



## Water and forests in the Mediterranean hot climate zone: a review based on a hydraulic interpretation of tree functioning

Teresa S. David<sup>\*1,2</sup>, Clara A. Pinto<sup>1</sup>, Nadezhda Nadezhkina<sup>3</sup>, Jorge S. David<sup>2,4</sup>

<sup>1</sup>Instituto Nacional de Investigação Agrária e Veterinária I.P., Quinta do Marquês, Av. da República, 2780-159 Oeiras, Portugal <sup>2</sup>Centro de Estudos Florestais, Universidade de Lisboa, Tapada da Ajuda, 1349-017 Lisboa, Portugal <sup>3</sup>Institute of Forest Botany, Dendrology and Geobiocenology, Mendel University, Zemedelska 3, 613 00 Brno, Czech Republic <sup>4</sup>Instituto Superior de Agronomia, Universidade de Lisboa, Tapada da Ajuda, 1349-017 Lisboa, Portugal

### Abstract

**Aim of the study:** Water scarcity is the main limitation to forest growth and tree survival in the Mediterranean hot climate zone. This paper reviews literature on the relations between water and forests in the region, and their implications on forest and water resources management. The analysis is based on a hydraulic interpretation of tree functioning.

**Area of the study:** The review covers research carried out in the Mediterranean hot climate zone, put into perspective of wider/global research on the subject. The scales of analysis range from the tree to catchment levels.

**Material and methods:** For literature review we used Scopus, Web of Science and Google Scholar as bibliographic databases. Data from two *Quercus suber* sites in Portugal were used for illustrative purposes.

**Main results:** We identify knowledge gaps and discuss options to better adapt forest management to climate change under a tree water use/availability perspective. Forest management is also discussed within the wider context of catchment water balance: water is a constraint for biomass production, but also for other human activities such as urban supply, industry and irrigated agriculture.

**Research highlights:** Given the scarce and variable (in space and in time) water availability in the region, further research is needed on: mapping the spatial heterogeneity of water availability to trees; adjustment of tree density to local conditions; silvicultural practices that do not damage soil properties or roots; irrigation of forest plantations in some specific areas; tree breeding. Also, a closer cooperation between forest and water managers is needed.

**Keywords:** tree hydraulics; tree mortality; climate change; forest management; water resources.

**Citation:** David, T.S., Pinto, C.A., Nadezhkina, N., David, J.S. (2016). Water and forests in the Mediterranean hot climate zone: a review based on a hydraulic interpretation of tree functioning. *Forest Systems*, Volume 25, Issue 2, eR02. <http://dx.doi.org/10.5424/fs/2016252-08899>.

**Received:** 01 Nov 2015. **Accepted:** 06 Apr 2016

**Copyright** © 2016 INIA. This is an open access article distributed under the terms of the Creative Commons Attribution-Non Commercial (by-nc) Spain 3.0 Licence, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.

**Funding:** The author(s) received no specific funding for this work.

**Competing interests:** The authors have declared that no competing interests exist.

**Correspondence** should be addressed to Teresa S. David: [teresa.david@iniav.pt](mailto:teresa.david@iniav.pt)

### The Mediterranean climate and forest vegetation

Mediterranean-type climate occurs in the Mediterranean Basin, California, central Chile, the Cape region of South Africa, and southwestern and southern Australia (Di Castri, 1991). Wet winters are coupled with dry and moderate/hot summers. Our work will be mainly focused on the driest areas that correspond to the *Csa* climate type of the Köppen-Geiger classification - Mediterranean Hot (Peel *et al.*, 2007; Spinoni *et al.*, 2015). In Europe, these areas mainly occupy the southern parts of Portugal, Spain, Italy, Greece and Turkey, characterized by a negative annual balance

between the evaporative atmospheric demand (potential evapotranspiration) and rainfall, increasing from north to south. In most of these areas aridity is increasing (FAO aridity index, average annual ratio between rainfall and potential evaporation is decreasing) (Spinoni *et al.*, 2015). Therefore, actual evapotranspiration is restricted by water availability, and streamflow represents only a small fraction of annual rainfall (David *et al.*, 1994; Huxman *et al.*, 2005). Furthermore, water scarcity imposes limits on many activities, such as urban and industrial supply, agricultural production and ecosystem maintenance.

Forest trees need water to survive, grow, provide timber and non-timber products, and ecosystem ser-

vices. Water is up taken from the rhizosphere, transported through the vascular system and evaporated to the atmosphere through leaf stomata (transpired water). Transpiration keeps stomata open to allow the intake of carbon dioxide required for photosynthesis and growth – the so called trade-off of water for carbon (Choat *et al.*, 2012; Buckley & Mott, 2013; Manzoni *et al.*, 2013). In the Mediterranean hot climate zone, transpiration is the main component of annual evapotranspiration (around 75%) (Paço *et al.*, 2009).

During the seasonal hot summer drought, vegetation is prone to some degree of water and heat stress and has evolved a series of adaptive strategies to survive and grow under such conditions (Chaves *et al.*, 2003; 2009; Baldocchi & Xu, 2007; Sardans & Peñuelas, 2013), and to maximize the use of scarce resources. The reviews by Chaves *et al.* (2003; 2009) bring together information from whole plant level to gene expression, proteomics, metabolomics and biochemical signalling in plant response to drought. In this work, we aim at a different/complementary approach to the “water and forests” issue. The scale of analysis is from the tree to the stand and catchment levels; and the scope essentially based on the theoretical background of the physics of water movement and water balance.

The ongoing climate change, linked to an increase in the frequency, intensity and duration of droughts, is threatening the productivity and survival of many Mediterranean ecosystems facing rapid changes in the habitat. In what concerns trees, mortality is increasing (Barbeta *et al.*, 2015; Doblás-Miranda *et al.*, 2015) though this is not a specific situation of the Mediterranean region. Other forest trees from different biomes, even from humid regions where a relative increase in drought is occurring, are facing similar problems (Allen *et al.*, 2010, 2015; Choat *et al.*, 2012; Engelbrecht, 2012; Grant *et al.*, 2013; Millar & Stephenson, 2015). Many are liable to suffer mega-disturbances over the long term (Millar & Stephenson, 2015), contracting from more arid conditions and expanding to wetter regions (Larter *et al.*, 2015). Despite that, the trend and magnitude of tree mortality and forest decline still remain largely unquantified due to the absence of an adequate global-scale monitoring system (Allen *et al.*, 2010; Millar & Stephenson, 2015). Nowadays, the primary goal for forest management is probably to try to minimize the effects of these changes (Grant *et al.*, 2013; Millar & Stephenson, 2015). This implies a better understanding of tree physiological responses to drought (Larter *et al.*, 2015). Among these, the assessment of tree vulnerability to drought is crucial to improve prediction of forest mortality and species range limits (Børja *et al.*, 2013; Urli *et al.*, 2013).

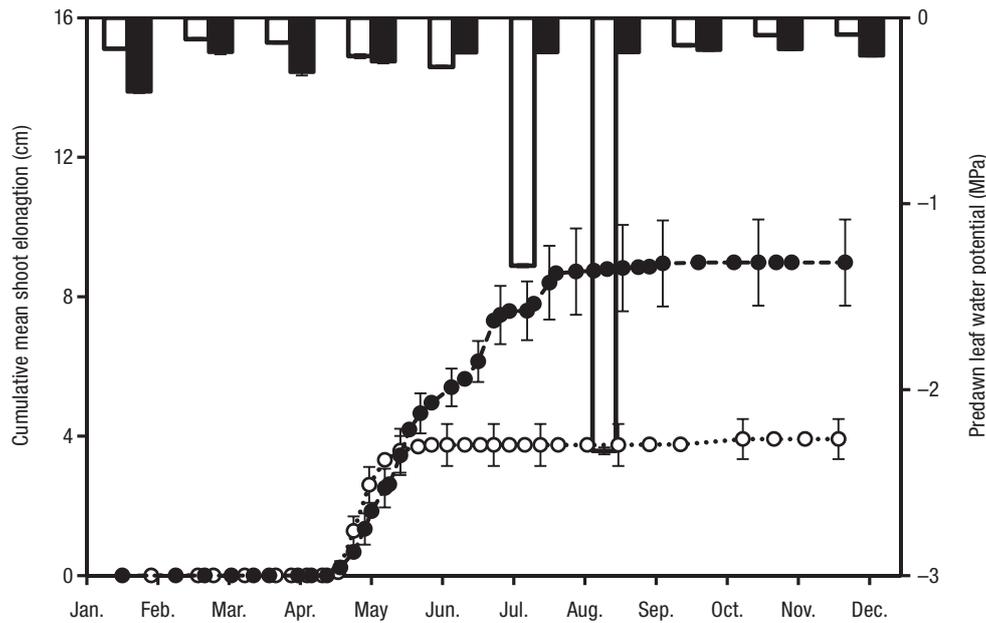
## Tree strategies to withstand drought

Through evolution and natural selection Mediterranean trees have developed structural and physiological attributes to cope with drought (Chaves *et al.*, 2003; Baldocchi & Xu, 2007; Sardans & Peñuelas, 2013). These short- and long-term features aim at maintaining a favourable balance between water lost through leaves (regulating stomatal and hydraulic conductivity, leaf nitrogen/photosynthetic capacity, reducing the size and/or increasing the thickness of leaves, constraining leaf area index by establishing a canopy with low tree density) and water uptaken by roots (maximizing water uptake by tapping deep water sources). These macro-evolutionary features are usually complemented by a high intra-specific genetic variability which also favours drought adaptation (Breda *et al.* 2006; Aranda *et al.*, 2014; Nardini *et al.*, 2014; Ramírez-Valiente *et al.*, 2015).

Based on a hydraulic interpretation of tree functioning and on a large dataset gathered in Portuguese cork oak ecosystems (montados), under different climatic and edaphic conditions (site 1 - central Portugal and site 2 - southern Portugal), we will illustrate some of the drought adaptive strategies of evergreen species to withstand the harsh summer drought. Cork oak (*Quercus suber* L.) is one of the native species to the western Mediterranean Basin, occupying over 1.3 million hectares in the Iberian Peninsula (about 61% of its total area worldwide). Portugal and Spain contribute to about 80% of the world cork production and exports (APCOR, 2014).

Site water availability influences shoot growth as evidenced in Figure 1. When roots access water during the whole year, even during summer, predawn leaf water potential ( $\psi_{l,pd}$ ) remains high throughout the year and shoot growth expands into summer (site 1, black symbols); when trees suffer some degree of summer water stress (drop in predawn leaf water potential), shoot growth ceases at the onset of  $\psi_{l,pd}$  decline (a small drop started by the end of May-June, followed by more pronounced ones in July and August) and cumulative shoot growth is reduced (site 2, white symbols).

When a severe water imbalance occurs (water losses far exceeding water uptake), causing xylem water potential to drop below a critical threshold, a cascade of multiple failures in multiple subsystems (hydraulic failure, carbon starvation, susceptibility to pests and diseases) may occur (McDowell *et al.*, 2008; Anderegg *et al.*, 2012; O’Grady *et al.*, 2013; Zeppel *et al.*, 2013; Millar & Stephenson, 2015), ultimately resulting in tree death. Hydraulic failure (increase of embolised xylem conduits that fail to transport water to tree crowns) is considered the main cause of plant



**Figure 1.** *Q. suber* cumulative shoot elongation (circles) at two sites with different water availability in Portugal (predawn leaf water potentials, bars): site 1, no summer stress (black symbols); site 2, stress in summer (white symbols). Error bars are standard errors. (Adapted from Pinto *et al.*, 2011).

mortality (Urli *et al.*, 2013). When hotter temperatures combine with drought, the risk of tree mortality increases (Allen *et al.*, 2015).

## Control of water losses

### *Stomatal closure*

Among the short-term responses to control water losses, stomatal regulation of leaf gas exchange plays a key role. Stomata adjust their aperture in response to multiple environmental factors, modulating transpiration and consequently determining the rate of soil water depletion (Damour *et al.*, 2010). Multiple signal transduction mechanisms are involved and substantial interaction exists among the signalling pathways (Buckley & Mott, 2013). Hydraulic and biochemical signals are involved in stomatal control (Tardieu *et al.*, 2010; Torres-Ruiz *et al.*, 2015). Yet, the integrated understanding of stomatal control is still poor (Brodribb & McAdam, 2011), and therefore modelling approaches remain fragmental (Damour *et al.*, 2010; Tombesi *et al.*, 2015). The hydraulic theory states that under water deficit (decrease in soil water potential or increase in atmospheric demand) stomata close to prevent the formation of xylem embolisms (Damour *et al.*, 2010). Stomata can then be viewed as pressure regulators, buffering the drop of xylem water potential and the consequent risk of massive xylem embolism and catastrophic hydraulic failure (Tombesi *et al.*, 2015).

In isohydric species (most Mediterranean trees), stomata closure maintains leaf water potentials at a safe constant daily minimum level during drought (Damour *et al.*, 2010). This is exemplified in Table 1 for *Q. suber* (site 2, southern Portugal). At the same site, daily maximum canopy conductance ( $g_{c,max}$ , dependent on stomatal conductance and leaf area index) significantly decreased in summer (Table 1). Despite the seasonal variation in water availability, stomata closure maintained midday leaf water potential ( $\psi_{l,md}$ ) at a constant minimum around -3 MPa under high evaporative demand (vapour pressure deficit,  $VPD$ , above 1500 Pa), irrespective of seasons or years (Table 1).

The above mentioned interpretation of stomatal closure is based on the assumption that stomatal behaviour is solely determined by hydraulic signals, which is obviously simplistic. However, this approach seems to conform to stomatal behaviour under field conditions (Bond & Kavanagh, 1999). Some authors argue that hydraulic signals are the main effector of stomatal response (Brodribb & Cochard, 2009).

Following this hydraulically-based framework of tree functioning, transpiration ( $E$ ) can be modelled by the Darcy Law (Wullschleger *et al.*, 1998; Sperry, 2000):

$$E = k (\psi_s - \psi_l) \quad [1]$$

where  $k$  is the hydraulic conductance in the root-leaf pathway,  $\psi_s$  is the water potential in soil/subsoil near the roots (assumed equal to  $\psi_{l,pd}$ ), and  $\psi_l$  is the leaf

**Table 1.** Average values (2 years; for days with  $VPD$  greater than 1500 Pa) of maximum daily canopy conductance ( $g_{c,max}$ ) and leaf water potential at predawn ( $\psi_{l,pd}$ , usually considered a surrogate of soil/subsoil water potential near roots) and midday ( $\psi_{l,md}$ ), for spring and summer (*Q. suber*, site 2). (Adapted from David *et al.*, 2007). Values between brackets are standard errors.

	$g_{c,max}$ (mm s <sup>-1</sup> )	Leaf Water Potential (MPa)	
		Predawn ( $\psi_{l,pd}$ )	Midday ( $\psi_{l,md}$ )
Spring	5.244 (±0.156)	-0.16 (±0.05)	-2.85 (±0.12)
Summer	1.086 (±0.067)	-1.75 (±0.57)	-2.80 (±0.13)

water potential. This approach views the ascending water flow in trees, during transpiration, as driven by the difference in water potential between leaves and soil/subsoil near the roots ( $\psi_s - \psi_l$ ). According to equation (1), the minimum constant  $\psi_l$  imposed by stomata closure during drought ( $\psi_{l,md}$ ) determines the maximum plateau for transpiration ( $E_{max}$ ). This plateau also depends on  $\psi_s$  ( $\approx \psi_{l,pd}$ ) and  $k$  (decreases in  $\psi_l$  and  $\psi_s$  can also reduce hydraulic conductance when some degree of xylem embolism occurs). As soil/subsoil dries out in summer,  $\psi_{l,pd}$  decreases (Table 1) and so  $E_{max}$  plateau (Figure 2) due to a smaller difference in water potential. This is clearly shown for the same *Q. suber* trees referred above (Figure 2).

Similar patterns of  $E_{max}$  decrease during prolonged drought have been reported for many other species and

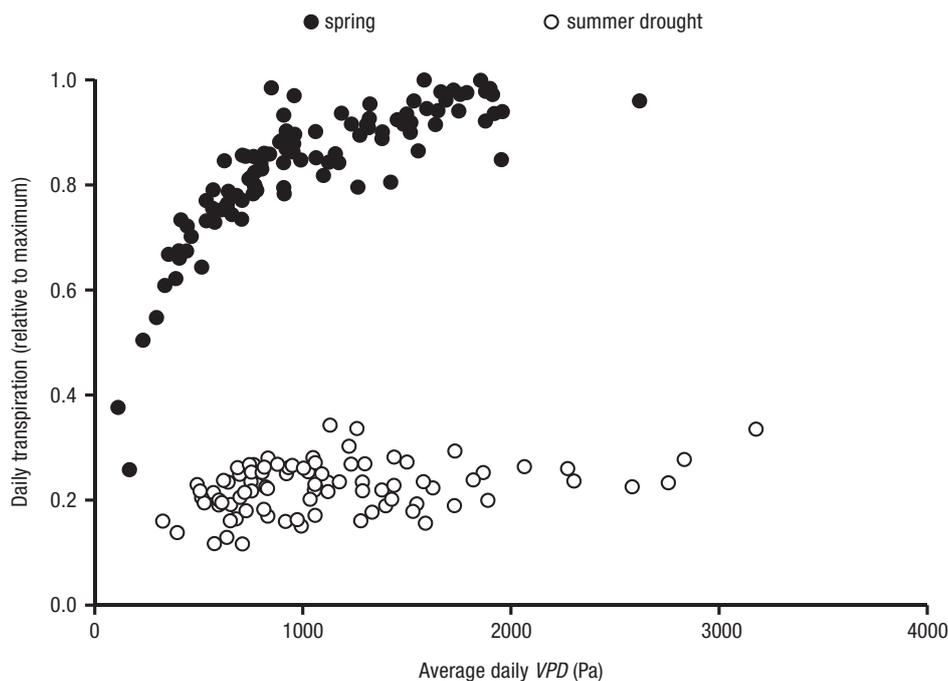
sites in the Mediterranean region (e.g., Infante *et al.* (1997) for *Q. ilex* near Seville, Spain).

Manzoni *et al.* (2013) predicted maximum transpiration plateaus ( $E_{max}$ ) with a reasonably accuracy ( $R = 0.88$ ) for different species, functional types, plant sizes and climates through a hydraulically based model.

### Leaf shedding

In addition to stomatal control, the decrease in the transpiring leaf area is also an effective drought adjustment in Mediterranean species (Limousin *et al.*, 2012). In a strictly hydraulic point of view, short-term leaf shedding may be regarded as a mechanism to further reduce transpiration when stomata fail to regulate  $\psi_l$ . Under severe water stress embolism is liable to occur, starting preferentially in the more vulnerable xylem of leaf shoots and small roots. These organs act as hydraulic fuses (safety valves), localizing failure to relatively cheap and replaceable organs, preventing disruption in the major conduits of the axial transport and diminishing the risks of hydraulic rupture (Jackson *et al.*, 2000; Zufferey *et al.*, 2011; Bucci *et al.*, 2003). Experimental results obtained by Vilagrosa *et al.* (2003) for seedlings of *Pistacia lentiscus* and *Quercus coccifera* seem to support this functional hydraulic trait.

Although this interpretation is simple and appella-tive, care must be taken since the mechanisms underlying leaf area adjustment are not yet fully understood



**Figure 2.** Variation on the maximum plateau of daily transpiration (heat dissipation sap flow method) between spring and summer for *Q. suber* at site 2 (southern Portugal).

(Limousin *et al.*, 2012). These authors have found that leaf area index declined rapidly in a *Quercus ilex* plot subjected to artificial throughfall exclusion (19% in relation to a control plot, after 7 years of treatment). Kurz-Besson *et al.* (2014) also observed a reduction in leaf area in *Q. suber* trees in response to the extreme drought of 2005 (leaf area dropped by 10.4% in an ambient treatment plot and 14.7% in a dry treatment plot subjected to 20% rainfall-exclusion).

## Maximizing water uptake

### Root systems/ Water sources

In addition to reducing water losses through leaves, trees adapted to drought invest in extensive and deep root systems. The first work to clearly unravel this strategy of increasing biomass allocation to below-ground tissues, as the environment becomes more severe, was that of Canadell *et al.* (1996). Maximum rooting depth was found to increase in arid environments and in environments with a long dry season. Mean maximum rooting depth of sclerophyllous Mediterranean trees (including mainly *Eucalyptus* spp. and *Quercus* spp.) was about 12.6 m (Canadell *et al.*, 1996). Deep rooting habit has also been reported for *Pinus pinea*, whose roots were damaging the Jewish catacombs of Villa Torlonia (Rome) at a depth of 8-10 m below soil surface (Caneva *et al.*, 2009). The evolutionary trait of evergreen Mediterranean oaks to preferentially allocate growth to root biomass is clear from the early stages of acorn germination, as illustrated in Figure 3 for *Quercus suber* seedlings from natural regeneration. After germination acorns quickly develop a strong taproot to facilitate access to water and permit seedlings to allocate reserves (Pausas *et al.*, 2009).



**Figure 3.** Root development in *Quercus suber* seedlings from natural regeneration.

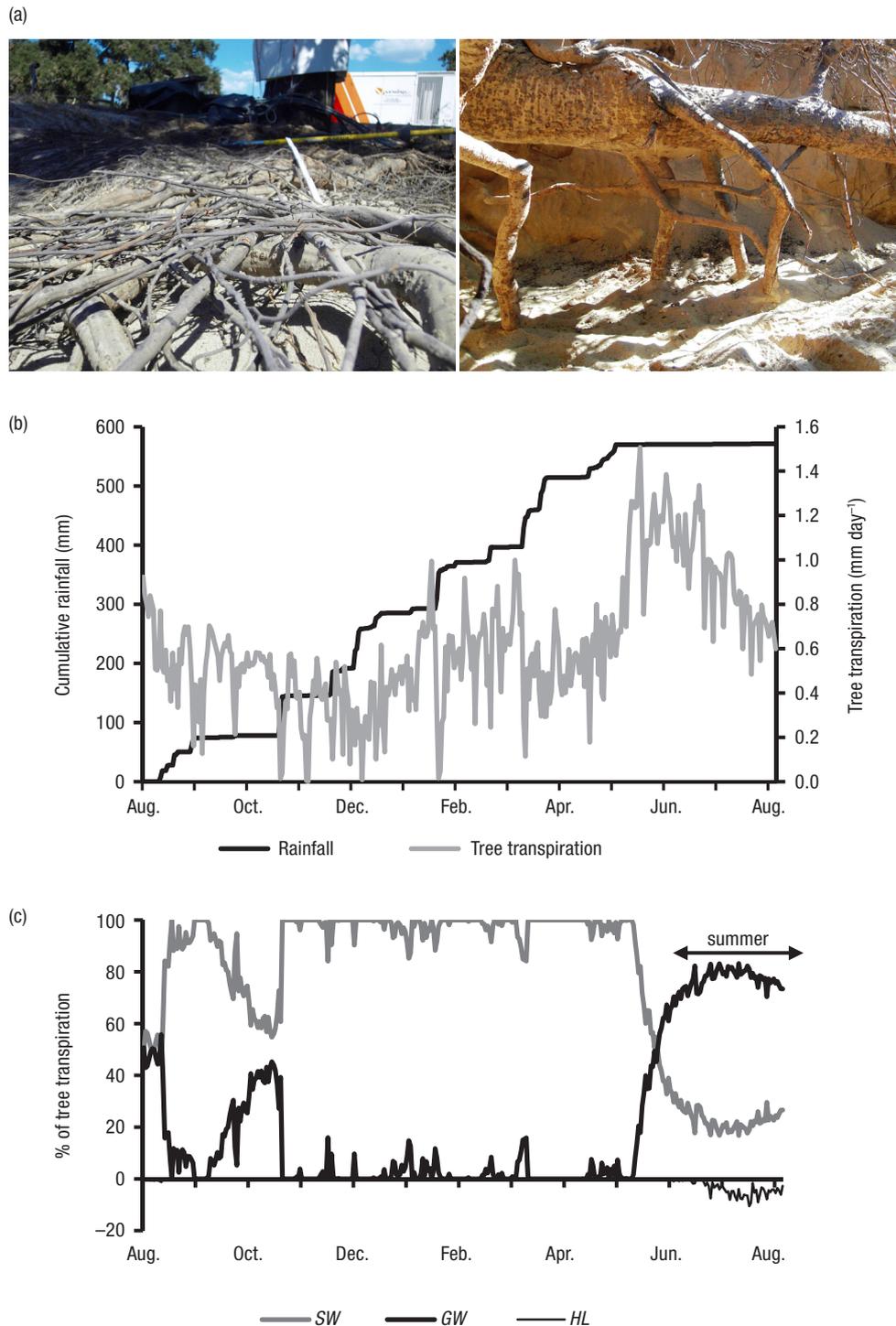
Deep rooting allows trees to maximize water uptake, exploring larger and deeper water reservoirs. This strategy is particularly important for evergreen trees that must survive a dry season. Several studies confirmed that Mediterranean oaks (*Quercus suber* and *Quercus ilex* in the Iberian Peninsula and *Quercus douglasii* in California) use this deep rooting strategy to tap water from groundwater reservoirs, whenever the superficial soil is dry and the water table is within the reach of the deep roots (David *et al.*, 2004, 2007, 2013; Lubczynski & Gurwin, 2005; Miller *et al.*, 2010; Barbeta *et al.*, 2015). This drought avoidance trait has also been observed in Australia (Zencich *et al.*, 2002; O'Grady *et al.*, 2006), South Africa (Le Maitre *et al.*, 1999), China (Yin *et al.*, 2015) and even in temperate forests during occasional droughts (Dolman, 1988). In these studies the evidence of groundwater uptake by tree roots was supported by different measuring techniques: lysimeters, sap flow measurements in stems and roots, stable isotopes and groundwater fluctuations. Since the soils in the Mediterranean region are frequently shallow and with low water retention capacity, the access of roots to groundwater (larger and more efficient water reservoir for inter-seasonal and inter-annual rainfall transference) may be critical for tree survival and growth.

Figure 4 shows the dimorphic root system of *Q. suber* trees at site 1 (dense network of superficial roots connected to sinker roots, Figure 4a), which enabled the access to different water sources in space and time, preventing summer water stress and maintaining tree growth (Figure 4b, Figure 1). During most of the year trees used soil water (when available), but relied on groundwater uptake through sinker roots when top soil dried out in summer (Figure 4c). The same pattern of tree water use was observed by Dolman (1988) in Netherlands and Gou & Miller (2014) in California. During the dry summer period, tree roots also performed night-time hydraulic lift (HL, passive movement of water through roots from groundwater to the top soil, in response to the difference in water potential between the two water storages, which is much lower in the dry top soil) (Nadezhkina *et al.*, 2010; Prieto *et al.*, 2012). The amount of water hydraulically lifted was small (Figure 4c) but ecologically important to mobilise the nutrients stored in the top soil, incorporating them in the transpiration flux of the following day. HL may also allow the maintenance of plant-plant interactions by providing water to the understorey vegetation (facilitation mechanism), as observed in a Mediterranean ecosystem (Peñuelas & Fillela, 2003).

When the soil is shallow, and roots only access soil water, severe water stress is liable to develop during

a single/short drought event. The access of roots to groundwater may have an efficient buffering effect on the impact of drought on trees (Gou & Miller, 2014). It is important to be aware that root access to groundwater does not depend solely on tree species but also on water table depth, nature of the underlying

rock (fractured rocks facilitate the penetration of deep roots (David *et al.*, 2004, 2007)), and on the spatial homogeneity/heterogeneity of these features. This may be one of the possible causes of the frequent patchy nature of drought-induced tree mortality (Barbeta *et al.*, 2015).



**Figure 4.** (a) Dimorphic structure of *Q. suber* root system at site 1 (central Portugal); (b) cumulative rainfall and daily tree transpiration; (c) relative daily contribution of soil water (*SW*), groundwater (*GW*) and hydraulic lift (*HL*) to tree transpiration (heat dissipation and heat field deformation sap flow methods). (Adapted from David *et al.*, 2013).

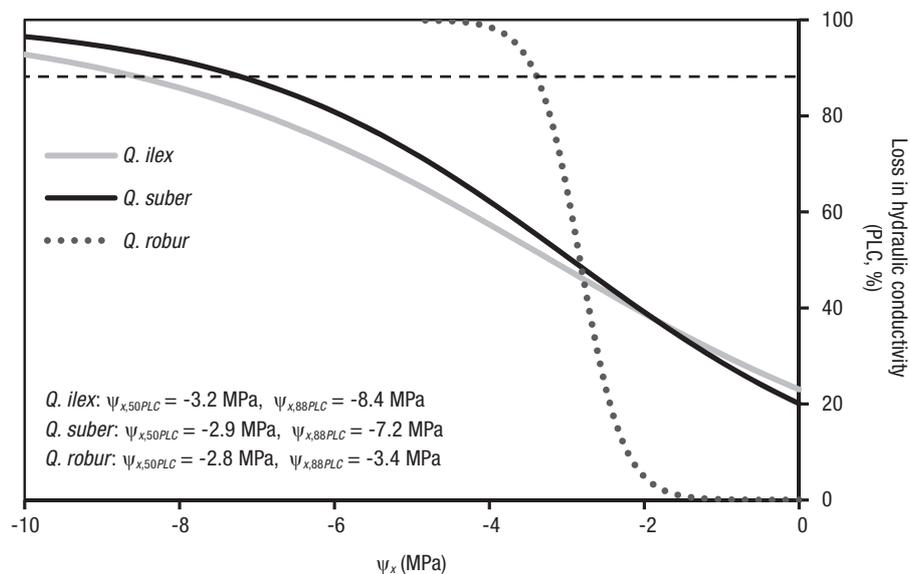
## Xylem vulnerability to drought-induced embolism

Under severe drought, major drops in xylem water potential (low negative pressures) may induce the formation of embolisms (sucked/trapped air) in the xylem conduits, reducing their water transport capacity (xylem conductance). As a consequence, water supply to leaves, photosynthesis and tree growth are reduced. In extreme situations, below a species-specific water potential threshold, catastrophic/generalised embolism may eventually lead to tree death (Choat *et al.*, 2012; Wheeler *et al.*, 2013).

Mortality risk triggered by drought-induced embolism can be assessed by vulnerability curves (VCs), plotting the percentage loss of hydraulic conductivity (PLC) versus xylem water potential ( $\psi_x$ ). The most common indexes to express embolism resistance are  $\psi_{x,50PLC}$  and  $\psi_{x,88PLC}$ , i.e., the xylem pressures inducing 50% and 88% loss of hydraulic conductivity. When  $\psi_x$  falls below these embolism thresholds, accelerated, non-recoverable embolism is liable to occur, leading to long-term reductions in productivity, tissue damage, and ultimately death (Choat *et al.*, 2012; Urli *et al.*, 2013). Brodrribb *et al.* (2010) and Urli *et al.* (2013) demonstrated that in conifers and angiosperms death occurred when trees experienced PLC losses in stems greater than 50% or 88%, respectively.

Figure 5 shows the vulnerability curves for shoots of two Mediterranean evergreen oaks (*Q. suber* and *Q. ilex*) and one temperate maritime deciduous oak (*Q. robur*).  $\psi_{x,88PLC}$  values of *Q. ilex* and *Q. suber* shoots (non-return embolism threshold for angiosperms) are more negative than those of the temperate maritime oak (Urli *et al.*, 2013). The more negative values of  $\psi_{x,88PLC}$ , together with the lower VC slopes estimated for *Q. suber* and *Q. ilex*, reflect their higher tolerance to drought-induced embolism (Tyree & Cochard, 1996; Domec & Gartner, 2001; Urli *et al.*, 2013).

The ability of trees to survive and recover from periods of drought, related to xylem resistance to embolism, is largely determined by xylem structure (Jansen *et al.*, 2009; Choat *et al.*, 2012; Brodrribb *et al.*, 2014). A more tolerant xylem (i.e., less vulnerable to embolism) is usually characterized by smaller inner diameters of xylem conduits, with smaller and lesser inter-conduit connections (Hacke *et al.*, 2006; Jansen *et al.*, 2009; Lens *et al.*, 2011; Martínez-Vilalta *et al.*, 2012). At the tissue level, there is a strong correlation between vulnerability to cavitation and mechanical strength parameters (Lens *et al.*, 2011). Greater wood density (reinforced conduit walls) seems related to the avoidance of vessel implosion under low negative pressures during drought (Hacke *et al.*, 2001; Nardini *et al.*, 2014). However, an intensive debate is still going on about the mechanisms underlying the relationship between drought resistance and xylem anatomy (e.g.



**Figure 5.** Vulnerability curves (VCs) of shoots of two Mediterranean evergreen oaks (*Quercus suber* - full black line and *Q. ilex* - full grey line), and one temperate oak *Q. robur* (dashed grey line). VCs were obtained from mature trees, using the air-dehydration method and fitting an exponential sigmoid equation (Pammenter & Vander Willigen, 1998). Values of  $\psi_{x,50PLC}$  and  $\psi_{x,88PLC}$  for the 3 species are given as inserts. Dashed horizontal line through PLC = 88 % defines the threshold of non-return catastrophic embolism for angiosperms. (Adapted from Cochard *et al.*, 1992; Pinto *et al.*, 2012; Urli *et al.*, 2013).

wood density, wall thickness, vessel size, pit membrane structure, and vessel grouping) (Hajek *et al.*, 2014).

The comparison of the hydraulic safety margins (difference between the minimum xylem water potential experienced in the field and species-specific embolism thresholds) enables the assessment of their risk of mortality under drought (Choat *et al.*, 2012; Delzon & Cochard, 2014). In the two cork oak sites reported above trees seemed well adapted to local water availability, operating with large safety margins above the non-return xylem cavitation threshold: minimum  $\psi_x$  values under field conditions, estimated from  $\psi_{l,pd}$  and  $\psi_{l,md}$ , were 5.45 and 4.68 MPa above  $\psi_{x,88PLC}$ , in sites 1 and 2 respectively (Pinto *et al.*, 2012).

### Intra-specific variation and plasticity in hydraulic traits

As referred, a high intra-specific variability for the aforementioned features also favours drought adaptation. In *Q. suber*, intra-specific variability has been studied on leaf traits related to drought (Ramírez-Valiente *et al.*, 2009; 2011; 2015), but corresponding information on rooting depth and xylem vulnerability to drought-induced embolism is still not available in literature. Ramírez-Valiente *et al.* (2009; 2011; 2015) have shown that leaf traits related to drought tolerance, namely specific leaf area (*SLA*), leaf size and nitrogen leaf content, vary significantly between different populations of *Q. suber*. Their recent work (Ramírez-Valiente *et al.*, 2015) shows that specific maternal *Q. suber* families with low *SLA* have growth benefits in dry years, whereas families with large leaf sizes are favoured in mesic years, highlighting the potential role of intra-population variability for the selection of better adapted genotypes to different weather conditions. These authors also found that *SLA* and leaf size were particularly plastic in *Q. suber* in response to annual rainfall variations, though the adaptive significance of this plasticity could not be confirmed.

### Adaptation measures for managing forests under enhanced drought

Human influences have shaped the structure and composition of Mediterranean woodlands impacting on forest management and land-use practices (Doblas-Miranda *et al.*, 2015). However, some of these practices are no longer adequate and must be adapted to the ongoing environmental changes, particularly in view of water availability regarded as the most limiting factor for survival, productivity and ecosystem diversity (Engelbrecht, 2012). Despite the aforementioned adap-

tive traits of Mediterranean forest trees, climate change might surpass their drought resistance limits in many places (Nardini *et al.*, 2014). Although we cannot alter climate at the local level (it is a global issue), forest management options can help to mitigate some of the negative impacts (Valladares *et al.*, 2014).

Adaptation measures should rely on the evaluation of the risks that Mediterranean forests are/will face, through improved drought monitoring, early warning systems, and mapping of areas representing different levels of risk. Also, water use priorities (water requirements for people and for the environment) need to be set in order to manage and use water in a sustainable way (Iglesias & Garrote, 2015). Forest management measures should be tailored to site-specific conditions, namely preventing damages to the evolutionary tools that Mediterranean trees have developed to survive drought. They should also be preferentially directed to situations where the greatest positive effects are expected (Millar & Stephenson, 2015).

### Examples of some of the possible approaches to better adapt forest management to water scarcity

To start with, the mapping of zones with distinct water availability to trees is critical to frame any locally adapted management strategy (Orellana *et al.*, 2012). The spatial evaluation of water availability can be based on several variables and parameters, such as annual and seasonal rainfall and future foreseen changes (estimated by global climatological models), soil water storage capacity and soil water dynamics, and hydrogeology (water capacity and dynamics of the groundwater storage, and identification of areas of potential access of roots to the water table). While data for climatic and edaphic mapping can be obtained easily in most cases, information on groundwater is uncommon. For this particular purpose, both spatial surveys and modelling are important. Several models are available to estimate the dynamics of groundwater use by tree transpiration (Gou & Miller, 2014; Orellana *et al.*, 2014; Pinto *et al.*, 2014). The large-scale mapping of zones where roots might have or not access to groundwater (groundwater dependent ecosystems) has been most frequently done indirectly, through remote sensing techniques coupled with geographic information systems (Howard & Merrifield, 2010; Gou *et al.*, 2015; Yin *et al.*, 2015). However, these two technological tools are not yet widely applicable and require further development and validation.

As described above, one of the evolutionary traits that trees have developed to cope with drought, not

only under Mediterranean climate but also in semi-arid regions, is deep and extensive rooting. Management practices should not damage or destroy roots to prevent decoupling trees from water and nutrient sources. This is particularly relevant in evergreen oaks in dehesas and montados, where a low density tree stratum coexists with pasture or crops in the open spaces. Ploughing, which has a damaging effect on tree root systems (superficial roots are connected to sinkers, see Figure 4), should be avoided as well as soil compaction promoted by heavy machinery or livestock overpressure (Hillel, 1982; Nadezhdina *et al.*, 2012; David *et al.*, 2013). Ploughing activities and livestock browsing have also been found to affect negatively cork oak natural regeneration (Pausas *et al.*, 2009; Arosa *et al.*, 2015), and may contribute to the spread of diseases and modify the physical properties of soils (Bugalho *et al.*, 2009). Therefore, minimum tillage techniques are recommended (David *et al.*, 2013). Furthermore, soil conservation practices capable of improving soil surface infiltration and of maintaining high soil water holding capacities are of paramount relevance, particularly in the Mediterranean agroforestry systems where soils are usually shallow and poor in organic matter (Grant *et al.*, 2013). Mulching using debris can also be used to improve soil conditions and reduce soil evaporation (Grant *et al.*, 2013; Jiménez *et al.*, 2016), particularly in agroforestry systems.

Another drought adaptation trait is the reduction of the transpiring area (leaf area and low tree density). Forests from southern Europe tend to be sparser than those from northern Europe. In the Mediterranean region, forest intensification due to land abandonment has increased the competition for water and therefore the likelihood of drought-induced forest die-off (Doblas-Miranda *et al.*, 2015). Several authors report evidence that forest thinning can mitigate the drought effects on forest growth and tree mortality (Gracia *et al.*, 1999; Linares *et al.*, 2010; Giuggiola *et al.*, 2013; Grant *et al.*, 2013; Kerhoulas *et al.*, 2013). Competition between trees may amplify the climatic-driven drought stress and further predispose forests to decline (Linares *et al.*, 2010). Therefore, tree density should be well balanced with the local water availability, considering the water storages that may supply roots (unsaturated/saturated soil/groundwater). However, stand density reductions can, in some cases, adversely affect the soil macro-detritivore assemblages and soil functioning (Henneron *et al.*, 2015). Further experimentation and research is needed on this issue. Shrub encroachment can also contribute to enhance competition for water, particularly in extremely dry years (Caldeira *et al.*, 2015).

Since water is the main limiting factor for tree growth, irrigation has frequently been considered a possible solution to promote plant productivity in the Mediterranean region. Irrigation has been traditionally used for agricultural crops. Intensively managed olive orchards expanded in the last two decades increasing the development of irrigation strategies balancing water saving, tree vigour and olive oil production (Fernandez *et al.*, 2013; Girón *et al.*, 2015). In the case of forests, there is experimental evidence of increased stem diameter growth in response to irrigation (Mayor & Rodà, 1994), particularly when groundwater is not within the reach of roots (Kurz-Besson *et al.*, 2014). However, irrigation has not been used in an extensive manner in forests. Yet, it seems appealing for tree species that supply raw material to highly competitive industrial uses. In Portugal, such examples are *Eucalyptus globulus*, that supplies the pulp and paper industry, and *Quercus suber* that supplies the industrial production of bottle wine stoppers. However, irrigation impacts on product quality and on ecological and economical sustainability are still missing in international literature. Irrigation might change the paradigm on how some Mediterranean forests (and species) are viewed, particularly in the case of cork oak. These will be intensive forest plantations, grown in very specific places within the existing irrigation project areas or in their vicinity. Research, experimentation, technological development/adaptation, and legislation adaptations will be required, in the case of a successful pursue of this trend.

Tree populations contain substantial genetic variability in tolerance to drought and heat stress, which maximizes their potential to withstand and adapt to biotic and abiotic stresses (Aranda *et al.*, 2014; Allen *et al.*, 2015; Doblas-Miranda *et al.*, 2015). Therefore, genetic breeding and phenotypic selection may be extremely useful in providing more resilience to drought (Allen *et al.*, 2015). However the study of the genetic intra-specific features with functional implications on drought tolerance is complex and results will be lagged in time, particularly in slow growing trees (Allen *et al.*, 2015; Aranda *et al.*, 2015). Given the underlying complexities it seems needed to intensify cross-disciplinary research among different disciplines such as genetics, genomics, and functional ecophysiology (Doblas-Miranda *et al.*, 2015). The maintenance of high genetic diversity within natural populations is also important to maximize their potential to withstand disturbances (Doblas-Miranda *et al.*, 2015). However, it is still an unresolved question whether the existing genetic variability is sufficient to compensate for the fast and large predicted changes in drought and heat in many locations (Nardini *et al.*, 2014; Allen *et al.*, 2015).

## Managing water resources in the Mediterranean hot climate zone: a competing dilemma

In the previous sections we have analysed the “water and forest” issue mainly in the perspective of sustaining the productivity and resilience of forest ecosystems. We will now frame it in the broader perspective of water resources management. In fact, the limited water resources in the Mediterranean hot climate zone are not only a constraint for biomass production, but also for other water-dependent human activities such as urban supply, industry and irrigated agriculture. The primary space scale to look at these water issues is the catchment. According to the simplified annual catchment water balance (Hewlett, 1982), part of the rain that falls in the catchment area is evaporated to the atmosphere and the remainder flows out of the catchment through the channel streamline. As referred, the water used through transpiration (the largest component of evapotranspiration in Mediterranean hot climate forests (Paço *et al.*, 2009)) is not a loss since it is the “cost” of photosynthesis: higher transpiration means higher carbon sequestration and higher biomass production. Due to the usually negative balance between the annual atmospheric evaporative demand and rainfall in the Mediterranean hot climate zone, annual streamflow is low and can decline to zero in dryer areas and/or during dryer years (David *et al.*, 1994). Streamflow is mostly generated in the wet season (autumn/winter) when the water balance is temporarily positive. Although small, catchment streamflow plays a paramount role in the downstream supply to urban populations, industry and irrigated agriculture. Vegetation cover (species and density) in the catchment area may affect the amount of streamflow through its action on evapotranspiration (Bosh & Hewlett, 1982; Zhang *et al.*, 2001). If we aim to maximize the biomass production in the catchment ecosystem, transpiration will increase resulting in a lower downstream flow. For example, a poplar plantation on a Mediterranean catchment (Santa Coloma River, NE Spain) where tree roots accessed the water table was estimated to reduce summer streamflow by about 46% (Folch & Ferrer, 2015). Conversely, a water table drawdown caused by groundwater pumping caused a decline in leaf water potential followed by leaf mortality and branch die-back in a groundwater-dependent *Populus deltoids* stand in Denver, Colorado, USA (Cooper *et al.*, 2003). These examples typify some of the conflicts that might arise in water limited regions (such as the Mediterranean) between the maintenance of ecosystems and other anthropogenic water demanding activities.

The definition of priorities for water use under these competing conditions is complex and may be controversial. For instance, and in contrast to the widely held view that forest management should emphasize the provision of water for downstream uses, Grant *et al.* (2013) argue that the maintenance of forest health might be a priority in the context of a changing climate, even if at some expense to downstream water supply.

However, under extreme hot droughts, all the components of the catchment water balance are liable to be affected, impacting on both ecosystems and anthropogenic activities. In fact, the unprecedented, prolonged hot drought that California is facing - four consecutive years of water shortfall and high temperatures, lead to massive groundwater overdraft, decline in unique ecological ecosystems, cutbacks to farmers, reductions in hydroelectricity generation, and a range of voluntary and mandatory urban water restrictions (Cook *et al.*, 2015; Mann & Gleick, 2015).

Water resources planning options should be ultimately determined by the objectives considered as the most relevant, and decision-making should always be based on a good scientific perception about the conflicts and trade-offs that are involved. Under the present circumstances, a close cooperation between forest and water managers seems clearly a must in the Mediterranean region.

## References

- Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH *et al.*, 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecol Manag* 259: 660-684. <http://dx.doi.org/10.1016/j.foreco.2009.09.001>
- Allen CD, Breshears DD, McDowell NG, 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6(8): art129. <http://dx.doi.org/10.1890/ES15-00203.1>
- Anderegg WRL, Berry JA, Field CB, 2012. Linking definitions, mechanisms, and modeling of drought-induced tree death. *Trends Plant Sci* 17: 693-700. <http://dx.doi.org/10.1016/j.tplants.2012.09.006>
- APCOR, 2014. Anuário da APCOR 2014. Santa Maria de Lamas, Santa Maria da Feira, Portugal. 78 pp.
- Aranda I, Ramirez-Valiente JA, Rodríguez-Calcerrada J, 2014. Functional features in the response to drought by *Quercus* species: inter- and intra-specific variation. *Ecosistemas* 23(2): 27-36.
- Arosa ML, Ceia RS, Costa SR, Freitas H, 2015. Factors affecting cork oak (*Quercus suber*) regeneration: acorn sowing success and seedling survival under field conditions. *Plant Ecol Divers* 8 (4): 519-528. <http://dx.doi.org/10.1080/17550874.2015.1051154>

- Baldocchi DD, Xu L, 2007. What limits evapotranspiration from Mediterranean oak woodlands-The supply of moisture in the soil, physiological control by plants or the demand by the atmosphere? *Adv Water Resour* 30: 2113-2122. <http://dx.doi.org/10.1016/j.advwatres.2006.06.013>
- Barbeta A, Mejía-Chang M, Ogaya R, Voltas J, Dawson TE, Peñuelas J, 2015. The combined effects of a long-term experimental drought and an extreme drought on the use of plant-water sources in a Mediterranean forest. *Global Chang Biol* 21: 1213-1225. <http://dx.doi.org/10.1111/gcb.12785>
- Bond BJ, Kavanagh KL, 1999. Stomatal behaviour of four woody species in relation to leaf-specific hydraulic conductance and threshold water potential. *Tree Physiol* 19: 503-510. <http://dx.doi.org/10.1093/treephys/19.8.503>
- Børja I, Světlík J, Nadezhdin V, Čermák J, Rosner S, Nadezhdina N, 2013. Sap flow dynamics as a diagnostic tool in Norway spruce. *Acta Hort* 991: 31-36. <http://dx.doi.org/10.17660/ActaHortic.2013.991.3>
- Bosch JM, Hewllett JD, 1982. A review of catchment experiments to determine the effect of vegetation changes on water yield and evapotranspiration. *J Hydrol* 55: 3-23. [http://dx.doi.org/10.1016/0022-1694\(82\)90117-2](http://dx.doi.org/10.1016/0022-1694(82)90117-2)
- Breda N, Huc R, Granier A, Dreyer E, 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Ann For Sci* 63, 625-644. <http://dx.doi.org/10.1051/forest:2006042>
- Brodribb TJ, Cochard H, 2009. Hydraulic failure defines the recovery and point of death in water-stressed conifers. *Plant Physiol* 149: 575-584. <http://dx.doi.org/10.1104/pp.108.129783>
- Brodribb TJ, McAdam SAM, 2011. Stomatal (mis)behaviour. *Tree Physiol* 31(10): 1039-1040. <http://dx.doi.org/10.1093/treephys/tpr100>
- Brodribb TJ, Bowman DMJS, Nichols S, Delzon S, Burrell R, 2010. Xylem function and growth rate interact to determine recovery rates after exposure to extreme water deficit. *New Phytol* 188: 533-542. <http://dx.doi.org/10.1111/j.1469-8137.2010.03393.x>
- Brodribb TJ, McAdam SAM, Jordan GJ, Martins SCV, 2014. Conifer species adapt to low-rainfall climates by following one of two divergent pathways. *Proc Natl Acad Sci USA* 111: 14489-14493. <http://dx.doi.org/10.1073/pnas.1407930111>
- Bucci SJ, Scholtz FG, Goldstein G, Meinzer FC, Sternberg L, 2003. Dynamic changes in hydraulic conductivity in petioles of two savanna tree species: factors and mechanisms contributing to the refilling of embolized vessels. *Plant Cell Environ* 26: 1633-1645. <http://dx.doi.org/10.1046/j.0140-7791.2003.01082.x>
- Buckley TN, Mott KA, 2013. Modelling stomatal conductance in response to environmental factors. *Plant Cell Environ* 36: 1691-1699. <http://dx.doi.org/10.1111/pce.12140>
- Bugalho MN, Plieninger T, Aronson J, Ellatifi M, Crespo DG, 2009. Open woodlands: a diversity of uses (and overuses). In: *Cork Oak Woodlands on the Edge: Ecology, Biogeography, and Restoration of an Ancient Mediterranean Ecosystem*; Aronson J, Pereira JS, Pausas JG (eds). pp: 33-45. Island Press, Washington DC, USA.
- Caldeira MC, Lecomte X, David TS, Pinto JG, Bugalho MN, Werner C, 2015. Synergy of extreme drought and shrub invasion reduce ecosystem functioning and resilience in water-limited climates. *Scientific Reports* 5. <http://www.nature.com/articles/srep15110>
- Canadell J, Jackson RB, Ehleringer JR, Mooney HA, Sala OE, Schulze ED, 1996. Maximum rooting depth of vegetation types at the global scale. *Oecologia* 108: 583-595. <http://dx.doi.org/10.1007/BF00329030>
- Caneva G, Galotta G, Cancellieri L, Savo V, 2009. Tree roots and damages in the Jewish catacombs of Villa Torlonia (Roma). *J Cult Herit* 10: 53-62. <http://dx.doi.org/10.1016/j.culher.2008.04.005>
- Chaves MM, Maroco JP, Pereira JS, 2003. Understanding plant responses to drought—from genes to the whole plant. *Funct Plant Biol* 30: 239-264. <http://dx.doi.org/10.1071/FP02076>
- Chaves MM, Flexas J, Pinheiro C, 2009. Photosynthesis under drought and salt stress: regulation mechanisms from whole plant to cell. *Ann Bot* 103: 551-560. <http://dx.doi.org/10.1093/aob/mcn125>
- Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R, Bucci SJ, Feild TS, Gleason SM, Hacke UG *et al.*, 2012. Global convergence in the vulnerability of forests to drought. *Nature* 491: 752-755. <http://dx.doi.org/10.1038/nature11688>
- Cochard H, Breda N, Granier A, Aussenac G, 1992. Vulnerability to air embolism of three European oak species (*Quercus petraea* (Matt) Liebl, *Q pubescens* Willd, *Q robur* L). *Ann Sci For* 49(3): 225-233. <http://dx.doi.org/10.1051/forest:19920302>
- Cook BI, Ault TR, Smerdon JE, 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. *Science Advances* 1. <http://advances.sciencemag.org/content/1/1/e1400082>
- Cooper DJ, D'Amico DR, Scott ML, 2003. Physiological and morphological response patterns of *Populus deltoides* to alluvial groundwater pumping. *Environ Manage* 31: 215-226. <http://dx.doi.org/10.1007/s00267-002-2808-2>
- Damour G, SImonneau T, Cochard H, Urban L, 2010. An overview of models of stomatal conductance at the leaf level. *Plant Cell Environ* 33: 1419-1438. <http://dx.doi.org/10.1111/j.1365-3040.2010.02181.x>
- David JS, Henriques MO, David TS, Tomé J, Ledger DC, 1994. Clearcutting effects on streamflow in coppiced *Eucalyptus globulus* stands in Portugal. *J Hydrol* 162: 143-154. [http://dx.doi.org/10.1016/0022-1694\(94\)90008-6](http://dx.doi.org/10.1016/0022-1694(94)90008-6)
- David TS, Ferreira MI, Cohen S, Pereira JS, David JS, 2004. Constraints on transpiration from an evergreen oak tree in southern Portugal. *Agr For Meteorol* 122: 193-205. <http://dx.doi.org/10.1016/j.agrformet.2003.09.014>
- David TS, Henriques MO, Kurz-Besson C, Nunes J, Valente F, Vaz M, Pereira JS, Siegwolf R, Chaves MM, Gazarini LC, David JS, 2007. Water-use strategies in two co-occurring Mediterranean evergreen oaks: surviving the summer drought. *Tree Physiol* 27: 793-803. <http://dx.doi.org/10.1093/treephys/27.6.793>
- David TS, Pinto CA, Nadezhdina N, Kurz-Besson C, Henriques MO, Quilhó T, Cermak J, Chaves MM, Pereira JS,

- David JS, 2013. Root functioning, tree water use and hydraulic redistribution in *Quercus suber* trees: A modeling approach based on root sap flow. *Forest Ecol Manag* 307: 136-146. <http://dx.doi.org/10.1016/j.foreco.2013.07.012>
- Delzon S, Cochard H, 2014. Recent advances in tree hydraulics highlight the ecological significance of the hydraulic safety margin. *New Phytol* 203: 355-358. <http://dx.doi.org/10.1111/nph.12798>
- Di Castri F, 1991. An ecological overview of the five regions with a mediterranean climate. In: *Biogeography of Mediterranean Invasions*; Groves RH, di Castri F (eds). pp: 3-16. Cambridge Univ. Press, Cambridge, UK. <http://dx.doi.org/10.1017/CBO9780511525544.002>
- Doblas-Miranda E, Martínez-Vilalta J, Lloret F, Álvarez A, Ávila A, Bonet FJ, Brotons L, Castro J, Curiel Yuste J, Díaz M, *et al.*, 2015. Reassessing global change research priorities in mediterranean terrestrial ecosystems: how far have we come and where do we go from here? *Glob Ecol Biogeogr* 24(1): 25-43. <http://dx.doi.org/10.1111/geb.12224>
- Dolman AJ, 1988. Transpiration of an oak forest as predicted from porometer and weather data. *J Hydrol* 97: 225-234. [http://dx.doi.org/10.1016/0022-1694\(88\)90117-5](http://dx.doi.org/10.1016/0022-1694(88)90117-5)
- Domec JC, Gartner BL, 2001. Cavitation and water storage capacity in bole xylem segments of mature and young Douglas-fir trees. *Trees-Struct Funct* 15: 204-214. <http://dx.doi.org/10.1007/s004680100095>
- Engelbrecht BMJ, 2012. Forests on the brink. *Nature* 491. <http://www.nature.com/nature/journal/v491/n7426/full/nature11756.html>
- Fernández JE, Perez-Martin A, Torres-Ruiz JM, Cuevas MV, Rodríguez-Domínguez CM, Elsayed-Farag S, Morales-Sillero A, García JM, Hernández-Santana V, Díaz-Espejo A, 2013. A regulated deficit irrigation strategy for hedgerow olive orchards with high plant density. *Plant Soil* 372 (1-2): 279-295. <http://dx.doi.org/10.1007/s11104-013-1704-2>
- Folch A, Ferrer N, 2015. The impact of poplar tree plantations for biomass production on the aquifer water budget and base flow in a Mediterranean basin. *Sci Total Environ* 524-525: 213-224. <http://dx.doi.org/10.1016/j.scitotenv.2015.03.123>
- Girón IF, Corell M, Martín-Palomo MJ, Galindo A, Torrecillas A, Moreno F, Moriana A, 2015. Feasibility of trunk diameter fluctuations in the scheduling of regulated deficit irrigation for table olive trees without reference trees. *Agric Water Manage* 161: 114-126. <http://dx.doi.org/10.1016/j.agwat.2015.07.014>
- Giuggiola A, Bugmann H, Zingg A, Dobbertin M, Rigling A, 2013. Reduction of stand density increases drought resistance in xeric Scots pine forests. *Forest Ecol Manag* 310: 827-835. <http://dx.doi.org/10.1016/j.foreco.2013.09.030>
- Gou S, Miller G, 2014. A groundwater-soil-plant-atmosphere continuum approach for modelling water stress, uptake, and hydraulic redistribution in phreatophytic vegetation. *Ecohydrology* 7(3): 1029-1041. <http://dx.doi.org/10.1002/eco.1427>
- Gou S, Gonzales S, Miller GR, 2015. Mapping potential groundwater-dependent ecosystems for sustainable management. *Groundwater* 53(1): 99-110. <http://dx.doi.org/10.1111/gwat.12169>
- Gracia CA, Tello E, Sabaté S, Bellot J, 1999. GOTILWA: an integrated model of water dynamics and forest growth. In: *Ecology of Mediterranean evergreen oak forests*; Roda F, Retana J, Gracia CA, Bellot J (eds). pp: 163-179. Springer-Verlag, Berlin, Germany. [http://dx.doi.org/10.1007/978-3-642-58618-7\\_12](http://dx.doi.org/10.1007/978-3-642-58618-7_12)
- Grant GE, Tague CL, Allen CD, 2013. Watering the forest for the trees: an emerging priority for managing water in forest landscapes. *Front Ecol Environ* 11: 314-321. <http://dx.doi.org/10.1890/120209>
- Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloh KA, 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126: 457-461. <http://dx.doi.org/10.1007/s004420100628>
- Hacke UG, Sperry JS, Wheeler JK, Castro L, 2006. Scaling of angiosperm xylem structure with safety and efficiency. *Tree Physiol* 26: 689-701. <http://dx.doi.org/10.1093/treephys/26.6.689>
- Hajek P, Leuschner C, Hertel D, Delzon S, Schudt B, 2014. Trade-offs between xylem hydraulic properties, wood anatomy and yield in *Populus*. *Tree Physiol* 34: 744-756. <http://dx.doi.org/10.1093/treephys/tpu048>
- Henneron L, Aubert M, Bureau F, Dumas Y, Ningre F, Perret S, Richter C, Balandier P, Chauvat M, 2015. Forest management adaptation to climate change: a Cornelian dilemma between drought resistance and soil macro-detritivore functional diversity. *J Applied Ecol* 52: 913-927. <http://dx.doi.org/10.1111/1365-2664.12440>
- Hewlett JD, 1982. *Principles of Forest Hydrology*. The University of Georgia Press, Athens, Georgia, USA. 183 pp.
- Hillel D, 1982. *Introduction to Soil Physics*. Academic Press: London, UK. 364 pp.
- Howard J, Merrifield M, 2010. Mapping groundwater dependent ecosystems in California. *PLoS ONE* 5 (6). <http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0011249>
- Huxman TE, Wilcox BP, Breshears DD, Scott RL, Snyder KA, Small EE, Hultine K, Pockman WT, Jackson RB, 2005. Ecohydrological implications of woody plant encroachment. *Ecology* 86: 308-319. <http://dx.doi.org/10.1890/03-0583>
- Iglesias A, Garrote L, 2015. Adaptation strategies for agricultural water management under climate change in Europe. *Agric Water Manage* 155: 113-124. <http://dx.doi.org/10.1016/j.agwat.2015.03.014>
- Infante JM, Rambal S, Joffre R, 1997. Modelling transpiration in holm-oak savannah trees: scaling up from the leaf to the canopy. *Agr For Meteorol* 87: 273-289. [http://dx.doi.org/10.1016/S0168-1923\(97\)00033-6](http://dx.doi.org/10.1016/S0168-1923(97)00033-6)
- Jackson RB, Sperry JS, Dawson TE, 2000. Root water uptake and transport: using physiological processes in global predictions. *Trends Plant Sci* 5: 482-488. [http://dx.doi.org/10.1016/S1360-1385\(00\)01766-0](http://dx.doi.org/10.1016/S1360-1385(00)01766-0)
- Jansen S, Choat B, Pletsers A, 2009. Morphological variation of intervessel pit membranes and implications to xylem function in angiosperms. *Am J Bot* 96(2): 409-419. <http://dx.doi.org/10.3732/ajb.0800248>

- Jiménez MN, Fernández-Ondoño E, Ripoll MÁ, Castro-Rodríguez J, Huntsinger L, Navarro FB, 2016. Stones and organic mulches improve the *Quercus ilex* L. afforestation success under Mediterranean climatic conditions. *Land Degrad Develop* 27: 357–365. <http://dx.doi.org/10.1002/ldr.2250>
- Kerhoulas LP, Kolb TE, Hurteau MD, Koch GW, 2013. Managing climate change adaptation in forests: a case study from the U.S. Southwest. *J Applied Ecol* 50: 1311–1320. <http://dx.doi.org/10.1111/1365-2664.12139>
- Kurz-Besson C, Lobo-do-Vale R, Rodrigues ML, Almeida P, Herd A, Grant OM, David TS, Schmidt M, Otieno D, Keenan TF *et al.*, 2014. Cork oak physiological responses to manipulated water availability in a Mediterranean woodland. *Agr For Meteorol* 184: 230–242. <http://dx.doi.org/10.1016/j.agrformet.2013.10.004>
- Larter M, Brodribb TJ, Pfautsch S, Burrell R, Cochard H, Delzon S, 2015. Extreme aridity pushes trees to their physical limits. *Plant Physiol* 168: 804–807. <http://dx.doi.org/10.1104/pp.15.00223>
- Lens F, Sperry JS, Christman MA, Choat B, Rabaey D, Jansen S, 2011. Testing hypotheses that link wood anatomy to cavitation resistance and hydraulic conductivity in the genus *Acer*. *New Phytol* 190(3): 709–723. <http://dx.doi.org/10.1111/j.1469-8137.2010.03518.x>
- Le Maitre DC, Scott DF, Colvin C, 1999. A review of information on interactions between vegetation and groundwater. *Water SA* 25(2): 137–152.
- Limousin JM, Rambal S, Ourcival J-M, Rodríguez-Calcerada J, Pérez-Ramos IM, Rodríguez-Cortina R, Misson L, Joffre R, 2012. Morphological and phenological shoot plasticity in a Mediterranean evergreen oak facing long-term increased drought. *Oecologia* 169: 565–577. <http://dx.doi.org/10.1007/s00442-011-2221-8>
- Linares JC, Camarero JJ, Carreira JA, 2010. Competition modulates the adaptation capacity of forests to climatic stress: insights from recent growth decline and death in relict stands of the Mediterranean fir *Abies pinsapo*. *J Ecol* 98: 592–603. <http://dx.doi.org/10.1111/j.1365-2745.2010.01645.x>
- Lubczynski MW, Gurwin J, 2005. Integration of various data sources for transient groundwater modeling with spatiotemporally variable fluxes - Sardon study case, Spain. *J Hydrol* 306: 71–96. <http://dx.doi.org/10.1016/j.jhydrol.2004.08.038>
- Mann ME, Gleick PH, 2015. Climate change and California drought in the 21st century. *Proc Natl Acad Sci USA* 112(13): 3858–3859. <http://dx.doi.org/10.1073/pnas.1503667112>
- Manzoni S, Vico G, Katul G, Palmroth S, Jackson RB, Porporato A, 2013. Hydraulic limits on maximum plant transpiration and the origin of the safety-efficiency trade-off. *New Phytol* 198: 169–178. <http://dx.doi.org/10.1111/nph.12126>
- Martínez-Vilalta J, Mencuccini M, Alvarez X, Camacho J, Loepfe L, Piñol J, 2012. Spatial distribution and packing of xylem conduits. *Am J Bot* 99: 1189–1196. <http://dx.doi.org/10.3732/ajb.1100384>
- Mayor X, Rodà F, 1994. Effects of irrigation and fertilization on stem diameter growth in a Mediterranean holm oak forest. *Forest Ecol Manag* 68(1): 119–126. [http://dx.doi.org/10.1016/0378-1127\(94\)90143-0](http://dx.doi.org/10.1016/0378-1127(94)90143-0)
- McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams DG, Yezzer EA, 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol* 178: 719–739. <http://dx.doi.org/10.1111/j.1469-8137.2008.02436.x>
- Millar CI, Stephenson NL, 2015. Temperate forest health in an era of emerging megadisturbance. *Science* 349: 823–826. <http://dx.doi.org/10.1126/science.aaa9933>
- Miller GR, Chen X, Rubin Y, Ma S, Baldocchi DD, 2010. Groundwater uptake by woody vegetation in a semiarid oak savanna. *Water Resour Res* 46, W10503 <http://dx.doi.org/10.1029/2009WR008902>
- Nadezhdina N, David TS, David JS, Ferreira MA, Dohnal M, Tesar M, Gartner K, Leitgeb E, Nadezhdin V, Cermak J *et al.*, 2010. Trees never rest: the multiple facets of hydraulic redistribution. *Ecohydrology* 3: 431–444. <http://dx.doi.org/10.1002/eco.148>
- Nadezhdina N, Prax A, Cermak J, Nadezhdin V, Ulrich R, Neruda I, Schlaghamersky A, 2012. Spruce roots under heavy machinery loading in two different soil types. *Forest Ecol Manag* 282: 46–52. <http://dx.doi.org/10.1016/j.foreco.2012.06.054>
- Nardini A, Lo Gullo MA, Trifilo P, Salleo S, 2014. The challenge of the Mediterranean climate to plant hydraulics: responses and adaptations. *Environ Exp Bot* 103: 68–79. <http://dx.doi.org/10.1016/j.envexpbot.2013.09.018>
- O'Grady AP, Cook PG, Howe P, Werren G, 2006. Groundwater use by dominant tree species in tropical remnant vegetation communities. *Aust J Bot* 54(2): 155–171. <http://dx.doi.org/10.1071/BT04179>
- O'Grady AP, Mitchell PJM, Pinkard EA, Tissue DT, 2013. Thirsty roots and hungry leaves: unravelling the roles of carbon and water dynamics in tree mortality. *New Phytol* 200: 294–297. <http://dx.doi.org/10.1111/nph.12451>
- Orellana F, Verma P, Loheide SP, Daly E, 2012. Monitoring and modeling water-vegetation interactions in groundwater-dependent ecosystems. *Rev Geophys* 50, RG3003 <http://dx.doi.org/10.1029/2011RG000383>
- Paço TA, David TS, Henriques MO, Pereira JS, Valente F, Banza J, Pereira FL, Pinto C, David JS, 2009. Evapotranspiration from a Mediterranean evergreen oak savannah: the role of trees and pasture. *J Hydrol* 369: 98–106. <http://dx.doi.org/10.1016/j.jhydrol.2009.02.011>
- Pammenter NW, Vander Willigen C, 1998. A mathematical and statistical analysis of the curves illustrating vulnerability of xylem to cavitation. *Tree Physiol* 18: 589–593. <http://dx.doi.org/10.1093/treephys/18.8-9.589>
- Pausas JG, Marañón T, Caldeira M, Pons J, 2009. Natural Regeneration. In: *Cork Oak Woodlands on the Edge*; Aronson J, Pereira JS, Pausas JG (eds). pp: 115–124. Island Press, Washington DC, USA.
- Peel MC, Finlayson BL, McMahon TA, 2007. Updated world map of the Köppen-Geiger climate classification. *Hydrol Earth Syst Sci* 11: 1633–1644. <http://dx.doi.org/10.5194/hess-11-1633-2007>

- Peñuelas J, Fillela I, 2003. Deuterium labelling of roots provides evidence of deep water access and hydraulic lift by *Pinus nigra* in a Mediterranean forest of NE Spain. *Environ Exp Bot* 49(3): 201-208. [http://dx.doi.org/10.1016/S0098-8472\(02\)00070-9](http://dx.doi.org/10.1016/S0098-8472(02)00070-9)
- Pinto CA, Henriques MO, Figueiredo JP, David JS, Abreu FG, Pereira JS, Correia I, David TS, 2011. Phenology and growth dynamics in Mediterranean evergreen oaks: Effects of environmental conditions and water relations. *Forest Ecol Manag* 262(3): 500-508. <http://dx.doi.org/10.1016/j.foreco.2011.04.018>
- Pinto CA, David JS, Cochard H, Caldeira MC, Henriques MO, Quilhó T, Paço TA, Pereira JS, David TS, 2012. Drought-induced embolism in current-year shoots of two Mediterranean evergreen oaks. *Forest Ecol Manag* 285: 1-10. <http://dx.doi.org/10.1016/j.foreco.2012.08.005>
- Pinto CA, Nadezhkina N, David JS, Kurz-Besson C, Caldeira MC, Henriques MO, Monteiro FG, Pereira JS, David TS, 2014. Transpiration in *Quercus suber* trees under shallow water table conditions: the role of soil and groundwater. *Hydrol Process* 28(25): 6067-6079. <http://dx.doi.org/10.1002/hyp.10097>
- Prieto I, Armas C, Pugnaire FI, 2012. Water release through plant roots: new insights into its consequences at the plant and ecosystem level. *New Phytol* 193(4): 830-841. <http://dx.doi.org/10.1111/j.1469-8137.2011.04039.x>
- Ramírez-Valiente JA, Lorenzo Z, Soto A, Valladares F, Gil L, Aranda I, 2009. Elucidating the role of genetic drift and natural selection in cork oak differentiation regarding drought tolerance. *Mol Ecol* 18: 3803-3815. <http://dx.doi.org/10.1111/j.1365-294X.2009.04317.x>
- Ramírez-Valiente JA, Valladares F, Huertas AD, Granados S, Aranda I, 2011. Factors affecting cork oak growth under dry conditions: local adaptation and contrasting additive genetic variance within populations. *Tree Genet Genomes* 7: 285-295. <http://dx.doi.org/10.1007/s11295-010-0331-9>
- Ramírez-Valiente JA, Valladares F, Delgado A, Nicotra AB, Aranda I, 2015. Understanding the importance of intrapopulation functional variability and phenotypic plasticity in *Quercus suber*. *Tree Genet Genomes* 11: 35. <http://dx.doi.org/10.1007/s11295-015-0856-z>
- Sardans J, Peñuelas J, 2013. Plant-soil interactions in Mediterranean forest and shrublands: impacts of climatic change. *Plant Soil* 365: 1-33. <http://dx.doi.org/10.1007/s11104-013-1591-6>
- Sperry JS, 2000. Hydraulic constraints on plant gas exchange. *Agr Forest Meteorol* 104(1): 13-23. [http://dx.doi.org/10.1016/S0168-1923\(00\)00144-1](http://dx.doi.org/10.1016/S0168-1923(00)00144-1)
- Spinoni J, Vogt J, Naumann G, Carrao H, Barbosa P, 2015. Towards identifying areas at climatological risk of desertification using the Köppen–Geiger classification and FAO aridity index. *Int J Climatol* 35: 2210-2222. <http://dx.doi.org/10.1002/joc.4124>
- Tardieu F, Parent B, Simonneau T, 2010. Control of leaf growth by abscisic acid: hydraulic or non-hydraulic processes? *Plant Cell Environ* 33: 636-647. <http://dx.doi.org/10.1111/j.1365-3040.2009.02091.x>
- Tombesi S, Nardini A, Frioni T, Soccolini M, Zadra C, Farinelli D, Poni S, Palliotti A, 2015. Stomatal closure is induced by hydraulic signals and maintained by ABA in drought-stressed grapevine. *Scientific Reports* 5. <http://www.nature.com/articles/srep12449>
- Torres-Ruiz JM, Diaz-Espejo A, Perez-Martin A, Hernandez-Santana V, 2015. Role of hydraulic and chemical signals in leaves, stems and roots in the stomatal behaviour of olive trees under water stress and recovery conditions. *Tree Physiol* 35(4): 415-424. <http://dx.doi.org/10.1093/treephys/tpu055>
- Tyree MT, Cochard H, 1996. Summer and winter embolism in oak – impact on water relations. *Ann Sci Forest* 53: 173-180. <http://dx.doi.org/10.1051/forest:19960201>
- Urli M, Porté AJ, Cochard H, Guengant Y, Burlett R, Delzon S, 2013. Xylem embolism threshold for catastrophic hydraulic failure in angiosperm trees. *Tree Physiol* 33: 672-683. <http://dx.doi.org/10.1093/treephys/tpt030>
- Valladares F, Benavides R, Rabasa SG, Diaz M, Pausas JG, Paula S, Simonson WD, 2014. Global change and Mediterranean forests: current impacts and potential responses. In: *Forests and Global Change*; Coomes DA, Burslem DFRP, Simonson WD (eds). pp 47-75. Cambridge University Press, UK. <http://dx.doi.org/10.1017/CBO9781107323506.005>
- Vilagrosa A, Bellot J, Vallejo VR, Gil-Pelegrín E, 2003. Cavitation, stomatal conductance, and leaf dieback in seedlings of two co-occurring Mediterranean shrubs during an intense drought. *J Exp Bot* 54(390): 2015-2024. <http://dx.doi.org/10.1093/jxb/erg221>
- Wheeler J, Huggett B, Tofte A, Fulton R, Holbrook NM, 2013. Cutting xylem under tension or supersaturated with gas can generate PLC and the appearance of rapid recovery from embolism. *Plant Cell Environ* 36: 1938-1949. <http://dx.doi.org/10.1111/pce.12139>
- Wullschlegel SD, Meinzer FC, Vertessy RA, 1998. A review of whole-plant water use studies in trees. *Tree Physiol* 18: 499-512. <http://dx.doi.org/10.1093/treephys/18.8-9.499>
- Yin L, Zhou Y, Huang J, Wenninger J, Zhang E, Hou G, Dong J, 2015. Interaction between groundwater and trees in an arid site: Potential impacts of climate variation and groundwater abstraction on trees. *J Hydrol* 528: 435-448. <http://dx.doi.org/10.1016/j.jhydrol.2015.06.063>
- Zencich SJ, Froend R, Turner JV, Gailitis V, 2002. Influence of groundwater depth on the seasonal sources of water accessed by *Banksia* tree species on a shallow, sandy aquifer. *Oecologia* 131: 8-19. <http://dx.doi.org/10.1007/s00442-001-0855-7>
- Zeppel MJB, Anderegg WRL, Adams HD, 2013. Forest mortality due to drought: latest insights, evidence and unresolved questions on physiological pathways and consequences of tree death. *New Phytol* 197: 372-374. <http://dx.doi.org/10.1111/nph.12090>
- Zhang L, Dawes WR, Walker GR, 2001. Response of mean annual evapotranspiration to vegetation changes at catchment scale. *Water Resour Res* 37(3): 701-708. <http://dx.doi.org/10.1029/2000WR900325>
- Zufferey V, Cochard H, Ameglio T, Spring J-L, Viret O, 2011. Diurnal cycles of embolism formation and repair in petioles of grapevine (*Vitis vinifera* cv. Chasselas). *J Exp Bot* 62: 3885-3894. <http://dx.doi.org/10.1093/jxb/err081>