and competition over water is challenging because of the lack of effective approaches for accessing and monitoring root distribution and activity. In this context, stable isotopes are excellent eco-hydrological tracers that allow characterizing the dynamics of water uptake patterns in trees and shrubs. Here, we studied biotic interactions for water uptake between two typical Mediterranean tree species, Aleppo pine (*Pinus halepensis*) and holm oak (*Quercus ilex*), coexisting in a mixed forest. We measured stable isotope composition (δ18O and δ2H) of xylem water in all trees found in the studied stand during one growing season, covering an exceptionally long summer drought and subsequent recovery. We applied point-process statistics together with stand density information to evaluate tree-to-tree interactions for water use. In pines, we observed a clear uncoupling between soil and xylem water isotope composition after two months of persistent drought. Conversely, the isotope composition of xylem water in oaks tracked observed changes in the soil during the first two months of drought, but began to depart from soil values after three months. These results suggest that during drought the oaks were able to keep active for longer using alternative soil water sources, not available for the pines. Point-process statistics revealed more positive isotope compositions at distances below 4–6 m, but only between con-specific individuals (i.e. pine-pine, oak-oak). These intra-specific responses were first seen in the pines (after two months of drought) and subsequently in oaks (after three months), coinciding with the onset of soil-xylem uncoupling for each species. On the other hand, the isotope composition of individual oaks decreased with increasing neighbor pine density, but increased in response to oak density. Conversely, the pines showed more positive values with increasing oak density. Our results suggest that the use of shallow water in oaks is limited by the presence of pines, which force them to shift to deep-soil water use, whereas pines have more restricted access to deep water in the presence of oaks, leading to more positive isotope values. According to the dynamics of interaction patterns, we conclude that inter-specific differences in pine-oak mixed forests hold two components: a static, spatial component determined by root distribution, and a dynamic, physiological component related to water uptake capacity within the soil profile.

1. Introduction

The composition and dynamics of forest systems in the Mediterranean basin are likely to undergo substantial changes due to the predicted increase in frequency of drought and heatwaves for the next decades (IPCC, 2013). In this region, subtle variations in water availability may have profound effects at the ecosystem level (Bellot et al., 2004; Filella and Peñuelas, 2003b; Zavala et al., 2000). A typical situation in coastal ranges along the western Mediterranean basin is the formation of pine-oak mixed forests (Gil et al., 1996; Klein et al., 2013). Mediterranean pines, as water-saving, drought-avoiding species, shares space and resources with drought-tolerant, less conservative species such as evergreen oaks (Lookingbill and Zavala, 2000; Zavala et al., 2000, 2011). Traditionally, pine-oak mixed forests have been considered as transient states in ecological succession towards an oak-dominated climax vegetation (Rivas-Martínez, 1987). However, increasing evidence points towards niche segregation as a mechanism determining the long-term persistence of these

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http://dx.doi.org/10.1016/j.foreco.2016.10.025
0378-1127/

communities (Zavala et al., 2000; Zavala and Zea, 2004). Yet, it is a matter of debate whether facilitation or competition define species co-existence (Díaz-Sierra et al., 2010; Maestre et al., 2005; Valladares et al., 2015; Zavala and Bravo de la Parra, 2005), and how resource scarcity could promote or inhibit these two processes (Brooker et al., 2008; Craine and Dybzinski, 2013). Recent studies have shown that water scarcity increases competition for water in mixed forests (Grossiord et al., 2014), reducing the potential benefits of species co-existence (Jucker et al., 2014). Conversely, other works show evidence of facilitation processes in water-limited environments, e.g. hydraulic lift by deep-rooted species favoring neighbor shallow-rooted species (Prieto et al., 2012; Rodríguez-Robles et al., 2015). So far, studies based on large-scale gradients do not provide a clear answer regarding the ecological effects of water availability on Mediterranean communities (see e.g. Grossiord et al., 2014). Species-specific seasonal patterns in transpiration rates, together with a distinct ability to retrieve water at different soil depths or matrix potentials, may cause an alternation between competition, niche segregation and facilitation patterns during the growing season (Bellot et al., 2004; Prieto et al., 2012; Rodríguez-Robles et al., 2015). In particular, the highly dynamic nature of water uptake patterns in Mediterranean forests (Barbeta et al., 2015; Klein et al., 2013, 2014b; Voltas et al., 2015) claims for complementary, stand-based studies, in order to consider dynamic tree-to-tree interactions in the use of water resources (Comas et al., 2015; Zavala and Bravo de la Parra, 2005).

Understanding the dynamics of inter- and intra-specific belowground interactions and competition for water is challenging because of the lack of effective approaches for accessing and monitoring root distribution and water uptake in trees (Jackson et al., 1996; Maeght et al., 2013; Rewald and Leuschner, 2009). In this context, stable isotopes constitute a powerful tool to examine short-term variability in plant water uptake (Dawson et al., 1993). Due to isotope fractionation during evaporation, and the different contribution of seasonal precipitation to soils, streams and groundwater, we can find differences in isotopic signatures between the soil surface water and the groundwater, as well as along the soil profile (Dawson et al., 1993; Ehleringer et al., 1991; Gat, 1996; Máguas et al., 2011; Tang and Feng, 2001). Additionally, the interaction with the mineral and organic substrate can cause additional fractionation of water among different water pools within the soil (Chen et al., 2016a; Meißner et al., 2014; Oerter et al., 2014; Palacio et al., 2014). Taking advantage of this variability, isotopic tracing has revealed the use of contrasting water sources among neighbour plants, generally associated to species-specific traits (e.g. Chen et al., 2016b; David et al., 2007; Filella and Peñuelas, 2003b; Máguas et al., 2011; Moreno-Gutiérrez et al., 2012; Yang et al., 2011), but also showing intra-specific variation, e.g. due to ontogenic or genetic variability (Dawson, 1996; Voltas et al., 2015). The main advantage of stable isotope tracing is that it can catch the highly dynamic nature of plant water uptake, showing variations from daily to seasonal time-scales (Barbeta et al., 2015; Filella and Peñuelas, 2003b; Holst et al., 2010; Máguas et al., 2011; Palacio et al., 2014; Volkmann et al., 2016; Voltas et al., 2015), often revealing intra- and inter-specific ecological interactions like competition (Comas et al., 2015; Dawson, 1996; Moreno-Gutiérrez et al., 2015) or facilitation through hydraulic redistribution (Dawson, 1996; Filella and Peñuelas, 2003a; Prieto et al., 2012).

In a recent work (Comas et al., 2015), we applied point-process statistics to examine the spatial patterns of stable isotope composition of xylem water in a mixed stand of Aleppo pine (*Pinus halepensis* Mill.) and holm oak (*Quercus ilex* L.) during summer drought. We did not identify inter-specific interactions and, therefore, we concluded that these species occupy distinct niches for water uptake, at least under conditions of limited water availability. However, we determined neither to what extent these conclusions held throughout the growing season nor the underlying processes for this apparent niche segregation.

In the present study, we hypothesize that inter-specific interactions for water uptake in pine-oak mixed stands are determined by two components: (1) a static, spatial component related to constitutive differences between species (i.e. due to contrasting root distribution); and (2) a dynamic component triggered by water scarcity and linked to differential (physiological) drought responses. Therefore, the main aim of this study is to determine whether clear spatial niche segregation within the soil precludes any inter-specific interaction throughout the growing season, or rather there is prevalence of a more dynamic physiological component, leaving room for competition and/or facilitation mechanisms under certain conditions. For this purpose, we characterized the temporal evolution of spatial interactions for water uptake during one growing season in a mixed pine-oak stand, integrating information from stable isotope composition in soil and xylem water, remote-sensing and other physiological indicators.

2. Material and methods

2.1. Site description

The study area was a mixed forest of holm oak and Aleppo pine located in the Montsant range, northeastern Iberian Peninsula (41° 19′ 47.3″ N, 0° 50′ 2.6″ E, 750 m a.s.l). The site is close to the optimal distribution range for both species (topo-climatic suitability index >0.8; http://www.opengis.uab.cat/IdoneitatPI/). The climate in the region is Mediterranean temperate with continental tendency, with a mean annual precipitation of 515 mm and mean annual temperature of 12.3 °C. It is characterized by a dry and a relatively warm summer (summer precipitation of 90 mm, mean temperature of 20.9 °C) and wet spring and autumn seasons. The forest stand originated from natural regeneration of pine and oak in a former agricultural terrace which, according to the age of the oldest individuals, was abandoned >100 years ago. Understory vegetation is relatively scarce and current regeneration of both species is rare. According to USDA soil taxonomy (Soil Survey Staff, 2010), soil is a loamy-skeletal, carbonatic, termic, active calcic pachic haploxeroll, with soil depths ranging from 20 cm to 50 cm approximately.

2.2. Remote sensing and meteorological data

Meteorological data was obtained from the nearest automatic agro-meteorological station (Ulldemolins, 4 km), maintained by the *Servei Meteorològic de Catalunya*. The station provides a continuous record of precipitation (P), air temperature, humidity, global radiation and wind speed, as well as a set of derived variables, including hourly estimations of Penman-Monteith-FAO reference Evapotranspiration (ETo) (following Allen et al., 1998). We estimated daily changes in soil water storage (SWS, in mm) using a simple water balance model (Botey et al., 2011), which assumes additive increments during wet days ($P \geqslant ETo$) until reaching maximum soil water storage (SWS_{max}), and exponential decay during dry days ($P < ETo$):

$$P_i \geqslant ETo_i \Rightarrow SWS_i = SWS_{i-1} + P_i - ETo_i \quad (1)$$

$$P_i < ETo_i \Rightarrow SWS_i = SWS_{i-1} \times e^{-(ETo_i - P_i)/SWS_{max}} \quad (2)$$

$$SWS_i \geqslant SWS_{max} \Rightarrow SWS_i = SWS_{max} \quad (3)$$

where SWS_i and SWS_{i-1} stand for SWS at days i and $i-1$, respectively, and ETo_i and P_i are daily accumulated values of ETo and P