Species-specific water use by forest tree species: From the tree to the stand

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ABSTRACT

Forests play a critical role in the hydrological cycle making the study of water use by trees and forest stands of prime importance in the global change context .Very negative effects of increasing and more intense droughts on forest vegetation have been described over the last decades. Symptoms of disease and decline have been associated with changed precipitation patterns in many forests particularly in European temperate and Mediterranean regions. Intra- and inter-specific differences in both physiology and morphology exert a large but not well understood influence on the water balance of forest ecosystems, further affecting their vulnerability to drought. Stand structure and composition influences rainfall interception, runoff and water fluxes of the whole ecosystem. Both expanding plantations of renovated interest for biofuel industry and natural and semi-natural forests must be managed in a sustainable way on the basis of their water consumption. We review the role of key drivers on forest water use such as species composition, tree canopy status of each of them and species specific sensitivity to soil water scarcity. Specifically we discuss the role of these factors for natural forest, but with references also to forest plantations. Water scarcity is expected to be one of the largest societal problems worldwide in the near future, so water use by natural and planted forest ecosystems has become a central subject in current research agendas.

1. Introduction

Forest lands cover wide areas in the world, being one of the main actors in the global hydrological cycle. Trees, the key individual component of forests, have distinct characteristics, such as secondary growth and long lifespan, that differentiate them from other kinds of plants such as annual weeds or crops in terms of water use and must be considered for management purposes. The idiosyncratic characteristics of forest trees impact upon the water economy at the ecosystem level depending on the composition and structure of the particular forest community (Asbjornsen et al., 2011; Dierick and Holscher, 2009).

Water use by trees is controlled basically at the interphase leaf–atmosphere by a strict regulation of leaf stomatal conductance to water vapour. This role of stomatal performance in regulating the flux of water through the soil–plant continuum is common to most plants. Unlike herbaceous species, however, forest tree species must attain not only hydration of aboveground organs, but also functionality of the hydraulic system assuring the continuity of the water column from soil to leaves (Meinzer et al., 2009; Salleo et al., 2000; Tyree and Sperry, 1988). The interplay between stomatal control of water losses and maintenance of function in the hydraulic pathway has important consequences for the development of different strategies. Tree species range in its performance from isohydric to anisohydric strategies depending on whether they prioritize under dry conditions hydraulic safety or gas exchange respectively (Franks et al., 2007; Tardieu and Simonneau, 1998; Kumagai and Porporato, 2012).

However, water use by forest tree species goes beyond the specific differentiation in terms of sensitivity to environmental factors. Forest communities attain a functional and structural complexity that contributes to emergent properties at different scales. Thus, water is not only managed according to the species-specific response to factors such as water in soil and atmosphere or radiation inputs into the forest ecosystem. Dominance and hierarchical position of individual trees in the stand (Martin et al., 1997; Granier et al., 2000), and other elements such as the coupling to atmospheric conditions of the different tree crowns within the functional unity of the canopy, play important roles in the final water budget of the ecosystem (Jarvis and McNaughton, 1986). The proper structure of the stand in terms of stratification on different size and age classes (Martin et al., 1997; Delzon and Loustau, 2005) and

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the origin of individuals (e.g., seed-origin vs. resprouts from coppice), are elements that modulate the amount and type of water used by forests (Asbjornsen et al., 2011).

Forest vegetation has been seen to be quite vulnerable to the negative effects of climate change, particularly in terms of increasing intensity and recurrence of dry periods (IPCC 2007). The negative effect of increasing dry periods will be reinforced by a parallel increase in temperature, further magnifying the effects of drought. Consequences of water stress are especially relevant for broad-leaved temperate species not well adapted to droughts, as was notorious after the heat wave of 2003 that affected wide forest areas in Central Europe (Leuzinger et al., 2005; Bréda et al., 2006; Geßler et al., 2007). The presence of extreme dry periods might be common worldwide in the future, impacting very negatively the sustainability and productivity of forests already threat by drought such as those at the rear edge of their geographical distribution; this has been well documented for some areas of the Mediterranean Basin (Jump et al., 2006; Linares et al., 2010). The capacity of forest trees to cope with dry periods is conditioned by the many factors linked to the species specific use of water (Oren et al., 1999a,b; Martínez-Vilalta et al., 2003; Leuzinger et al., 2005), and to the structure of the forests in terms of size and age classes, and tree density (Granier and Bréda, 1996; Granier et al., 2000; Moreno and Cubera, 2008). All these factors can be controlled and considered in the adaptive forest management since they have a direct effect on the water budget of trees remaining after intervention in forest stands (Bréda et al., 1995; Bladon et al., 2006; Gyenge et al., 2011). Water use has not been considered a target in many afforestation programs, which are typically more centred in either increasing productivity or optimizing forests as carbon sinks. The expected increase in the importance of water as a limiting factor for the future of many forests supports its inclusion as a priority in the planning of new forest systems. However, gaps in knowledge may prevent an effective inclusion of water as a management priority in many cases.

We carry out an overview of some of the main factors influencing water use by forest ecosystems, from basic functional mechanisms involved in the regulation of the water use by trees to changes in the land use. Though, we acknowledge previous reviews that have dealt with specific key issues in relation to water use by trees (i.e. see Bréda et al., 2006) to build upon them, and to identify important gaps and challenges for future research.

2. Importance of species specific physiological mechanisms

2.1. Physiological control of water use by forest tree species

The need of controlling water losses by a fine tuning of leaf stomatal regulation has been, as in other kind of plants, one of the most important selective forces of evolution of forest tree species (Franks and Beerling, 2009; Lawson et al., 2011). Probably, stomatal conductance is one the most relevant and complex plant physiological processes, acting during plant evolution as a crossroad in the interplay between carbon fixation and water loss. Daily and seasonal response of leaf stomatal conductance to water vapour (g_{wv}) establishes clear differences between forest tree species coexisting at a given site (Fig. 1). The response is highly variable according to the differential species sensitivity to climatic events such as drought (Aranda et al., 2000; Mediavilla and Escudero, 2003; Tenhunen et al., 1990), or atmospheric factors such as evaporative demand (Bladon et al., 2006).

The need to maintain functionality of hydraulic system through long living periods is probably one of the most singular and particular characteristics of forest tree species with regard to other plant groups. In this respect, the relationship between the response of

leaf stomatal conductance, and the functionality of the hydraulic pathway through water movements within the tree, has emerged in the last decades as one of the most important points in the understanding of water use by trees (Johnson et al., 2011; Meinzer et al., 2009). Like other plants, stomatal regulation in trees must allow conservation of hydration of aboveground tissues. Stomatal performance also operates, in the specific case of forest tree species, maintaining the hydraulic system functionality within margins of security from catastrophic dysfunction (Brodribb and Cochard, 2009; Tyree and Sperry, 1989). There are numerous examples where the stomata closure, as drought intensify, runs in parallel with a decrease of the hydraulic efficiency into the water pathway of trees. Thus, it is common to observe a decrease in the leaf stomatal conductance to water vapour coupled to the loss of efficiency in the hydraulic system at different points in the continuum soil–tree–atmosphere. For instances, Aranda et al. (2005) observed a seasonal decrease in g_{wv} of beech leaves at the top of the canopy as dry intensified at the end of summer (Fig. 1). It was followed by a parallel drop of hydraulic efficiency in the continuum soil–plant–atmosphere, arriving almost to a 50% when comparing the beginning of summer with the peak of drought. Similar results are frequently signed for most forest tree species, and points out to the complex interplay between maintenance of the water supply to leaves and the risk of hydraulic failure from tensions developed within the xylem (Meinzer et al., 2009; Salleo et al., 2000; Tyree and Sperry, 1988). Under extreme droughts, the hydraulic failure can make trees to sacrifice branches and show symptoms of crown die-back (Rood et al., 2000; Sperry et al., 1998). This particular characteristic of the water conducting system has fostered the development of very different hydraulic designs in the evolution of woody plants, rendering not only very different xylem anatomies, but also different leaf hydraulic designs (Brodribb and Holbrook, 2006; Sack and Holbrook, 2006). Furthermore, hydraulic function has been underscored and is now claimed, together with the maintenance of a positive carbon balance, as the basis to understand the success of woody plants during acute water stress periods (Breshears et al., 2009; McDowell, 2011). In this respect, functioning of the hydraulic system is directly connected to the capacity of maintaining a positive carbon balance (McDowell et al., 2008; Woodruff and Meinzer, 2011). However, the matter is under debate, at least with regard to the role played by starvation of stored non-structural C compounds for tree survival (Bréda et al., 2006; Sala et al., 2010). The expected depletion of carbon balance with water stress is not always in accordance with empirical data (Körner, 2003; Villar-Salvador et al., 2004; William et al., 2012). Endogenous tree factors such as age (Genet et al., 2010), height (Woodruff and Meinzer, 2011), sensitivity of species to water stress (Tissue and Wright, 1995; Latt et al., 2001; Piper and Fajardo, 2011) and seasonal coupling between supply and demand of carbon for growth (Walter et al., 2005; Smith and Stitt, 2007), are all factors modulating the final carbon balance of tree and their capacity to cope with extreme dry events in the long term (see Sala et al., 2012 for a recent review on the matter). Finally, whichever the direct physiological mechanisms implied in the weakening and final death of trees, either maintenance of the functionality of tree hydraulic system or starvation by depletion of carbon reserves, they represent the mechanistic basis underpinning the recently observed decline of forest tree species under water stress conditions worldwide (McDowell et al., 2008, though see Sala and Hoch, 2009; Sala et al., 2010). This issue is of great relevance as forest die-back in same cases (Carnicer et al., 2011), or even important phenomena of mortality (Linares et al., 2010) seem to have accelerated and aggravated in the last decades (Breshears et al., 2009; Allen et al., 2010; Linares et al., 2011). Whichever the ultimate mechanistic basis, it seems clear for trees hydraulic failure and impairment of an optimum carbon balance are both elements
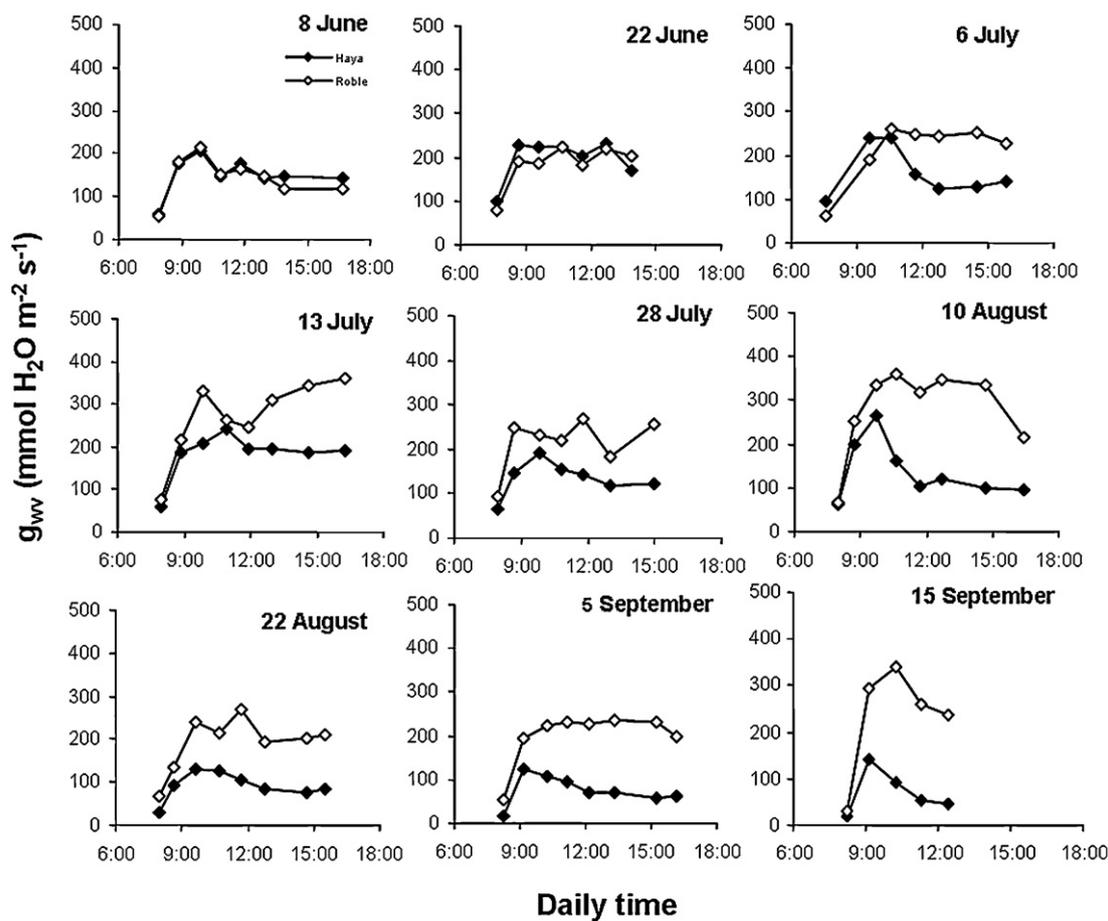
Fig. 1. Seasonal evolution in daily leaf stomatal conductance to water vapour (g_{wv}) for sun leaves at the top canopy in a mixed stand of beech (*F. sylvatica*) and sessile oak (*Q. petraea*) at the southern area distribution of both species in Europe. There was a progressive increase in drought intensity that peaked by the middle of September. Beech shows a progressive decrease in maximum daily g_{wv} that tends also to be earlier in the morning as drought intensifies. In the other hand, sessile oak showed a typical dome shaped daily evolution of g_{wv}, even for the most stressful dates when differences were maxima between both species. Data are for year 2000 at the beech-oak forest of Montejo de la Sierra (I. Aranda unpublished original data).

impacting the capacity to cope with acute drought events in the long term.

2.2. Integration of water use mechanisms at the tree and canopy levels

It should be noted that despite the large amount of information available, there is no current, successful mechanistic model accounting for the physiological basis and integrating the complex stomatal conductance performance in response to a multiplicity of endogenous and exogenous factors (Franks et al., 2007; Mott and Peak, 2010, 2011). Nonetheless, main environmental drivers, namely, soil moisture, air humidity and radiation, have been recognized historically as key factors eliciting different daily and seasonal patterns observed for g_{wv} within tree crowns and canopies (Jarvis and McNaughton, 1986).

The physiological functioning of leaves in the regulation of water losses is coupled to the physical control imposed by leaf size and form. Morphology of leaves conditions the leaf boundary layer resistance to water diffusion (Gates, 1968). Smaller leaves of trees would be adaptive under warmer environments preventing leaf heating over harmful temperatures. Thus, recent reports highlight also its impact on the transpiration consumption at the individual tree level (Bauerle and Bowden, 2011). Thought importance of the leaf boundary layer at the ecosystem level relies in the consideration of canopies as aggregate of leaves (Jarvis and McNaughton, 1986). In this respect, the aggregation of the

performance of different leaves into the crown in a unique functional unit, the canopy, results in the highest level of integration for transpiration, and where forest stand is viewed on the perspective of a big leaf (McNaughton and Jarvis, 1984). Although the overall flux of water through the continuum soil–tree–atmosphere is a very complex process, there are two main physical drivers exerting a control on the rates of water losses at the canopy scale under wet conditions, the physiological control and the boundary layer control over the canopy. Both impact the degree of coupling of tree canopy to the atmosphere (Wullschleger et al., 2000; Gyenge et al., 2011), and in particular to the two principal factors influencing evapotranspiration, the vapour pressure deficit surrounding vegetation and the incoming net radiation. After the inversion of the Penman–Monteith equation, and considering the flux of water into trees as water transpired, it is possible to estimate a physiological and aerodynamic canopy conductance to water vapour. Canopies integrate different structural and functional properties of individual leaves, but they do not result from the summing of those from individual leaves. The coupling to environmental factors of the aerodynamic and physiological conductance of canopy as a functional unity follows similar biophysical rules to those emerging from individual leaves (Jarvis and McNaughton, 1986). The coupling to the atmosphere is modulated daily from wind velocity, incoming radiation and VPD (Wullschleger et al., 2000), and seasonally from a high influence of the water deficit endured by trees (Granier et al., 2000; Kumagai et al., 2004). In this regard, the increase of canopy physiological conductance sensitivity to air water vapour deficit,

Table 1
Decoupling factor from conifer to tropical forest tree species. The ranges for some species represent variation according to time in the growing season or degree of canopy closure.

Species	Decoupling factor (Ω)	Type of vegetation	Study
Chamaecyparis obtusa	0.21	Temperate conifer forest	Kosugi et al. (2007)
Pinus ponderosa	0.20–0.32	Temperate conifer forest	Law et al. (2001)
Picea glauca	0.11–0.16	Mixed temperate forest	Bladon et al. (2006)
Betula papyrifera	0.19–0.36	Mixed temperate forest	Bladon et al. (2006)
Populus balsamifera	0.18–0.40	Mixed temperate forest	Bladon et al. (2006)
Fagus sylvatica	0.20–0.28	Broad-leaved temperate forest	Magnani et al. (1998)/Herbst (1995)
Fagus crenata	0.20–0.45	Broad-leaved temperate forest	Tateishi et al. (2010)
Cecropia longipes	0.90	Tropical rain forest	Meinzer et al. (1997)
Ficus insipida	0.82	Tropical rain forest	Meinzer et al. (1997)
Luehea seemannii	0.88	Tropical rain forest	Meinzer et al. (1997)
Spondias mombin	0.90	Tropical rain forest	Meinzer et al. (1997)
Eucalyptus grandis	0.12–0.40	Temperate forest	Mielke et al. (1999)
Populus hybrids	0.66	Temperate forest	Hinckley et al. (1994)
Nothofagus antarctica	0.07–0.14	Temperate forest	Gyenge et al. (2011)
Mixed dipterocarp forest	0.24–0.43	Tropical rain forest	Kumagai et al. (2004)
Acer rubrum	0.12–0.37	Broad-leaved temperate forest	Wullschleger et al. (2000)

as drought progresses, would be an effective manner to avoid the hydraulic failure in the soil–leaf–air pathway. Surface roughness of most forest canopies increase the degree of coupling to atmospheric conditions, and decrease the importance that aerodynamic conductance may play in controlling the overall water flux from vegetation to atmosphere (Jarvis and McNaughton, 1986). This is a fundamental difference of forest tree covers, mostly in temperate and Mediterranean areas, when compared to the smoothness of plant surfaces in grasslands or crops cultivars. However, even considering forest tree species as a group, there are important differences between conifers and temperate broad-leaved or tropical species (Martyn et al., 1998; Meinzer et al., 1993, 1997; Kumagai et al., 2004; Wullschleger et al., 2000), and even between different species within the same functional group (Leuzinger and Körner, 2007). Temperate broad-leaved forest tree species seems to be slightly decoupled from atmosphere (Table 1, and see Table 2 in Wullschleger et al., 1998), though this degree of decoupling is not as large as in tropical rainforest species. It translates in the later, into a higher importance of the control exerted by the physiological conductance to water vapour of the canopy for some forest tree species, transpiration becoming more dependent on the sensitivity of leaf stomata to changes in water vapour deficit of atmosphere.

Water use by forests has been ascertained mainly from the use of techniques such as leaf porometry (Goulden and Field, 1994), tree sap-flow (Oishi et al., 2008; Wullschleger et al., 2001), eddy covariance (Baldocchi and Ryu, 2011) and catchment water balance (Zhang et al., 2001; Nosetto et al., 2011). The overview of all these methods is beyond the scope of this work, and good reviews have been already published (see Goulden and Field, 1994; Baldocchi and Ryu, 2011; Kell et al., 2001; Wilson et al., 2001; Wullschleger et al., 1998). We are going to outline only briefly one of them: the sap flow record. This measurement is an intermediate methodological approach to dissect the use of water by forest tree species from the micro-scale at the leaf level (e.g. porometry), to the macro-scale represented by the whole ecosystem (e.g. eddy

covariance or catchment water balance). The response in terms of control of water use at the leaf level, and integrated through the full tree crown, result in different patterns in the water use at the integrative scale represented by a whole individual tree. Individual trees at the same place make use of water in different ways according to species (Martínez-Vilalta et al., 2003; Aranda et al., 2005; Poyatos et al., 2005, 2007), and hierarchical status of tree into the stand (Ryan et al., 2000). Measurement of sap flow density is one of the most extensively employed methods that allow discriminating water use by individual trees. The method has different technical approaches and methodological shortcomings (Köstner et al., 1998). Some of them related with the different patterns of sap flow profiling across sapwood depending on species, daily time lag between canopy transpiration and sap flow, or adjustment of the zero base line during nocturnal periods when sap flow is considered null. However, the technique allows resolving water consumption at the individual tree scale reasonably well, allowing to extrapolate to the overall forest stand after an affordable scaling exercise (Kaufmann and Kelliher, 1991; Schwärzel et al., 2009; Oishi et al., 2010). The approach has shortcomings as already mentioned, with some emerging ones as the nocturnal water fluxes, which have to be included in the water balance calculations (Oishi et al., 2008).

Once water is captured it moves through trees inhabiting the same forest in a very species-specific manner. This is linked in some cases to specific morphological traits such as leaf and rooting habits, namely deciduous versus evergreen leafing, and shallow vs. deep rooting patterns. The sensitivity of different species to environmental factors, specifically to soil water availability, evaporative demand or radiation, explain the different strategies in the sap flow on daily and seasonal temporal scales. An example is found when comparing the daily sap flow of two evergreen species, *Quercus ilex* and *Pinus nigra*, growing together in mixed stands at the mid-mountains of the Iberian Peninsula. Both species showed a decline in the daily sap flow from the beginning to the middle of

Table 2
Impact on water use of outstanding trees after forest thinning. It was observed an increased water use in most cases in the following years after the treatment.

| Species	Impact	Type of vegetation	Study
Picea glauca	Increase	Temperate Forest	Bladon et al. (2006)
Betula papyrifera	Moderate increase	Temperate Forest	Bladon et al. (2006)
Populus balsamifera	No change	Temperate Forest	Bladon et al. (2006)
Pinus pinaster	Increase	Mediterranean conifer forest	Jiménez et al. (2008)
Quercus petraea	Increase	Temperate Forest	Bréda et al. (1995)
Quercus ilex	Increase	Mediterranean angiosperm forest	Gracia et al. (1999)
Nothofagus antarctica	Increase	Temperate Forest	Gyenge et al. (2011)
Pinus sylvestris	Moderate decrease	Temperate conifer forest	Lagergren et al. (2008)
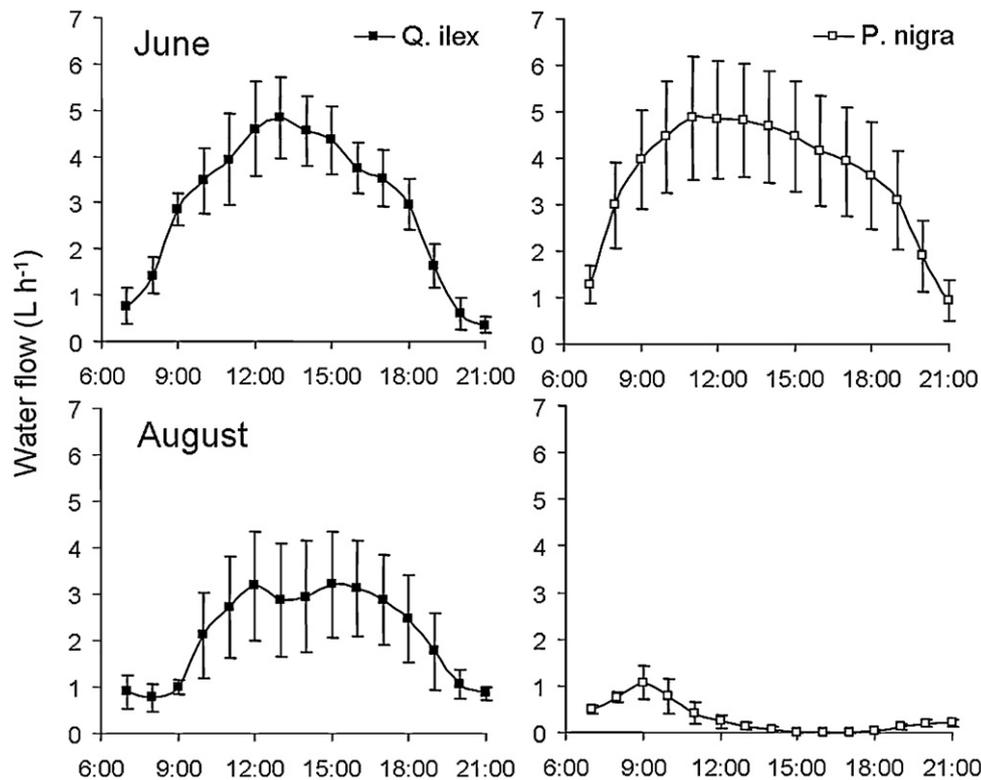
Fig. 2. Daily water sap flow in two typical Mediterranean forest tree species (*Quercus ilex* and *Pinus nigra*) recorded with the HBT technique. Two contrasted periods were considered, late spring (top graph) and mid summer (bottom graph). Pines suffered a much more acute decrease in summer water use than oaks. The trends represent the mean ± SD for four trees per species (A. Forner original unpublished data).

summer (Fig. 2). However, *P. nigra* maintained a much more conservative performance with regard to the water transpired, showing an acute depression in daily sap flow, making transpiration almost null around midday, which was not observed in *Q. ilex*. Similar segregation and differential performance among species inhabiting the same place has been frequently explored in many kinds of forest tree species, from temperate to tropical biomes.

Therefore water consumption by forest trees varies daily and seasonal among species according to seasonal changes in the relative extractable water, radiation and vapour pressure deficit (Oren et al., 1999a,b; Kumagai, 2011). Despite the well-known differentiation among forest tree species to climate and atmospheric factors, there has been a debate if the final water budget of forest stands is controlled purely by biophysical rules (West et al., 1999; Enquist, 2002; Meinzer et al., 2001; Meinzer, 2003). In this case, the proper application of general transformation scaling rules (i.e. relationship between sapwood and total leaf area) would result in the adjustment of the water use by different tree species to a similar pattern (Meinzer et al., 2001). Another example of confluence in the whole water used by different kind of species, was recently presented by Baldocchi et al. (2010). They observed a similar pattern in the overall annual water budget and carbon fixed when comparing evergreen vs. deciduous species in Mediterranean oak woodlands. It was concluded most important factor controlling, as much water use or carbon uptake, was leaf area index. Inter-annual modulation in the maximum interchange of water and carbon fluxes with the atmosphere according to leaf habit was given by the changes in leaf area index. Thus, and besides leaf habit could be considered to exert an important role on the fluxes of water and carbon in forest ecosystems, it seems that the species-specific response was blurred when the overall water used through the full growing season was considered. In this respect, deciduous species would compensate their shorter vegetative period by maximizing the consumption of

water during the wet spring months. However, as shown worldwide and from many studies, the sensitivity of each species to evaporative demand (Hinckley et al., 1978; Oren et al., 1999a,b), perturbations such as intense droughts (Leuzinger et al., 2005) and modification of tree physiological performance in the subsequent years to the perturbation (Bréda et al., 2006), are issues to consider at least in environments where water is one of the main limiting environmental factors at some times during the growing season, and different adaptive strategies may have evolved. In this regard, there are numerous examples showing how sensitivity to drought explain differential species-specific decreases in the water use by trees as dry period advances (Aranda et al., 2005; David et al., 2007; Kunert et al., 2010; Leuzinger et al., 2005; Oren and Pataki, 2001).

2.3. Other functional species-specific processes involved in the water use: capacitance, nocturnal water flux and hydraulic lift

Not only use, but also control and management of soil water differ from trees to other plant life styles. Unlike other plants, forest trees represent important aboveground reservoirs of water themselves (Scholz et al., 2007). Sapwood and elastic tissues of trees are the two main internal water storages. The relative importance of both compartments varies according to species (Kravka et al., 1999), tree size (Phillips et al., 2010), and soil water availability (Hernández-Santana et al., 2008; Betsch et al., 2011). Although, sapwood seems to be more relevant by conditioning daily tree water budget (Čermak et al., 2007). The impact of dry years on the amount of water withdrawn from both internal water storages has been assessed recently for *Fagus sylvatica* considering the exceptional drought of 2003 in Central Europe (Betsch et al., 2011). The contribution of water accumulated within trees to the overall daily water balance, and specifically to the transpiration stream, increased with the intensity of drought reaching almost a 70% at the

peak of the dry period (Betsch et al., 2011). However, its relevance as mechanism to avoid dry periods should be considered moderate, as most water depleted during diurnal hours must be replaced during the night in order to maintain hydration of aboveground tissues. Otherwise, a fast death of plant tissues would be expected from a fast dehydration. In fact, this recharge is lowered as water in soil gets scarcer (Giovannelli et al., 2007), showing the progressive difficulty to collect and replace internal water reservoirs as drought intensifies.

Until recently, water use by trees was considered to operate mainly during the daylight period. In the last years, this view is beginning to change, and nocturnal water flux has been described already for numerous forest tree species (Daley and Phillips, 2006; Fisher et al., 2007; Sellin and Lubenets, 2010). It can be a mere consequence of the recharge of internal water reservoirs on the first night hours, but also a consequence of incomplete stomatal closure during night (Caird et al., 2007; Fisher et al., 2007). After replacement of the internal reservoirs, the reason why trees assume costs of night-time water loss without simultaneous photosynthetic carbon gain remains unclear (Phillips et al., 2010). However, there are some possible benefits derived from this, such as the increase of nutrient availability to the plant (Caird et al., 2007), or provide oxygen to the respiring cells of the deep sapwood (Daley and Phillips, 2006). The nocturnal water transport has been quantified as a significant fraction of total daily water use although it depends on several factors including the particular species studied (Dawson et al., 2007). The value ranges from 4.9% to 7.3% in *Eucalyptus* species (Phillips et al., 2010) and it is established as 2.4%, 6.6% and 13% in *Acer rubrum*, *Quercus rubra* and *Betula papyrifera*, respectively (Daley and Phillips, 2006) and 6–8% in *Eucalyptus parramattensis* and *Angophora bakeri* (Zeppel et al., 2010). According to these values, the inter-specific variation in nocturnal water transport has been described to be lower than the intra-specific variation in some studies (Phillips et al., 2010; Zeppel et al., 2010). Another important factor that affects significantly to nocturnal sap flow is tree height (Pfautsch et al., 2011). Nevertheless, the factors that present higher correlations with nocturnal sap flow are the environmental ones. For example, it depends on the season, being higher when the soil water availability is not limited: up to almost 50% (commonly 35%) and 20–25% in *Eucalyptus victrix* in wet and dry season, respectively (Pfautsch et al., 2011). Thus, nocturnal transpiration is highest in sites with higher soil water content and less prone to atmospheric or soil water deficits (Dawson et al., 2007). The night-time water transport is highly correlated with vapour pressure deficit (Pfautsch et al., 2011; Zeppel et al., 2010), although there is some study where the product between the vapour pressure deficit and the wind speed are both the principal drivers (Phillips et al., 2010). Specifically, some studies indicate nocturnal transpiration is less than 10% of the daily sap flow (Daley and Phillips, 2006; Novick et al., 2009). This supports the idea nocturnal refilling is more important than night-time transpiration, which disagree with the study carried out by Zeppel et al. (2010) and where nocturnal sap flow depended mainly on transpiration.

The deep rooting patter of trees, unlike other plants, makes possible the movement of water from deep to shallow soil horizons. This specific water pumping property of trees, known as hydraulic lifting (Caldwell and Richards, 1989; Dawson, 1993), can have an important ecological role in terms of water redistribution in soils (Horton and Hart, 1998). Not only the water balance may be modulated by this process in some forest trees, but also hydraulic lift is affecting important ecological processes such as the facilitation of water use by individuals of different species and by juveniles of the same species (Brooks et al., 2006). Hydraulic lift was first observed in plants from dry sites such as deserts (Caldwell and Richards, 1989). Afterwards, there have been numerous reports describing this phenomenon for forest tree species from tropical rainforest to
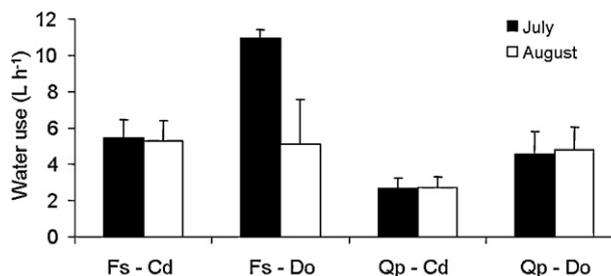

Fig. 3. Water is used by trees in Mediterranean mid-mountains conditions according to its hierarchical position in the stand. Sensitivity of species to the depletion of soil moisture as season advance is of prime importance as well. There were significant differences for *Fagus sylvatica* (Fs) and *Quercus petraea* (Qp) in the water use at midday, and whether dominant (Do) or co-dominant the status of tree in the stand. The differences were maintained only for Qp as the season progressed. Average values represent water use by trees at midday in three dates on July and August in the Beech-Oak forest of Montejo de la Sierra ($n = 4$, $\pm$S.E.). This forest represents one of the southernmost beech populations in west of Europe. (A. Forner original unpublished data.)

typical Mediterranean and temperate forests (Meinzer et al., 2004; Nadezhdina et al., 2008; Scholz et al., 2002). Yet the process seems to be species-specific as recently reported in a mixed beech-oak stand (Zapater et al., 2011).

3. The interacting influence of species identity, age, size, stand structure and management in the forest water use

Segregation of many forest tree species across ranges of soil and atmospheric moisture availability is linked to the control exercised over the water use, on the other hand related to the own sensitivity of different species to water scarcity (Baquedano and Castillo, 2006; David et al., 2007; Chirino et al., 2011). From Mediterranean to temperate and tropical areas, there is a plethora of strategies ranging from a characteristic isohydric performance to other fully anysohydric ones (Chirino et al., 2011; Kumagai and Porporato, 2012; Tardieu and Simonneau, 1998). In the first case a water saver performance is expected as soil moisture availability decreases, in the second one, a more water spender use of water is sustained by trees. A typical example is given by *Fagus sylvatica* and *Quercus petraea* under sub-Mediterranean conditions. The former has a very high sensitivity to the depletion of soil water supply, suffering higher decreases in sap flow density rates than *Q. petraea* as drought advances in summer months (Aranda et al., 2005; Jonard et al., 2011). However, most species would represent a point in what should be more considered a range of variation in the water economy management, than a strict double categorical classification (Franks et al., 2007).

Along with the species-specific strategy followed in the water use (Pataki and Oren, 2003), other factors are fundamental to understand the water balance of forests. In this respect, two important structural drivers influence water consumption. Height of tree and its hierarchical position in the stand determine total volume of water transpired (Fig. 3). Frequently, dominant trees maintain higher sap flow densities in the sapwood, together a higher spending of total water as consequence of higher inputs of radiation into tree crowns (Martin et al., 1997; Meinzer et al., 1999; Granier et al., 2000). Different sensitivity of leaf stomatal response to evaporative demand with tree height brings about also differences in the sap flow of tree (Woodruff et al., 2010). Even more, whether forest tree species grow in pure or mixed stands, it is also a factor that modifies the species-specific response and performance in terms of individual tree sap flow, conditioning the overall water use of stand in the last (Jonard et al., 2011).

Beyond the size of the tree and its dominance of the forest stand, its own age profoundly modulates its water use (Delzon and Loustau, 2005). As trees age, there is a progressive decrease in the movement of water per sapwood unit, explained by what has been termed "the hydraulic limitation hypothesis" (Ryan and Yoder, 1997; Ryan et al., 2006). The lost of efficiency through the hydraulic path as tree ages, in terms of lower leaf-specific hydraulic conductance, would explain a more water conservative performance at the leaf stomatal control level at the top of the tree crown. This has practical consequences on the water used by natural or artificial forests. If stands are structured according to young or old age tree classes impacts directly in the forest water budget. For a similar sapwood area, young trees tend to maintain higher rates of transpiration than old ones. In this respect, silviculture practices focuses to maintain short rotation systems might promote a more water spending use by outstanding trees (Lagergren and Lindroth, 2004; Forrester et al., 2010). In the same way, some perturbations as wildfires or intensive logging prompt transformation of old to re-growth forests or coppice, the direct impact being an increase in the water consumption by forest in subsequent years (Buckley et al., 2012; Macfarlane et al., 2010).

Therefore, modification in the structure of stand as a consequence of different management practices, impacts directly in the water used by the remaining trees (Bréda et al., 1995; Jiménez et al., 2008). Coppice or seedling re-establishment are two different forest management practices for regeneration of natural forests or plantations, both also influencing forest water economy in the following years after the silvicultural practice (Drake et al., 2012). The former involves a higher development of root system which translate into a better access to deep water resources from groundwater, together with larger water interception and stand-scale transpiration rate (Drake et al., 2012). This would result in a more wasteful water use in stands maintained in a permanent re-growth state as coppice, at least on the first years after logging and re-sprouting of stumps.

The need of a precise knowledge of the water consumption of forest tree species or specific stand structure, it is also extensible to the impact of some management practices such as forest thinning (Bréda et al., 1995; Gyenge et al., 2011; Moreno and Cubera, 2008). Silvicultural treatments where forest stand stocking is reduced bring about direct structural changes making more open the stand. This has an impact not only in the interrelationships among residual trees (Jiménez et al., 2008), and species in the case of mixed stands (Bladon et al., 2006; Herbst et al., 2008), but also on the surrounding microclimate conditions (Zheng et al., 2000). Its well established that a decrease in tree density prompt an immediate positive effect on remnant trees, increasing on many cases the use of resources such as water (Table 2), and improving growth in the subsequent years after stand stocking decrease (Bréda et al., 1995; Gracia et al., 1999; Lagergren et al., 2008). Amelioration of growth is clearly related with an increase in the water and radiation availability. However, it has been also observed on some cases, an abrupt change in the evaporative demand around remaining trees after cutting. This increases the xylem tension drop below the hydraulic margins of security for the hydraulic system of standing trees (Bladon et al., 2006). In the last, this could translate in a negative impact on the tree hydraulic system, provoking an increase of xylem dysfunction. The response is highly species-specific as shown by Bladon et al. (2006) from a variable retention partial harvesting stand experiment. Forest tree species making up the mixed stand responded in a very different way. There was an improved in the water use of residual trees in *Picea glauca* at the clear cutting plot, a moderate and slight increase in *Betula papyrifera* and the maintenance of the same water consumption between control and cleared plots for *Populus balsamifera*. In the case of *Populus* there was an increase in the risk of hydraulic failure after the thinning.

One the most important needs of information to assure management of new planted and natural forest in a sustainable way in the future is related to the water requirements of forests. The specific composition, along with structure, will be both the main drivers in the forest water use. This issue is especially relevant for areas of the world as tropical zones where basic information in the water use at the specific level is scarce (Kunert et al., 2010). Water is already a problem in wide areas of the world as the Mediterranean Basin. This obligates to have a good knowledge on the specie-specific water use at the tree level for plant materials used in reforestation programs, given the aforementioned different strategies followed by forest tree species. In order to assure sustainability of planted forest stands in the future, it is needed to ascertain how much water will be used by these new forest systems (Petzold et al., 2010), paying attention to the impact of natural hazards such as intensification of droughts in the water use by forest tree species in general (Martínez-Vilalta et al., 2003; Gartner et al., 2009). For instance, new plantations aimed to produce biomass as source for bioenergetic use, might increase the water consumed with regard traditional agricultural crops or natural forests (Gyenge et al., 2008; Petzold et al., 2010). Tricker et al. (2009) reported an increase in the annual water use by *Populus* trees in bioenergy plantation under the future higher air CO_2 levels expected in the next decades. This was despite the response, in terms of lower leaf stomatal conductance, followed the general pattern of decrease in the CO_2 enriched air treatment regarding ambient conditions. Increases in other factors such as total leaf biomass would compensate the lowering in the water use at the leaf level. If these data are confirmed, the result could be the establishment of new plant production systems that would not be sustainable in relation to available water resources at some places in the world (Delucchi, 2010). The picture could be worse considering the forecasted more extreme dry period that forests will have to withstand in areas as the Mediterranean (IPCC 2007), or even ample tropical zones.

4. Water use by forests and impact at the landscape scale

Trees exert a strong control over the terrestrial ecosystem water cycle through their effect on forest water use (Stoy et al., 2006). As a consequence, changes in land cover may lead to profound hydrological changes, affecting the water balance and the quantity and quality of water resources (Kume et al., 2007). During the last decade, afforestations have been proposed as a promising tool for carbon sequestration, but their full environmental consequences have not been considered. Regarding water budgets, current evidence suggests that tree plantations usually reduce stream flow and groundwater recharge (Farley et al., 2005; Nosetto et al., 2011), since tree covers present greater evapotranspiratory capacity than croplands and herbaceous covers (Farley et al., 2005; Huxman et al., 2005). The combination of deeper root systems extended growing seasons, higher transpiration rates, greater interception of precipitation and higher inputs of radiant energy because of lower albedos explain the higher evapotranspiration and lower deep drainage in forest compared to herbaceous covers or croplands (Kelliher et al., 1993; Canadell et al., 1996; Nosetto et al., 2011). Due to these hydrological impacts reforestations programs are considered as a land use activity that may threaten water resources security, particularly in some drought prone areas (Pacala and Socolow, 2004; Jackson et al., 2005). In a global synthesis study, Farley et al. (2005) showed that afforestation of grass and shrublands reduced annual runoff on average by 44% and by 31%, respectively. Similarly, stream flow reductions of up to 50% have been reported in the Ecuadorian Andes (Buytaert et al., 2007) after afforestation with *Pinus* plantations while a water budget study in Brazil demonstrated that 95% of the precipitation is evapotranspirated by *Eucalypt*

plantations (Almeida et al., 2007). However, positive effects related to the control of flooding or the improvement of the quality of water resources are also claimed as main arguments for reforestation programs. In some cases, due to higher root density, microfaunal activity and/or content of soil organic matter and litter, tree plantations may improve the porosity and capacity of water transport of soils, improving water infiltration and deep drainage, and reducing erosion and the volume of sediment, nutrients and salt volumes transported into river systems (Nosetto et al., 2007; Van Dijk and Keenan, 2007; Nosetto et al., 2011).

Replacement of native woody vegetation by tree plantations has also strong effect on the water cycle. Reforestation programs usually used fast-growing species which are characterized by higher productivity and biomass, but also by higher annual transpiration and rainfall interception, particularly for fast growing evergreen species such as pines and eucalypts (Farley et al., 2005). Gyenge et al. (2008) demonstrated significantly greater water use by ponderosa pine plantations compared to natives *Austrocedrus chilensis* forests in NW Patagonia. Hydraulic characteristics of *P. ponderosa* (higher canopy-stomatal, whole hydraulic conductances and specific hydraulic conductivity) allow high stomatal conductance for more hours a day than *A. chilensis* trees, and therefore greater transpiration. In a study of more than 600 observations, Jackson et al. (2005) found reductions stream flows by almost 52% when native vegetation was replaced by forest plantations. In some cases, establishment of plantations caused streams to dry completely, especially in drier regions.

By contrast to afforestation, deforestation usually leads to increases in stream flows and ground water recharge since evapotranspiration is considerably reduced (Farley et al., 2005; Nosetto et al., 2011). Native forest clearing for cropping in Australia and the Sahel has led to increased groundwater recharge, arising of water table levels due to the lower evapotranspiration rates of croplands (Schofield, 1992; Leblanc et al., 2008). Similarly, Nosetto et al. (2011) predict that replacement of large areas of dry forests by soybean crops in central Argentina would reduce evapotranspiration in a 30% and would almost increase three fold deep drainage fluxes.

Nevertheless, the impact of the hydrological changes generated by land-use changes varies depending on context where land use shifts occur (Van Dijk and Keenan, 2007; Nosetto et al., 2011). In drought prone regions the potential reductions of water resources caused by forest plantations are smaller in absolute terms than in humid regions, but the impact can be environmental, economical and socially more harmful due to the already scarce water availability. Even more, hydrological modification could trigger positive or negative impacts on water cycle depending on the context. For example, tree plantation in flooding-prone places may be positive, since it can reduce the risk of flooding and improve the soil drainage capacity. By contrast, afforestation in semiarid environments would reduce water availability even more. The replacement of forests by crops can improve stream flows and ground water recharge, but it could also cause the rise of water table levels, flooding and salinization (Archibald et al., 2006; Peck, 1978). In addition, for a given climatic condition, there are different options for developing sustainable forest management strategies in order to control or minimize the potential hydrological impacts of tree plantations: terrain conditions, planting arrangement, species physiology, water use efficiency, variation in stand age, spacing, site productivity, forestry operations, proportion of area planted, etc.

5. Main conclusions and remarks

Water is a keystone element influencing performance of forest tree species worldwide. The impact of water availability on the ecology and evolution of plants in general, has been one of the most important subjects of study for functional plant ecologists in the last decades. Main environmental factors influencing the species-specific water use by forest tree species, and the different functional strategies, are beginning to be elucidated. Nevertheless it must be recognized that there are important gaps in current functional knowledge regarding water use for many forest tree species, especially in tropical zones. Functional mechanisms governing water use at different scales of biological integration have been assessed in detail during the last decades. However, the complexity in the response to water availability, always interacting with other factors of the environment such as light or nutrients, and the proper structural complexity of forest ecosystems, explain the difficulties to implement water used by forest tree species as criteria in management practice. In any case, management of forests must guarantee the sustainability of forest stands in the future, taken into account the well documented relationship between forest health, tree growth and water availability. Management must make possible the difficult interplay between forests as water spenders and carbon fixing sinks. Some natural and artificial forest could be in serious risk of die-back and mortality of dominant trees as a consequence of a general harshening of climate in terms of more acute dry periods. This reinforces the urgent need to establish, despite the many aforementioned difficulties, the inclusion of water use as one of the main targets in the management of forest in the future, and within the context of a rapidly changing world. The issue is especially relevant for the new plantations planned to provide different goodness from biomass for bioenergetics purposes to soil protection from desertification.

Acknowledgements

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