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Disentangling the effects of ontogeny and environmental factors on xylem anatomy in a semiarid chamaephyte

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ABSTRACT

The hydraulic system of plants reflects a balance between efficiency and safety which is continuously adjusted along plant's life to guarantee survival under changing conditions. One of such adjustments is the formation of new conductive cells, so vessel traits along ring series reflect part of plant's hydraulic plasticity. In this work we disentangled the effects of ontogeny and environmental factors on wood anatomy of a semiarid chamaephyte, *Linum suffruticosum*. We sampled individuals on contrasting slope aspects in the Ebro valley (Spain), and measured ring width and vessel traits to obtain annually-resolved data series. General Additive Models (GAMs) were used to identify the variability associated to cambial age, slope aspect, and climatic factors: a shift towards a more efficient xylem configuration was observed at the eighth year of life; narrower rings characterized by higher vessel density and smaller vessel sizes were found at south-facing slopes; and low precipitation at the onset of the growing season resulted in safer vessel features. The combination of quantitative analysis of vessels along ring series and GAMs allowed a global understanding of xylem's functional plasticity; moreover, the need for adequately assessing ontogenetic and topographic effects when predicting plant distribution under global change scenarios was reinforced.

1. Introduction

Water plays a fundamental role in the life of a plant. Understanding how plants cope with water stress is becoming a major concern in the context of ongoing climatic change (IPCC, 2007), and it is particularly urgent for arid and semiarid environments. Given the strong negative potential involved in water extraction from the soil and its transport up to the leaves, plants hydraulic systems often run close to physical limits (Tyree and Zimmermann, 2002). Without some kind of safety mechanisms, air-seeding of gas may trigger cavitation and subsequent embolism, which would reduce transport efficiency, cause leaf desiccation and eventually plant death. On the other hand, over-developed safety mechanisms may result in reduced water transport and/or higher resource investment, and thus would reduce plant performance and competitive ability (McDowell, 2011; Sperry et al., 2008).

Plants show a range of responses occurring at different time scales to withstand fluctuating levels of water availability (Maseda and Fernandez, 2006), including stomatal closure (Tyree and Ewers, 1991; Zweifel et al., 2009), shifts in the shoot-to-root growth ratio (Klein et al., 2011), modifications of the leaf and sap area (Rigling et al., 2010), and changes in xylem anatomy (Tyree and Zimmermann, 2002). Performing adjustments in the topology, density, and size of conductive cells is an effective and relatively fast mechanism to regulate the delicate balance between cavitation risks and efficiency in water transport (Mauseth and Stevenson, 2004; von Arx et al., 2012). Thus, tree-ring series of cell anatomical features constitute a chronological archive of past plant–water relations (e.g., Fonti et al., 2010; Olano et al., 2012). Understanding the patterns of xylem adjustments to climate, and the relative importance of the different factors affecting xylem anatomy, is essential to anticipate the potential impacts of climatic change on plant performance. For example, the regional climatic signal may be modified by the effects of local site characteristics such as slope aspect; thus, in Northern Hemisphere semiarid environments, north-facing aspects show more favorable conditions for plant growth, since they receive less solar radiation than south-facing slopes (Bellot et al., 2004; Pueyo and Alados, 2007). In addition,

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changes in plant growth requirements that occur along the lifecycle can further confound the importance of climate. Such age-size-related trends, despite usually being considered noise in dendroclimatic studies, strongly influence wood structure (Domec and Gartner, 2002; Spicer and Gartner, 2001), particularly in short- to medium-lived plants such as sub-shrubs (Biondi and Queadan, 2008).

Despite largely neglected in dendrochronological literature, sub-shrubs constitute a dominant life form in arid and semiarid ecosystems. In fact, semiarid scrublands dominate vast areas of the landscape in the Mediterranean Basin, where water availability is low in general, and highly variable at contrasting spatial and temporal scales (Sher et al., 2004). The projected increase in the frequency and severity of droughts for this region (Schär et al., 2004) may strongly affect these ecosystems. Potentially drier and warmer conditions are expected to result in altered phenological timing (Llorens and Peñuelas, 2005), reduced growth and primary production (Ogaya et al., 2003), shifted recruitment patterns (Olano et al., 2011), and enhanced mortality rates (Allen et al., 2010; McDowell et al., 2008). Anatomical traits have also been correlated with water stress in shrub species (Jacobsen et al., 2007; Martínez-Cabrera et al., 2009).

In this study, we assessed radial growth and vessel traits in the chamaephyte *Linum suffruticosum* L., which inhabits low scrublands on both gypsum and calcareous soils in South-western Europe (Ockendon and Walters, 1968), thus being considered a gypsovag (*sensu* Meyer, 1986). Specifically, our aims were to a) better understand the relative contribution of age, slope aspect and climate to radial growth and xylem anatomical characteristics, and b) describe the adjustments in vessel size classes performed by the species in relation to site and climate conditions. To simultaneously assess the effect of multiple factors on annual ring characteristics, Generalized Additive Models (GAM) were used.

2. Materials and methods

2.1. Study site and species description

The study was conducted in the central Ebro Valley, North-eastern Spain (41° 41′N, 0° 46′W, 242 m a.s.l.). Climate is semi-arid Mediterranean, characterized by an intense summer drought and a mean annual rainfall of 320 mm. Mean annual temperature is 15.0 °C, with a mean minimum temperature in the coldest month of 2.4 °C and a mean maximum temperature in the hottest month of 31.5 °C (data from Zaragoza meteorological station, 41° 39′ 23″ N, 0° 52′ 45″ W, 208 m a.s.l.). Soils are developed on gypsum parent rocks, and consequently are rich in calcium sulfate. The landscape is characterized by low hills and flat-bottomed valleys, and is covered by a low open scrubland where *L. suffruticosum* is abundant.

Gypsum steppes occurring under semiarid climates are subjected to harsh environmental conditions, given their physically (Romão and Escudero, 2005) and chemically (Guerrero-Campo et al., 1999b) restrictive soils, and the existence of an intense summer drought (Olano et al., 2011). *L. suffruticosum* is an evergreen and medium-lived chamaephyte showing distinct rings and semi-ring-porous wood (Fig. 1). It grows up to 40 cm tall and constitutes a major component of gypsum steppes in South-western Europe (Ockendon and Walters, 1968). Vegetative and reproductive activity of the species takes place during spring and autumn; its longitudinal growth shows a main pulse from mid-February to the end of June, and a second pulse from September to November (Palacio and Montserrat-Martí, 2005). Radial growth extends from April to June (Camarero et al., 2013).

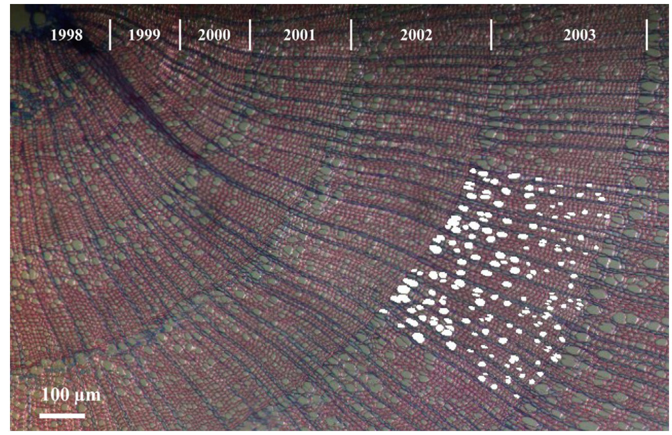

Fig. 1. Permanent histological cross-section of *L. suffruticosum*. Staining conducted with Alcian Blue (1% solution in 0.7 N HCl) and Safranin (1% water soluble); digital images captured with a Nikon D-90 digital camera mounted on a Nikon Eclipse 50i optical microscope. Scale (down left), dating (below the top), and identified vessels (on year 2003) are indicated.

2.2. Sampling, sample preparation and anatomical survey

Two samplings were performed in January 2010. A first sampling was performed at Villamayor (Zaragoza-Spain), where 20 dominant individuals per aspect were selected from the north-facing and south-facing slopes of a hill (N-site and S-site). Height and two canopy diameters were measured on each individual, and afterward plants were extracted. Root collars were cut and immediately stored in a fixative solution of formalin–ethanol–acetic acid (5:90:5).

Since the obtained chronology spanned a relative short period of time for standard dendrochronological climate-growth analysis, a second sampling of 20 dominant individuals was subsequently performed on the south-facing slope of a hill at Alfajarín (Zaragoza-Spain, 3 km away from Villamayor) by following the same sampling procedure. The Alfajarín site was characterized by harsher environmental conditions (steeper slope, rockier soil), and therefore we expected to obtain older individuals from it, since environmental stress is known to extend life spans as a result of reduced growth (Schweingruber and Poschlod, 2005). Such older individuals from Alfajarín allowed us to obtain temporal series long enough to reliably perform statistical correlations of residual growth-climate following classic techniques; the aim was exclusively to detect the most relevant climatic parameters determining ring width and vessel features in order to include them in the statistical analysis conducted with data from Villamayor (thus reducing the number of parameters included in the models, and at the same time ensuring the reliability of the selected climatic variables).

We acknowledge that, since an only field site was sampled and no replication of north- and south-facing slopes was included in the statistical analyses, our results must be taken with caution. Nevertheless, and given that aspect is one the major ecological factors acting at local scales in semiarid environments (Guerrero-Campo et al., 1999a; Pueyo and Alados, 2007), we are confident of the representativeness of our results.

Digital images of the cross-sections of root-collars were used to perform ring width measurements. Micro-sections 10 to 15 µm-thick were obtained by means of a sledge microtome (© H. Gärtner/F.H. Schweingruber, Birmensdorf, Switzerland), stained with Alcian Blue (1% solution in 0.7 N HCl) and Safranin (1% water soluble), and permanently embedded with Eukitt® glue (O. Kindler GmbH, Freiburg, Germany). Digital images were captured using a Nikon D-90 digital camera mounted on a Nikon Eclipse 50i optical