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Some positive effects of the fragmentation of holm oak forests: Attenuation of water stress and enhancement of acorn production

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ABSTRACT

The effects of fragmentation on acorn production should be mediated by their impacts on the physiological status of oaks during seed development particularly in water-limited systems, such as Mediterranean forests. The creation of forests edges reduces tree-to-tree competition, which may in turn temper water shortage during summer and, as a result, enhance acorn production. To test these two hypotheses we monitored acorn production and predawn water potential during the 2012–2014 period in two holm oak (*Quercus ilex*) forest archipelagos of the Iberian Peninsula.

Acorn production and fragmentation effects did not differ between localities despite of their contrasting climatic conditions (accumulated water deficit from April to August was a 60% higher in the South). In general, forest interiors showed a high proportion of non-producing trees (~50%) while trees at small forest fragments showed high acorn crops (acorn score ⩾3, ~40% of studied trees). Our results confirmed the expectation that intraspecific competition in small forest fragments was reduced, which alleviated summer water shortage of the trees studied. This reduced water stress entailed an increased acorn production. Overall, our results show that local processes such as fragmentation may counteract climatic differences among localities and could even override the impacts of increased aridity on acorn crops.

1. Introduction

Habitat loss, resource overexploitation and inadequate management are the main drivers of forest degradation in the Mediterranean Basin, and their impacts are expected to be intensified by climate change (Sala et al., 2000; Valladares et al., 2014). On one hand, summer water availability is one of the main limiting factors for plant growth in Mediterranean ecosystems (Flexas et al., 2014) and future scenarios of climate change predict an increase in drought intensity in the coming decades (IPCC, 2013). On the other hand, forest management can have pervasive effects on forest regeneration, which is driven by a complex interplay between habitat availability, isolation and edge effects (Valladares et al., 2014). Thus, knowledge on the combined effects of these different drivers is urgently needed in order to evaluate the actual vulnerability of Mediterranean forests to global environmental change (Doblas-Miranda et al., 2015).

Holm oaks (*Quercus ilex* ssp. *ballota*) are an ideal study system for addressing the combined effect of management and increased aridity on forest regeneration. Most holm oak forests are located in anthropogenic landscapes and either an increased summer drought, a given management regime or both may compromise holm oak reproduction (Espelta et al., 1995; Pérez-Ramos et al., 2010; Misson et al., 2011). Holm oaks are considered as tolerant to severe water shortage due to their deep root system (Moreno et al., 2005), to their ability to rapidly recover from tissue damage caused by the summer drought, and to their resprouting capability (Tognetti et al., 1998). However, when compared to other Mediterranean species, they are quite vulnerable to xylem cavitation and they actually function close to their point of hydraulic failure during the summer months (Martínez-Vilalta et al., 2002; Quero et al., 2011). In fact, high defoliation rates and dieback episodes have been registered after extreme drought events in holm oak forests (Peñuelas et al., 2000). Fruit production has been also linked to water availability during spring and summer months, despite complex masting processes that derive in high inter-annual variability in acorn crops. In general, moister springs involve higher investment on female flowers, which entails enhanced acorn production, but a very severe summer drought can lead to high abortion rates and constrain final acorn production (Ogaya and Peñuelas, 2007; Espelta et al., 2008; Pérez-Ramos et al., 2010; Misson et al., 2011; Rodríguez-Calcerrada et al., 2011; Sánchez-Humanes and Espelta, 2011; Fernández-Martínez et al., 2012; Garcia-Mozo et al., 2012). Thus, the increased aridity expected under a climate

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change scenario may hamper holm oak reproduction. In fact, rainfall exclusion experiments have shown that a 15–30% reduction in summer rainfall, which are similar to that expected by the end of the century for the Mediterranean basin (AEMET, 2009), can significantly constrain acorn production (Pérez-Ramos et al., 2010; Rodríguez-Calcerrada et al., 2011; Sánchez-Humanes and Espelta, 2011; IPCC, 2013).

Concomitantly to climatic conditions, management practices such as tree coppicing, tree thinning and shrub clearance, or fragmentation can affect water availability of individual holm oak trees (Terradas, 1999; Moreno and Cubera, 2008; Campos et al., 2013). In dense multi-stemmed stands, increased competition for resources limits oak growth and sexual reproduction (Rodríguez-Calcerrada et al., 2011; Sánchez-Humanes and Espelta, 2011). Selective thinning of the weaker stems has been proposed as a management strategy for natural restocking since it stimulates tree growth (e.g. Retana et al., 1992; Mayor and Roda, 1993). However, thinning effects on acorn production seem minor (Rodríguez-Calcerrada et al., 2011; Sánchez-Humanes and Espelta, 2011). Another way of buffering the negative effects of summer drought on holm oak water status is tree clearance (Moreno and Cubera, 2008). For instance, trees in savanna-like woodlands (dehesas and montados) show acorn crops one order of magnitude higher than those found in forest habitats (Pulido and Díaz, 2005; Díaz, 2014). Therefore, management effects on holm oaks acorn production seems to be driven by local changes in intraspecific competition, which modulates the negative effects of summer drought.

Among management regimes, fragmentation is widely spread in the Iberian Peninsula, where agricultural intensification has led to the replacement of large continuous holm oak forests by archipelagos of isolated fragments embedded in a cereal cropland matrix (Santos and Tellería, 1998). Forest fragmentation has well-known negative effects on acorn dispersal and seedling recruitment (Santos and Tellería, 1997; Morán-López et al., 2015). However, the creation of forest edges may entail lower intraspecific competition, and thus could temper oak water stress during summer (Moreno and Cubera, 2008). If this was the case, forest fragmentation could have positive effects on acorn production (Carevic et al., 2010). To test this hypothesis we (1) monitored acorn crops in two holm oak forest archipelagos of the Iberian Peninsula during three consecutive years (2012–2014), and (2) evaluated whether fragmentation effects on acorn production depended on changes in intraspecific competition for water resources during summer.

2. Material and methods

2.1. Study area

The two holm oak archipelagos studied are located in the northern and southern Plateaux of the Iberian Peninsula (Fig. A1) — an extensive treeless agricultural region where cereal cultivation has reduced the original forest cover to about a 7–8% of the land area (Santos and Tellería, 1998). Besides, past exploitation for firewood has led to a coppice structure of large forests and small fragments.

Fieldwork in the southern plateau was carried out in the vicinity of Quintanar de la Orden (39°35′N, 02°56′W; 870 m.a.s.l.) within an area of 38,500 ha. The dominant tree is the holm oak (121 stems per ha) with the understory composed by shrubby Kermes oak *Q. coccifera* and shrub species typical from xeric Mesomediterranean localities (e.g. *Rhamnus lycioides*, *R. alaternus*, *Cistus ladanifer*, *Asparagus acutifolius*). Average canopy radius of holm oaks in Quintanar de la Orden is 3.02 m (±0.28). Annual precipitation and mean temperature are 421 mm and 14 °C, respectively.

Fieldwork in the northern plateau was undertaken in an area of 66,500 ha around Lerma (41°58′N, 03°52′W; 930 m asl). The dominant tree is also holm oak (424 stems per ha), with isolated Lusitanian oak *Quercus faginea* and Spanish juniper *Juniperus thurifera* and understory shrubs typical from wetter and cooler Supramediterranean localities (e.g. *Cistus laurifolius*, *Genista scorpius*, *Thymus zygis*). Average canopy radius of holm oaks in Lerma is 2.26 m (±0.13). Annual precipitation is 567 mm and annual mean temperature is 11 °C. In both localities, the dominant soils are classified as Cambisols (calcics) (WRB, 2007) with 17% sand, 39% silt and 44% clay for the southern region and 11% sand, 42% silt and 47% clay for the northern region (Flores-Renteria et al., 2015).

2.2. Experimental design and tree measurements

In each locality we selected three large forest fragments (>100 ha), in which we defined forest interiors and edges. Edges were defined as forest areas closer than 60 m from the cultivated border, being interiors the remaining forest (García et al., 1998). Edge plots were selected along long straight borders to avoid influences of border geometry on edge effects (Fernández et al., 2002). Besides, we selected 10 and 11 small forest fragments in the northern and southern locality, respectively (mean ± SE 0.047 ± 0.031 and 0.031 ± 0.024 ha in the south and north, respectively). Hence, three fragmentation categories were defined — forest interior, forest edge and small fragments — in each locality — northern and southern plateaus.

In a pilot study carried out in 2011 we observed that site-specific variability on acorn production stabilized at sample sizes of about 75 (25 trees per fragmentation level). Therefore, we established a sampling effort of 30 randomly selected trees per fragmentation level and locality (total sample size = 180). During 2012–2013–2014 crop size of focal trees was visually estimated using a semi-quantitative scale ("acorn score") with five classes- 0 (no acorns), 1 (<10% of the canopy covered by acorns), 2 (10–50%), 3 (50–90%) and 4 (>90%) (Díaz et al., 2011; Koenig et al., 2013). The large number of trees sampled forced the use of visual surveys, which are less time-consuming than seed traps and are highly correlated with quantitative measures (Koenig et al., 2013; Carevic et al., 2014b).

In mid-August 2012 and 2013 we measured predawn water potential (Ψ_{pd}) of focal trees. In each locality, we sampled 90 focal trees (30 per fragmentation level) along six days. On average, 15 trees were measured each day following a randomized factorial design with respect to fragmentation category. Measurements were conducted on two twigs per tree and then averaged. Excised twigs were collected into sealable plastic bags, with air saturated of humidity and CO_2, and kept refrigerated and in dark (Pérez-Harguindeguy et al., 2013). All measurements were performed by means of a Scholander chamber (Scholand et al., 1965).

In each focal tree we estimated intraspecific competition as the proportion of area within a radius of 20 m from focal trees covered by other canopies (Oppie, 1968). Area of influence was fixed to 20 m because it is an intermediate value between maximum horizontal extension of oak roots in savanna-like woodlands (33 m, Moreno et al., 2005) and those found in forest stands (10 m, Rewald and Leuchner, 2009). High stem density in the northern locality together with a multi-stem structure of focal trees forced us to use transects as a proxy of area of influence (4 transects per tree —N, S, E, W directions). We also measured canopy radius (average of four measures per tree) and number of stems per stump since both variables could covary with intraspecific competition and affect tree water status and acorn production of individual trees (e.g. Sánchez-Humanes and Espelta, 2011; Rodríguez-Calcerrada et al., 2011).

2.3. Meteorological data

Meteorological data for the 2012–2014 period were obtained from the closest weather stations belonging to the Spanish