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Xylem anatomical traits reveal different strategies of two Mediterranean oaks to cope with drought and warming

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ABSTRACT

Performance and survival of Mediterranean trees depend on their capacity to cope with water stress. In harsh environments, xylem growth strategies are critical to ensure efficient water transport, though these are largely unknown for many species, including most Mediterranean oaks. We investigated xylem anatomical traits in tree-ring series of deciduous *Quercus ithaburensis* and *Q. boissieri* in the South-Eastern Mediterranean Basin to assess xylem response to climate variability, with special attention to dry and warm years and to temperature increase over the last decades. Abundant precipitation and low temperature during the wet season (November–April) benefited xylem formation of both species. However, intra-ring analysis revealed different patterns, as the size of early-formed vessels in *Q. boissieri* was related to previous-year ring, while in *Q. ithaburensis* it was strongly affected by current wet season conditions. During dry years, vessel size and number in *Q. ithaburensis* were strongly reduced, but they fully recovered in the following year (high resilience). Conversely, *Q. boissieri* vessels were barely reduced during dry or warm years (high resistance). Different strategies allow both species to overcome dry and warm years, but their capacity to withstand long-term warming seems to differ. *Q. ithaburensis* xylem traits did not evidence any trend over the last few decades, while *Q. boissieri* was facing a decline in some traits. Our analysis suggests that the growth strategies of *Q. ithaburensis* would be effective under future drier conditions, while temperature increase could induce a hydraulic deterioration and a potential decline in the less fit *Q. boissieri*.

1. Introduction

As a global warming hotspot, the Mediterranean basin will likely be affected by increased temperature, reduced precipitation, and enhanced frequency of extremely dry spells (Giorgi and Lionello, 2008; IPCC, 2014). This could have dramatic consequences on terrestrial biomes and on the survival and distribution of tree species (Petit et al., 2005; Matesanz and Valladares, 2014). As migration and genetic adaptation are relatively slow processes for long-living organisms like trees, morphological and physiological adjustment would be critical to cope with a dryer climate (Sultan, 2000; Bussotti et al., 2014; Lloret et al., 2016). Given the importance of this, a large research effort has been made to elucidate Mediterranean species structural traits and adaptive strategies to withstand drought (Lo Gullo and Salleo, 1988; Nardini and Pitt, 1999; Ogaya et al., 2011; Matías et al., 2012). Currently, most attention has been paid to short-term physiological and metabolic processes that determine plant capacity to overcome summer drought (David et al., 2007; McDowell et al., 2008; Quero et al., 2011; Niinemets and Keenan, 2014), especially at the leaf level. However, xylem hydraulic properties also play a role in the survival or mortality of plants during drought (Martínez-Vilalta et al., 2002; Limousin et al., 2012). Additional knowledge on xylem formation mechanisms, including strategies to deal with climate variations and extreme events, is therefore required to assess how climate change will affect Mediterranean species. Trees unable to produce safe and efficient conductive tissues under altered environmental conditions will experience hydraulic deterioration and a consequent physiological decline, which could trigger mortality (Levanic et al., 2011; Camarero et al., 2015). Indeed, hydraulic system failure has been indicated as a major cause of tree species dieback in the Mediterranean area (Nardini et al., 2014; Pellizzari et al., 2016).

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Different genera, species within a genus, and ecotypes within a species, have distinctive xylem anatomical traits adapted to prevailing environmental conditions, which influence their ecological amplitude (Baas and Carlquist, 1985; Fahn et al., 1986). The genus *Quercus* comprises many species with specific morphological and physiological traits, including very different xylem structure (Tessier et al., 1994; Nardini and Tyree, 1999). Some species present drought-adaptive traits to survive at the dry limit of broadleaved trees in the Mediterranean area. However, while Mediterranean oaks will likely replace less drought-tolerant species in most of Central and Southern Europe under warming climate (Hanewinkel et al., 2013), a drastic reduction in productivity and distribution in some dry Mediterranean regions (Di Filippo et al., 2010; Bussotti et al., 2015; Natalini et al., 2016) raises a doubt on *Quercus* species capacity to cope with warming at the dry limit of their natural distribution.

To elucidate how oaks respond to climate, an increasing number of studies have investigated secondary growth and xylem anatomy of different species in the Mediterranean region (e.g., Cherubini et al., 2003; Garcia-Gonzalez and Fonti, 2006; Gea-Izquierdo et al., 2012; González-González et al., 2015). However, knowledge on intra-seasonal growth mechanisms, strategies to withstand drought, or current and carry-over xylem response to dry events, is still scant for most oak species (Pèrez-de-Lis et al., 2016), especially in the Eastern Mediterranean.

With this study, we aimed at increasing knowledge on *Quercus* strategies to cope with drought in the Mediterranean area, by investigating xylem response to climatic variability, a critical aspect for assessing the genus vulnerability to climate change. We analyzed xylem anatomical traits along tree-ring series in two deciduous oak species at the south-eastern limit of genus distribution (Dufour-Dror and Ertas, 2004), *Q. ithaburensis* Decne. subspecies *ithaburensis* and *Q. boissieri* Reut., to test the following hypotheses: (1) being in a water-limited area for tree growth, xylem traits of both the species are related to precipitation variability, but the response magnitude and timing depend on the species and local conditions; (2) being naturally adapted to the local environment, they possess – possibly different – strategies to produce efficient vessels during and after dry and warm years; (3) despite neither species evidencing any symptoms of decline, growth rates and some xylem traits have been negatively affected over the last decades by unprecedented climate warming.

2. Material and methods

2.1. Investigated species and study area

Q. ithaburensis Decne. (hereafter QUIT) is a deciduous oak widely distributed in the East-Mediterranean area. The subspecies *ithaburensis* (Tabor oak) typically grows in open stands in lowlands up to 500 m a.s.l. between Israel, Jordan and Syria (Dufour-Dror and Ertas, 2004; Schiller et al., 2007; Cooper et al., 2014). Despite being considered winter deciduous, Ne'Eman (1993) reports a wide morphological and phenological variability within the species, and Kaplan and Gutman (1999) indicate that a few individuals (10–15%) keep their leaves during winter. The wood is ring- to semi-ring-porous (Fahn et al., 1986). Three study sites were surveyed, at a distance of a few kilometres apart in the Lower Galilee: Alonei Abba (32°73′N, 35°18′E, 140 m a.s.l.); Bet Zarzir (32°73′N, 35°20′E, 180 m a.s.l.); Qiryat Tiv'on (32°71′N, 35°13′E, 140 m a.s.l.). All three sites feature open woodlands with oak Trees 6–8 m tall on flat or gently slopes ($<$ 10%).

Soils are Brown Rendzina (Rendolls and Xerorthents in the American classification, Dan et al., 1972; Singer, 2007), developed over a 0.5–2 m deep *Nari* layer, i.e. a hard crust developing on top the soft chalk rock during pedogenic processes. Due to the irregular topography of the *Nari* crust, numerous soil pockets occur up to 1.5 m deep. Through them, tree roots penetrate the rock below which serves as a water reservoir during the summer season (Herr et al., 2000, 2016). Moisture tension at the end of the summer in the Brown Rendzina soil, at 20 cm depth, is around 20–40 bar, enabling roots survival (Singer, 2007). Lower Galilee is classified as Dry subhumid, and mean aridity index in the study sites is 0.61 (UNEP, 1992). High temperature and the typical Mediterranean precipitation regime determine a long dry period between April and October (Fig. 1).

Q. boissieri Reut. (Boissier oak, hereafter QUBO) is a deciduous oak distributed between western Iran, Turkey, Syria, Lebanon, and Israel, mainly between 500 and 1200 m a.s.l. (Danin, 1992). The wood is generally ring-porous, sometimes semi-ring-porous (Fahn et al., 1986). All the samples were collected in open woodland in the Golan highlands (Merom Golan, about 60 km from *Q. ithaburensis* sites; 33°13′N, 35°76′E, 960 m a.s.l.), where 8–10 m tall individuals occur in mixture with other broadleaf species (mainly *Q. calliprinos* Webb). The land is flat or gently sloping

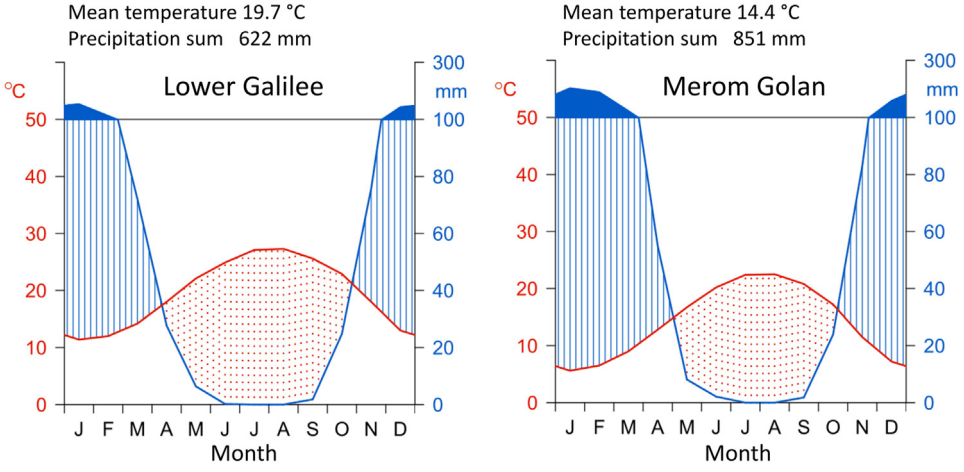

Fig. 1. Walter-Lieth ombrothermic diagrams for Lower Galilee (left), the *Q. ithaburensis* sample site, and Merom Golan (right), the *Q. boissieri* sample site. Lower Galilee weather data comes from Tavor Kadoorie climate station, 145 m a.s.l., and Allone Abba–Waldheim rain station, 170 m a.s.l. Merom Golan data comes from Merom Golan Picman Man climate station, 942 m a.s.l.