

The challenge of the Mediterranean climate to plant hydraulics: Responses and adaptations



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ABSTRACT

Mediterranean-type biomes characterized by warm summers with a distinct drought period lasting from 2 up to 10 months occur in several world regions including the Mediterranean basin, S-California, Chile, S-Africa and SW-Australia. All these areas are covered by a peculiar and hyper-diverse vegetation dominated by evergreen trees and shrubs with small and coriaceous leaves. Drought adaptation of Mediterranean plants relies on different mechanisms including deep rooting patterns, avoidance or resistance of cavitation-induced embolism, compensation or repair of embolism-induced hydraulic damage. The complementarity and/or co-occurrence of these physiological traits in different species inhabiting Mediterranean biomes is probably the basis for high plant biodiversity in these fascinating habitats. Ongoing climate changes, leading to enhanced frequency and intensity of drought episodes in Mediterranean biomes, represent a major threat to future conservation of these fragile ecosystems, especially if future harsher climate conditions will overcome the drought resistance limits of Mediterranean plants. Current knowledge about drought resistance mechanisms as well as about processes leading to decline and death of woody plants under extreme climatic conditions is revised and directions for future research are suggested.

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1. Introduction

Mediterranean-type ecosystems are among the most biodiversity-rich spots over the planet (Cowling et al., 1996). Long-term climate stability, leading to increased opportunities for species evolution coupled to low rates of species extinctions (Sniderman et al., 2013), as well as heterogeneity of geological substrates and topography (Bradbury, 1981) have likely represented important factors promoting the development and persistence of hyper-diverse sclerophyllous floras in the seasonally arid climates of the Mediterranean basin, S-California, Chile, S-Africa and SW-Australia (di Castri, 1981). Mediterranean biomes are also predicted to be among those most exposed to potentially harmful effects of climate change (Giorgi and Lionello, 2008). In fact, recent episodes of anomalous drought and heath waves have already shown the potentially large impact of modification of temperatures and water regimes on Mediterranean vegetation (Martinez-Vilalta et al., 2002a; Matusik et al., 2013).

Mediterranean-type biomes represent transitional habitats between temperate and tropical regions, and as such comprise

plant species with different biogeographical origin, both survivors of previous tropical or temperate vegetation as well as representative of taxa that evolved within the Mediterranean climate itself. Although the climate similarities in Mediterranean-like regions have led to a fascinating convergence in the overall appearance of vegetation and landscape, it is not surprising that such an extreme taxonomic, evolutionary and biogeographic diversity has also led to substantial diversity in terms of functional responses/adaptation of plant species to the specific climatic features of Mediterranean areas. This review will especially focus on the Mediterranean basin region, but similarities between different Mediterranean biomes, as well as divergence of functional traits within biomes will also be addressed, with special reference to plant adaptation to seasonal water stress, representing one of the distinctive traits of the Mediterranean-type climate.

2. Plants facing the Mediterranean-type climate: isohydry, anisohydry, and rooting depth

The Mediterranean-type climate has been defined in different ways, according to different authors. However, there is general consensus about the importance of some key features of Mediterranean climate including the concentration of most rainfall in winter, the year-to-year variability of precipitation, intensive solar radiation

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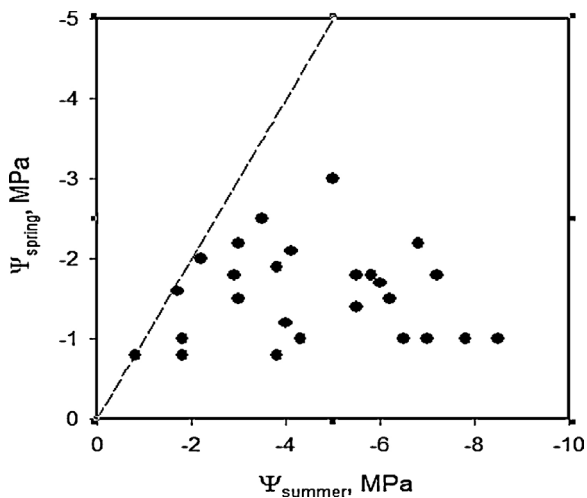


Fig. 1. Relationship between leaf water potential as measured at the end of spring rains (Ψ_{spring}) and after the summer drought (Ψ_{summer}) in different Mediterranean species. Each point represents a different species. The dashed line indicates the 1:1 relationship. Data were gathered from the literature (see text for details).

and, most importantly, the occurrence of mild to hot summers with a distinct drought period lasting from 2 up to 10 months. In the last decades, extreme summer drought events have been reported to occur at a significantly higher frequency (de Dios et al., 2007), and current evidence suggests that typical Mediterranean summer drought stress might further tend to increase in duration and/or intensity (Giorgi and Lionello, 2008).

Arid and semi-arid habitats are widespread from deserts to tropical forests and, hence, drought is not a specific feature of the Mediterranean biome. However, in contrast to plant species inhabiting the above listed regions that often display a drought-deciduous leaf habit (Sperry and Hacke, 2002; Jolly and Running, 2004), Mediterranean plants generally maintain their foliage physiologically active even during prolonged summer drought (Pignatti, 1978; Cowling and Campbell, 1980). Such a behaviour obviously requires the development of specific adaptive strategies addressed at maintaining sufficient plant water contents or tolerating substantial water losses and tissue dehydration. In the classical literature (Levitt, 1980), Mediterranean plant species were classified into two main categories, namely: (a) drought avoiding species, in turn divided into “water savers” limiting water loss by reducing stomatal opening and “water spenders” as capable of extracting water from the soil to a similar extent of water evaporation and, (b) “drought tolerant” undergoing large variation of plant water potential in phase with environmental changes in this variable. This classification roughly corresponds to the actually widespread categorization of plants in “isohydric” vs “anisohydric” species. The former group actually maintains plant water status (water potential and/or water content) relatively constant under drought stress conditions, while the latter displays large water potential fluctuations while maintaining relatively high gas exchange rates even during arid season. This binary classification is somewhat arbitrary, as in reality a continuous spectrum of plant hydraulic strategies can be observed in Mediterranean plants, ranging from nearly perfect isohydric behaviour, to mild anisohydry and finally to strong anisohydry (Salleo and Lo Gullo, 1990; West et al., 2012).

A convenient quantification of the relative degree of isohydry/anisohydry can be performed by comparing leaf water potential values recorded at the end of spring (Ψ_{spring}), when water is generally well available even in the upper soil layers, to values recorded at the end of the summer drought period (Ψ_{summer}). Fig. 1 reports such a comparison for several different species measured in different Mediterranean biomes around the globe (data

from Martínez-Vilalta et al., 2002b; Llorens et al., 2003; Serrano and Peñuelas, 2005; Bhaskar et al., 2007; David et al., 2007; Quero et al., 2011). It is clear that while some species maintain a strict control of their leaf water status during the arid season, so that Ψ_{summer} is very close to Ψ_{spring} , other species undergo ample fluctuations of their water status, with Ψ_{summer} being even 7 MPa lower than Ψ_{spring} . The co-existence of such contrasting water use strategies reflects the co-occurrence of diverse functional groups in Mediterranean environments like evergreen sclerophyllous trees, evergreen sclerophyllous shrubs and sub-shrubs, semi-deciduous shrubs and perennial herbs (Galmés et al., 2007). Moreover, the ‘hydraulic’ diversity in this particular semiarid ecosystem likely also reflects contrasting species’ evolutionary histories. Moreno-Gutiérrez et al. (2012) have suggested that the anisohydric behaviour is more typical of Quaternary taxa that appeared and evolved under proper Mediterranean climatic conditions, while isohydric strategy would be more common in evergreen sclerophylls that evolved under pre-existing tropical climate during the Tertiary.

Leaf water status fluctuations reflect the balance between water uptake at the root level and water loss at the leaf level. The former is dictated by soil water availability as well as root morphological and physiological properties (Nardini et al., 2002), while the latter is largely controlled by stomatal behaviour under variable evaporative demand (Jones, 1998). Rooting depth of vegetation types is known to vary on a global scale, with deepest rooting patterns occurring in seasonally water-limited ecosystems and warm-temperate to tropical forests (Schenk and Jackson, 2002). According to Canadell et al. (1996), maximum rooting depth for sclerophyllous shrub-lands and forests ranges from minimum values between 1 and 2 m and maxima comprised between 23 and 40 m, with an average value of 5.2 ± 0.8 m. These data are in accordance with predicted rooting depth in seasonally arid environments, as based on an analysis of known relationships between climatic variables, soil variables and recorded occurrence of deep roots (Schenk and Jackson, 2005).

Several experimental lines of evidence support the existence of substantial heterogeneity of rooting habits in Mediterranean plants. As an example, Burgess (2006) reported the effects of a summer rain on transpiration response in eleven Mediterranean trees and shrubs co-occurring in Western Australia. The variation of transpiration rates of different species following the rain event varied from zero to a more than fivefold increase, indicating considerable variation in the water sources accessed by plants and suggesting substantial inter-specific differences in rooting depth. These findings have been recently confirmed by the analysis of xylem sap isotopic composition during the summer dry season, as performed by West et al. (2012) in a shrub-land community in South Africa and by Moreno-Gutiérrez et al. (2012) in an open woodland community in Southeastern Spain. In both ecosystems, co-existing plant species were shown to segregate along a continuous ecophysiological ‘water envelope’ defined by different access to deep water resources. Xylem sap $^2\delta\text{H}$ ranged from -20% to -10% in the first study and from -40% to -33% in the second one, with more negative values indicating access to deeper water sources.

Interestingly, spatial and temporal dynamics of water uptake patterns have been suggested to underlie the co-existence of different species and growth forms in the same habitat. As an example, co-existing *Quercus suber* and *Q. ilex* trees were shown to exploit different water pools on a spatial basis, as a likely consequence of their different rooting patterns (David et al., 2007). Moreover, Nardini et al. (1999) provided evidence that physiological activity of root systems of co-occurring *Quercus cerris* and *Q. suber* achieved maximum values in different time of the vegetative season, with *Q. cerris* absorbing more water per unit surface area in spring and *Q. suber* reaching maxima of water uptake during late summer and early autumn. These findings suggest that the enormous floristic

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