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

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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.

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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; Doblas-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 (Borja 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 uptake 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; Anderigg 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
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 ($g_{c,\text{max}}$, 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 ($\psi_{l,\text{md}}$) 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):

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

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

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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). 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 appellative, care must be taken since the mechanisms underlying leaf area adjustment are not yet fully understood.

### 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 (ψ_{l,pd}, usually considered a surrogate of soil/subsoil water potential near roots) and midday (ψ_{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^{-1}) | Leaf Water Potential (MPa) |
|----------------------|---------------------------|
|                      | Predawn (ψ_{l,pd}) | Midday (ψ_{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 (ψ_{l} - ψ_{s}). According to equation (1), the minimum constant ψ_{l} imposed by stomata closure during drought (ψ_{l,md}) determines the maximum plateau for transpiration (E_{max}). This plateau also depends on ψ_{s} (=ψ_{l,pd}) and k (decreases in ψ_{l} and ψ_{s} can also reduce hydraulic conductance when some degree of xylem embolism occurs). As soil/subsoil dries out in summer, ψ_{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).

![Figure 2](image-url). 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).
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 sinkers 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) (Nadezhdina 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

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 belowground 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.

(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).

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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).
Water and forests in the Mediterranean hot climate zone

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 $\psi_{x,50}$PLC and $\psi_{x,88}$PLC, 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). Brodribb 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 ($Q. robur$). $\psi_{x,50}$PLC 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 $\psi_{x,88}$PLC 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; Brodribb 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](image-url)
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 \( \psi \), values under field conditions, estimated from \( \psi_{l,pd} \) and \( \psi_{l,msr} \), were 5.45 and 4.68 MPa above \( \psi_{\text{ABSLCS}} \) 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 adaptive 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 pursuit 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 & Gleich, 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.

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