Contrasting growth and water use strategies in four co-occurring Mediterranean tree species revealed by concurrent measurements of sap flow and stem diameter variations

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Abstract

Drought limits tree water use and growth of Mediterranean trees. However, growth and water use strategies are rarely addressed simultaneously across species and drought conditions. Here, we investigate the link between stem diameter variations and sap flow in four co-existing Mediterranean trees (*Pinus halepensis* Mill., *Quercus pubescens* Willd., *Quercus ilex* L. and *Arbutus unedo* L.), under relatively wet (2011) and dry (2012) conditions. Continuous stem diameter variations were converted to basal area increment (BAI) and de-trended to estimate tree water deficit (ΔW), an indicator of stem hydration. *P. halepensis* and *Q. pubescens* showed the most and the least conservative sap flow density (J_S) regulation under drought, respectively, with *Q. ilex* and *A.unedo* showing intermediate drought responses. All species, except *A. unedo*, showed some between-year variability in the environmental control of J_S. Seasonal stem shrinkage in response to drought (i.e. increasing ΔW) and subsequent trunk rehydration after rainfall (i.e. decreasing ΔW) occurred in all species. Vapour pressure deficit (VPD) and soil moisture (θ) interacted to determine seasonal variation in ΔW. Interestingly, in the dry year, 2012, more species-specific differences were found in the responses of ΔW to θ and VPD. Across species, J_S and ΔW began to decline at similar soil moisture thresholds, underpinning the tight link between J_S and ΔW under varying drought conditions. Annual BAI decreased proportionally more than tree-level transpiration (J_T) between the wet (2011) and the dry (2012) year, hence growth-based WUE ($WUE_{BAI}=BAI/J_T$) decreased for all species, albeit less acutely for *P. halepensis*. Overall, despite their contrasting leaf habit and wood type, the studied Mediterranean tree species show coordinated responses of transpiration, water storage dynamics and growth-based WUE which allow them to cope with seasonal and interannual drought.

Keywords: Automatic dendrometer, water availability, tree transpiration, tree water deficit, growth-based water use efficiency.

1. Introduction

Water availability is the most limiting factor for plants in Mediterranean forest ecosystems, where droughts occur every summer and display varying duration and intensity from year to year (Blondel and Aronson 1999). Despite that Mediterranean woody flora is generally regarded as drought-tolerant, extreme drought episodes and recent region-wide increases in aridity are already causing severe tree defoliation and increasing mortality rates in some species (Peñuelas et al. 2001, Carnicer et al. 2011, Ogaya et al. 2014). Given the projected increases in temperature and reductions in precipitation for the Mediterranean basin (Collins et al. 2013, Lindner et al. 2014), there is an urgent need to identify species-specific patterns in drought sensitivity of water-related physiological processes in Mediterranean forests.

The recent land-use history of Mediterranean forests has resulted in the coexistence of tree species of different functional type and evolutionary background, associated with contrasted successional stages (Romane and Terradas 1992). These species often show different leaf habits, wood anatomical properties and contrasting water use strategies. For example, early successional pines may show high rates of gas exchange under well-watered conditions, but they display a strict stomatal control under drought conditions (Borghetti et al. 1998, Maseyk et al. 2008). Evergreen sclerophyllous trees also display year-round transpiration and a wide range in stomatal control of transpiration during drought (Martínez-Vilalta et al. 2003, Mereu et al. 2009). In contrast, winter deciduous oaks must maximize gas exchange during a shorter growing season, resulting in relatively high transpiration rates throughout the summer (e.g. Baldocchi et al. 2009).

Likewise, drought responses of stem radial increment across Mediterranean tree species are also varied. After growth initiation in spring, summer drought slows down stem increments in most species. Cell division and enlargement and carbohydrate availability are reduced with increasing water stress (Zweifel et al. 2006), but drought sensitivity of these processes is species-dependent (Sanz-Pérez et al. 2009). As a result, some Mediterranean species enter a state of cambium quiescence in summer (Vieira et al. 2013) while others can keep growing, albeit at very small rates (Cherubini et al. 2003). Radial stem increments following autumn rains are mostly related to stem rehydration, but wood formation has also been shown in some Mediterranean species in early autumn (Camarero et al. 2010).

Transpiration-induced depletion of water stored in sapwood and bark tissues produces fluctuations in stem diameter at daily and seasonal timescales (Zweifel and Häsler 2001), which may result in prolonged stem shrinking during drought (e.g. Vieira et al. 2013). De-trended stem diameter fluctuations (tree water deficit, ΔW) provide a metrics of whole-tree water status relative to a fully hydrated state (Zweifel et al. 2005); ΔW values close to zero are indicative of ample water storage conditions within the trunk and ΔW increases as drought progresses. In absolute value, ΔW generally increases with vapour pressure deficit and decreasing soil water availability in a manner that is species-dependent (Zweifel et al. 2005, Drew et al. 2011, Köcher et al. 2013). In temperate forests, conifers usually display higher sensitivity of ΔW to soil water availability compared to co-occurring deciduous oaks (Zweifel et al. 2005, Zweifel et al. 2007), but little is known on the environmental controls of ΔW across Mediterranean tree species. Moreover, the link between sap flow and ΔW remains relatively unexplored, despite its potential to reveal species-specific differences in physiological regulation of transpiration (Zweifel et al. 2007).

Productivity and water use show different sensitivities to water availability, the former being more sensitive to water deficits (Hsiao 1973). This relative variability is conveniently encapsulated in water use efficiency (WUE), the ratio between productivity and water use (Jones 1992), where productivity can be expressed in terms of basal area increment (BAI) (Bréda and Granier 1996) or biomass production (Forrester et al. 2010). Isotopic- and gas exchange-based WUE measurements have indeed shown contrasted species-specific variation related to drought in Mediterranean forests (Ferrio et al. 2003), but a limited interannual variation (Damesin et al. 1998). However, neither of these measurements integrates both, the whole-plant level and the annual timescale, the relevant ecological scales to address patterns in forest resource use efficiency (Binkley 2004). The response of growth-based WUE to drought across species may be used to study the relative sensitivities of transpiration and growth to water deficits in different ecological contexts (McCarthy et al. 2011, Morán-López et al. 2014, Smith and Sperry 2014).

Here, we monitored seasonal sap flow and stem radius variations for almost two years in four tree species growing in a Mediterranean forest: the winter-deciduous sub-Mediterranean *Quercus pubescens* Willd., two evergreen sclerophyllous species (*Quercus ilex L.* and *Arbutus unedo* L.) and *Pinus halepensis* Mill., an early successional, drought-adapted pine. The main aim of this study is twofold: (1) to assess interspecific drought responses of sap flow, BAI and ΔW under relatively wet (2011) and dry (2012) conditions and (2) to study the coordination of growth and water use strategies in this ecological context using growth-based WUE. Pines often display a more conservative water use compared to co-occurring deciduous oaks (Poyatos et al., 2008; Zweifel et al., 2007), hence we hypothesized that (1a) *P. halepensis* would show the strongest reductions of sap flow and ΔW in response to drought (at the seasonal and annual scales), in contrast with *Q. pubescens*; for both, sap flow and Δ*W*, the sclerophyllous *Q. ilex* and *A. unedo* would show intermediate responses. Given the tight link between transpiration and Δ*W* (Zweifel et al., 2007), we also hypothesize a close correspondence between the soil moisture controls on both sap flow and Δ*W* across species and years (1b). Moreover, because of its drought-adapted character and its high priority for stem growth (Sanz-Pérez et al., 2009) we postulated that *P. halepensis* would show the highest BAI and the lowest BAI reduction in the dry year. We also expected that, given its preference for mesic habitats in the region (De Dios et al. 2009), *Q. pubescens* would show the higher BAI reduction under drought. Because of the different relative sensitivity of radial growth and water use in response to drought (e.g. Hsiao, 1973), we hypothesized that (3) annual BAI would decrease proportionally more than water use in the dry year of 2012, compared to 2011 across all species (i.e. WUE_{BAI} would decline). Finally, we hypothesized (4) that *P. halepensis*, because of its strict stomatal control, and *Q. pubescens*, because of its shorter leafy period, would display higher annual WUE_{BAI} compared to *A. unedo* and *Q. ilex*.

2. Materials and Methods

2.1. Study site, plot characteristics and environmental monitoring

Field measurements were conducted in the Can Balasc experimental site (41° 25’ 51.56’’ N, 2° 04’ 25’’ E, 270 m a.s.l.) located in the coastal massif of Collserola (NE Spain). Climate is typically Mediterranean with warm, dry summers and mild winters. Mean annual precipitation and temperature (1951-2010) are 608 mm and 15.2 °C, according to a spatially-explicit climatic database (Ninyerola et al. 2007a, Ninyerola et al. 2007b). Soils are predominantly developed above lithological strata of shales and granite (Espelta et al. 2008) and are *ca.* 50 cm deep; according to the USDA textural soil classification (Cosby et al. 1984), the soil type is sandy-loam. The study plot is located in a 0.7 ha stand area, dominated by holm oak (*Quercus ilex* L.), accompanied by pubescent oak (*Quercus pubescens* Mill.) and strawberry tree (*Arbutus unedo* L.). Some scattered Aleppo pines (*Pinus halepensis* Mill.) are also present, growing above the main canopy (Table 1). The understory is a dense stratum mainly consisting of *Pistacia lentiscus*, *Erica arborea* L., *Phillyrea latifolia* L., *Rhamnus alaternus*, *Cistus* pp, *Crataegus monogyna*, *Bupleurum fruticosum* and other less abundant species. A more detailed description of the stand's recent history can be found in Sperlich et al. (2014).

Sensors for measuring air temperature and relative humidity (HMP45C, Vaisala Oyj, Finland), precipitation (ARG100, Environmental Measurements Ltd., Sunderland, UK), solar radiation (SP1110 Skye Instruments Ltd., Powys, UK) and wind speed (05103-5, R.M. Young Company, Traverse City, MI, USA) were installed at a height of 3 m, in a clearing, located ca. 1 km from the plot. Vapour pressure deficit (VPD) was calculated from air temperature and relative humidity. Meteorological data were recorded every 30 seconds and stored as 15 minutes average in a data logger (CR800 Datalogger, Campbell Scientific, Inc., Logan, UT, USA). Average volumetric soil water content (θ) ($cm^3\ cm^{-3}$) in the upper 0-30 cm of soil was recorded continuously using five vertically-inserted frequency domain reflectometers (CS616, Campbell Scientific Inc.), installed randomly within the plot to obtain a representative measure of soil moisture for the whole plot.

2.2. Sap flow measurements

In September 2010, we installed sap flow sensors in trees selected to cover the range of diameter classes, except the smallest trees (<10 cm), which may be problematic for sap flow measurements and have the lowest contribution to stand transpiration (*Q. ilex* n=7, *Q. pubescens* *n*=7, *A. unedo* *n*=4 and *P. halepensis* *n*=3). In 2012, the number of operative sensors was reduced due to probe failure (*Q. ilex* *n*=5, *Q. pubescens* *n*=4, *A. unedo* *n*=3 and *P. halepensis* *n*=3). The measurement period for sap flow (and stem radial variations) spanned from February 2011 (DOY 50) until the end of the year 2012 (DOY 365).

Stem sap flow was monitored with constant thermal dissipation sensors constructed in our own laboratories according to Granier (1985, 1987). These two probes were installed at a height of 1.20 m, with a vertical separation of ca. 12 cm between them. To minimise the influence of natural temperature gradients in the stem, the installation was carried out in the north face side of each tree and isolated with aluminium-covered material to avoid direct solar radiation. Temperature differences (*dT*) were recorded at 30 s intervals and stored as 15 min average in a data logger (CR1000, Campbell Scientific, Inc.). The monitored trees had estimated sapwood depths of 42-45 mm for *A.unedo*, 44-48 mm for *P.halepensis*, 35-40 mm for *Q.pubescens*, and 47-69 mm for *Q.ilex*. Although this range of sapwood depths reduced the risk of underestimating sap flow due to the contact of the probe with non-conducting xylem, steep gradients in sap flow density within the probe length can also cause underestimation of average sap flow density (Clearwater et al 1999). Hence, we installed short sensors (10 mm) in all tree species except Aleppo pine (20 mm), which does not display a steep radial variation of sap flow within the outer ~20 mm of xylem (Cohen et al. 2008).

Natural temperature gradients were measured over 137 days to determine that the upper (95 %) and lower (5 %) quantiles were 0.3 ± 0.02 and 0.2 ± 0.02 ˚C (across-trees mean ± SE), suggesting only a minor effect on sap flow measurements (Do and Rocheteau 2002). Nevertheless, we accounted for the effect of natural temperature gradients by first modelling them as a function of environmental variables (including lagged variables) for each sensor. We then used these tree-specific models (across-trees average $R^2 = 0.44$) to predict natural temperature gradients in the stem and corrected the raw dT signal; corrected sap flow density was 3.5 ± 1.1 % (across-trees mean ± SE) larger than the uncorrected values. For a robust $dT_{\max}$ estimation (i.e. dT under zero flow) we selected the highest dT of the previous night, only if the average of the minimum evaporative demand was less than 0.05 kPa during 2 hours and the coefficient of variation of the four highest dT values was less than 0.5 %. When these conditions were not met, $dT_{\max}$ was linearly interpolated from nearby days (Oishi et al. 2008).

Sap flow density per unit sapwood area (J_S) (kg m^{-2} sapwood s^{-1}), was calculated following the original calibration derived empirically by Granier (1985, 1987), multiplied by a radial correction coefficient (C_r) to account for the spatial variation of sap flow along the xylem radius. C_r was obtained for each species from published values of generic radial patterns of sap flow (Table 1) (Cohen et al. 2008, Poyatos et al. 2008, Mereu et al. 2009, Aguadé et al. 2011). Instantaneous values of J_S were then averaged daily for each monitored tree. Missing data due to occasional sensor failure (17 ± 4 % of individual tree data) was gap-filled using linear regressions with other sensors, choosing the one displaying the best fit, according to R^2 (range between 0.7 and 0.9).

Whole-tree sap flow rates (J_T) (kg s^{-1}) were obtained by multiplying J_S by sapwood area (A_S) (m^2). As we could not core the trees with sap flow sensors due to the long-term nature of the experimental set-up, sapwood area was estimated from a linear regression between stem basal area (A_B) and A_S obtained in the bibliography for the same tree species within the same region (Martínez-Vilalta et al. 2003, Gracia et al. 2004, Poyatos et al. 2007, Aguadé et al. 2011). These estimations were validated using visual measurements based on wood translucency in fresh disks obtained in a nearby area *ca*. 8 km from the plot (Can Catà, Collserola Natural Park); we found an excellent agreement between literature-derived estimations and field measurements (see supplementary Figure S1).

2.3. Basal area increment, tree water deficit and growth-based water use efficiency

Automatic band dendrometers (DRL26, EMS Brno, Czech Republic), which measure the linear displacement of a stainless steel band embraced around the trunk, were used to monitor stem circumference variation continuously. Displacement has an accuracy of 1 µm over an adjusted range of 60 mm. Dendrometers were installed at height of about 1.30 m, above the sap flow sensors. Outer bark was removed before the installation of the instrument. Almost all trees with sap flow probes had a dendrometer installed (*Q. ilex n*=6, *Q. pubescens n*=6, *A. unedo n*=4 and *P. halepensis n*=3), recording data every 15 min. Dendrometer data were converted to stem diameter variations and to basal area increment (BAI) (cm^2). We also calculated the BAI of each monitored tree relative to its basal area at the beginning of 2011 (BAI/A_B).

Dendrometer time series were de-trended in order to extract growth-independent diameter fluctuations caused by changes in sapwood and bark water content as a result of the daily and seasonal dynamics of stored water in the transpiration stream (Zweifel et al. 2005, Drew et al. 2011). Tree water deficit (ΔW) was calculated as the difference between the constant growth line and stem actual diameter variations and provides an index of whole-tree water status (see supplementary Figure S3). Here we assume that, having defined ΔW as a ‘deficit’ relative to an optimal hydrated state ($\Delta W = 0$), the value of ΔW takes increasingly positive values as drought-stress increases, consistent with Zweifel et al. (2005). As we focused on the seasonal variation in ΔW, not the daily cycles, here we report daily-averaged values.

Total annual BAI was transformed into annual aboveground carbon production (AGC, kg C year^{-1}) per tree using site- and species-specific allometric equations and carbon concentration data from IEFC (Gracia et al. 2004). See supplementary Table S1 for details of the equations. We then aggregated annual tree-level J_T and calculated water use efficiency with respect to annual BAI (WUE_{BAI}=BAI/J_T) and with respect to aboveground carbon production (WUE_{AGC}= AGC/ J_T).

2.4. Data analysis

All statistical analyses were carried out with R Statistical Software version 3.0.2 (R Development Core Team 2010). We used mixed-effects models (package nlme), specifying tree identity as a random factor, to analyse environmental and species-specific controls on J_S and ΔW, and to analyse the relationship between J_S and ΔW (Pinheiro and Bates 2000). The functional relationship between J_S and VPD was analysed fitting a nonlinear mixed model (nlme function) expressed as:

$$J_S = b \cdot \ln(\text{VPD}) + a \qquad (1)$$

Where *a* is the sap flow when VPD is equal to 1 kPa and the slope *b* represents absolute J_S sensitivity to VPD. In this analysis, two individuals of *Q. pubescens* were not used due to lack of fit. In order to capture the VPD response without other variables col-limiting sap flow, we only included days with solar radiation > 50 W m^{-2} and $\theta > 0.15$ cm^2 cm^{-2}. We also calculated the ratio between parameters b and a (*b/a*) as a measure of relative sensitivity to VPD, in an analogous way to the well-known stomatal model by Oren et al. 1999.

The response of J_S to θ was analysed using a three-parameter sigmoid function, based on similar functional responses reported elsewhere (Duursma et al. 2008, Poyatos et al. 2013):

$$J_S = \frac{J_{S,\mathrm{Asym}}}{1+\exp[(\theta_{\mathrm{mid}}-\theta)/\theta_{\mathrm{scal}}]} \qquad (2)$$

Where $J_{S,\mathrm{Asym}}$ is the horizontal asymptote, θ_{mid} the value of θ where J_S is 50 % of $J_{S,\mathrm{Asym}}$ and θ_{scal} a scaling parameter. The value of θ_{scal} represents the difference between θ_{mid} and the value of θ at which J_S is 75 % of $J_{S,\mathrm{Asym}}$, with lower values of θ_{scal} representing a steeper curve (see supplementary Figure S2). In order to capture the θ response without evaporative demand col-limiting sap flow, we only included days solar radiation > 50 W m^{-2} and VPD > 0.5 kPa.

We analysed ΔW using a linear mixed model, with tree as a random factor and species, θ, and VPD and their interactions as fixed factors. Exploratory data analyses showed an exponential-shaped relationship between ΔW and θ, and therefore we log-transformed ΔW in this model. The response of J_S and ΔW was also analysed using a linear mixed model including the species factor and its interaction with (log-transformed) ΔW.

Model selection for J_S and ΔW responses was based on the minimisation of the Akaike Information Criterion (AIC); models within 2 units of AIC were considered equivalent and, in this case, we retained the more parsimonious one (i.e. the one with less parameters). We graphically inspected residual plots and implemented appropriate variance structures to minimise heteroscedasticity in the residuals (varPower structure in nlme/lme functions). In sap flow models, day of the year (DOY) was used as a continuous time covariate (corCAR1 in function nlme/lme functions). We assessed the statistical significance of fixed effects using Wald *t*-tests. For all statistical tests, significance was accepted at $P<0.05$. We calculated pseudo-R^2 values for linear mixed models, based on a likelihood ratio test between the target model and a null (intercept-only) model, as implemented in the R-package MuMIn (Bartoń 2014).

3. Results

3.1. Seasonal course of environmental variables and sap flow

Over the studied period, meteorology was typically Mediterranean (Figure 1a). For 2011 and 2012, the mean annual air temperature was similar to the climatic mean value of 15.2 ºC (1951-2010) but annual precipitation in 2011 (804 mm) was 32 % higher than the climatic average, whereas in 2012 it was 21 % lower (479 mm) (Figure 1c). In particular, the 2012 winter period presented 90 % less precipitation (25 mm) than the same period of 2011 (254 mm) and 36 % less compared to the climatic average. Low values of θ were achieved in both summer periods (*ca.* 0.12 $cm^3\ cm^{-3}$), but in 2012 these coincided with higher values of VPD (Figure 1a, d); mean daily VPD during summer 2011 was lower than in 2012 (0.9 and 1.2 kPa, respectively) (Figure 1a).

The seasonal patterns of sap flow showed high J_S rates during spring across species for both years, and drought-related reductions in J_S beginning in August 2011 and June 2012, respectively (Figure 2). Autumn rainfall and the consequent rise in θ, helped to recover sap flow rates (Figure 2), except for *Q. pubescens* which reduced J_S coinciding with leaf senescence and maintained some residual sap flow during the leafless winter period. During winter, *A. unedo* and *Q. ilex* were the species with highest values of J_S. Spring J_S values were lowest for *P. halepensis* in both years and highest for *Q. pubescens* in 2011 and for *Q. ilex* in 2012 (see supplementary Table S2 and Figure 2). *Q. pubescens* displayed a lower J_S drop from spring to summer (10 % in 2011 and 20 % in 2012) compared to the rest of species (25 – 40 % in 2011 and 50 – 75 % in 2012), and was able to maintain the highest summer J_S values. No significant differences in J_S for a given seasonal period were found between years for either *A. unedo* or *Q. ilex* (see supplementary Table S2). As for tree-level sap flow, *Q. ilex* showed higher J_T values than the rest of species, while *Q. pubescens*, in general, displayed the lowest values. Intermediate J_T values were found for *A. unedo* and *P. halepensis* (see supplementary Table S2 and Figure 2).

3.2. Environmental responses of sap flow across species and years

Daily J_S was positively and non-linearly related to θ for all species, plateauing at moderate moisture values (Figure 3a, b). For 2011 and 2012, the higher θ_{mid} values (i.e., the θ value at which sap flow is 50% of $J_{S,Asym}$) were observed for *P. halepensis*. The rest of the species showed lower θ_{mid} values and no significant differences were found between years (Table 2). In contrast, the species-specific patterns of $J_{S,Asym}$ did vary between years; in 2011, $J_{S,Asym}$ was significantly higher for *Q. pubescens*, *Q. ilex* showed higher $J_{S,Asym}$ compared to *P. halepensis*, whereas $J_{S,Asym}$ of *A. unedo* was similar to *Q. ilex* and *P.halepensis* (Table 2). In 2012, $J_{S,Asym}$ was significantly higher for *Q. ilex*, whereas *Q. pubescens* and *A. unedo* showed higher $J_{S,Asym}$ compared to *P. halepensis* (Table 2).

The relationship between J_S and VPD was also non-linear and well described by a logarithmic response (Figure 3c, d). The highest values of both VPD parameters were found for *Q. pubescens* in 2011 and *Q. ilex* in 2012. The slope of the relationship between J_S and VPD (parameter *b*) in 2011 was similar for *P. halepensis*, *Q. ilex* and *A. unedo* (Table 2). In contrast, in 2012, parameter *b* for *P. halepensis* was not significantly different from the value observed for *Q. pubescens*. *P. halepensis* always showed the highest values of *b/a* (i.e. higher relative sensitivity of J_S to VPD) while *Q.*

pubescens showed a high interannual variation in *b/a*. *A. unedo* and *Q. ilex* displayed similar and consistent values of *b/a* across years (Table 2).

3.3. Basal area increment across species and years

P. halepensis BAI was significantly higher than the rest of the species for both years (Table 3 and Figure 4a) but BAI/A_B revealed that all the species showed a similar seasonal pattern of BAI (Figure 4b). Spring rainfall in 2011 was followed by increases in BAI across species (Figure 4), while the onset of the 2011 summer period coincided with *ca.* 3 months of stem shrinkage for *A. unedo*, *Q. ilex* and, to a lesser extent, *Q. pubescens*. In contrast, *P. halepensis* appeared to maintain a nearly-constant BAI during the 2011 summer period. Autumn rainfall led to a quick stem swelling in all the species (Figure 4b). In 2012, the spring rise in BAI was much lower than in 2011 for all the species. The stem shrinkage period associated with the 2012 summer season was longer than in 2011 (at least *ca.* 4 months), but punctuated by small rainfall events that produced only transient stem refilling (Figure 4b). Stem shrinkage in 2012 was especially intense for *A. unedo*.

In 2011, *Q. pubescens* was the species with the highest values of annual BAI/A_B followed by *P. halepensis* (Table 3 and Figure 4b). Nevertheless, for 2012, significant differences among species were found, being *Q. pubescens* and *P. halepensis* the species with the highest values of BAI/A_B (Table 3 and Figure 4b). In 2012, most species showed significantly lower values than in 2011 (Table 3) and even some trees presented a negligible annual BAI (see supplementary Table S3). BAI reductions in 2012 compared to 2011 were around 90 % for *Q. ilex* and *A. unedo*, and 60 % for *P. halepensis*, but they were non-significant for *Q. pubescens*.

3.4. Environmental controls on ΔW

The seasonal course of daily ΔW was similar for all the species over the two study years (Figure 4c). The higher values of ΔW were observed during summer and autumn, coinciding with a decline in θ and the increase of VPD, although moderate values (~0.2-0.3 mm) were also observed during wintertime. The longest period with sustained high values of ΔW occurred in 2012, the intense drought year. In general, evergreen sclerophyllous species presented the highest values of ΔW (Figure 4c).

Daily ΔW was inversely and non-linearly related to θ for all species, approaching 0 (i.e. the fully hydrated state) at values of θ above *ca.* 0.15 cm^3 cm^{-3} (Figure 5). An increasing trend in ΔW with respect to VPD was observed more clearly for 2012 (Figure 5). The best models describing the variation in ΔW as a function of water supply and demand differed between years, and both included the species effect, the interaction between θ and VPD and the interaction between θ and species (Table 4), albeit this latter effect was not significant in 2011. In 2012, we detected an additional interaction between VPD and species (Table 4). Only at low values of θ, we observed that the relationship between ΔW and θ became steeper as VPD increased (Figure 6). *A. unedo* and *Q. ilex* displayed the strongest responses of ΔW to θ, and *Q. ilex* showed a particularly steep response in 2012. Likewise, ΔW only showed a clear increase with VPD when θ was low (see supplementary Figure S4); *P. halepensis* and *Q. pubescens* both displayed a low sensitivity of ΔW to VPD, whereas it was higher for *A. unedo* and *Q.ilex*. In general, for a given, low θ (0.11 cm^3 cm^{-3}) and moderate values of VPD = 1 kPa, ΔW was higher in 2012 compared to 2011 (see supplementary Figure S4).

3.5. Relationship between sap flow and ΔW

J_S declined nonlinearly with increasing ΔW, following a steeper relationship in 2012 compared to 2011 across all species, except for *Q. pubescens* (Figure 7a, b), which, at

ΔW of 50% of its year-specific maximum, maintained J_S at *ca.* 65% of the maximum value, when the rest of species only reached 25-40% (data not shown). The sensitivity of J_S to log-transformed ΔW varied across all species for 2012, while for 2011, *A. unedo* and *Q. ilex* (*P*=0.731), *Q. pubescens* and *Q. ilex* (*P*=0.051) and *Q. pubescens* and *P. halepensis* (*P*=0.362) showed no differences in the sensitivity of J_S to log ΔW (Table 5). Overall, *Q. ilex* and *A.unedo* showed the highest sensitivity of J_S to ΔW and *P. halepensis* and *Q. pubescens* showed the lowest.

3.6. Growth-based water use efficiency

Variation of WUE_{BAI} and WUE_{AGC} across years and species was identical (Table 3), hence we will only discuss WUE_{BAI} results. *P. halepensis* showed high BAI with comparatively low transpiration, leading to the highest values of WUE_{BAI} among the studied species for both years (Table 3). In contrast, *Q. ilex* presented higher transpiration as well as low growth, and therefore it showed low WUE_{BAI} during both years. *A. unedo* also showed low WUE_{BAI}, whereas *Q. pubescens* presented intermediate WUE_{BAI} values (Table 3). WUE_{BAI} reductions in 2012 compared to 2011 were strong in *Q. ilex* (89 %) and, *A. unedo* (85 %), compared to only 29 % for *P. halepensis*; a non-significant reduction of 58 % was observed for *Q. pubescens*.

4. Discussion

4.1. Sap flow: seasonal course and environmental controls

Seasonal variability in sap flow differed across species, and it was mainly associated with their leaf habit and response to drought. Deciduous *Q. pubescens* presented a residual sap flow during the leafless period, which could be attributed to transpiration through the bark (e.g. Stöhr and Lösch 2004) and to the fact that one *Q. pubescens* tree kept its leaves functional all year round. Remarkably, winter sap flow was generally higher than in summer for all three evergreen species (see supplementary Table S2), particularly *Q. ilex* and *A. unedo*.

Responses of sap flow to water supply and demand varied across species and most inter-annual variability was observed for *Quercus* species, which displayed the highest J_S, but showed opposite species-specific patterns with drought intensity. In the dry year (2012), *Q. ilex* increased $J_{S,Asym}$ and parameter *a*, because it displayed the highest fluxes in in late winter and spring, in response to frequent rainfall which maintained soil water availability during these periods (Figure 1c, d). In contrast, both $J_{S,Asym}$ and parameter *a* decreased in 2012 for *Q. pubescens*. Reduced precipitation during late autumn and early winter 2012 could have precluded the recharge of deep soil water, which is a preferred water source for the deciduous *Q. pubescens* (Valentini et al. 1992), causing a reduction in maximum sap flow rates.

P. halepensis and *Q. ilex* displayed a higher θ threshold for J_S reductions (i.e. higher θ_{mid}) (Table 2 and Figure 3), consistent with their strict stomatal control under soil drought (Borghetti et al. 1998, Tognetti et al. 1998, Maseyk et al. 2008). In contrast, *Q. pubescens* showed comparatively lower θ_{mid} values, and was less sensitive to declining soil moisture than co-occurring species, in agreement with patterns observed elsewhere (Poyatos et al. 2005, Zweifel et al. 2007) and with the general trend of ring-porous species being less sensitive to soil drying (Meinzer et al. 2013). Absolute sensitivity of J_S to VPD (parameter *b*) was higher in species with higher potential J_S (parameter *a*). Relative sensitivity (*b/a*) did not vary greatly between years, and only *P. halepensis*, in line with its more conservative water use, tended to show a higher value of *b/a*. *A. unedo* and *Q. ilex,* displayed similar J_S rates during spring and summer, consistent with findings in other Mediterranean locations (i.e. Gratani and Ghia 2002). *A. unedo* also showed a similar θ_{mid} value compared to *Q. ilex*, but presented a steeper reduction in J_{S} with lower θ (Table 2 and Figure 3), consistent with mixed drought responses observed for these two sclerophyllous species (Martínez-Vilalta et al. 2003, Mereu et al. 2009).

Overall, our results largely support our hypothesis 1a (comparatively stronger drought physiological responses in *P. halepensis*), but, remarkably, the physiological parameters controlling transpiration sensitivity to drought, especially the response to θ, only vary within a narrow range across species and years. In contrast, more structural traits (A_L:A_S, a, $J_{\mathrm{S,Asym}}$) display much higher variability. Our results also highlight the importance of timing of drought in driving differences in water use regulation between *Quercus* species, possibly related to water partitioning at different soil depths. Unfortunately, because of the limited number of available soil moisture probes and the compromise between horizontal and vertical sampling, the influence of deeper soil water content on our results could not be assessed. Nevertheless, the lack of soil moisture measurements over the entire soil profile is unlikely to have confounded our interpretation of drought responses. Firstly, soils are relatively shallow and soil moisture probes measure 60% of the total soil profile. Secondly, although trees may switch to deeper root water uptake during drought, especially in the fractured substrate underlying the study site, a recent study in a similar setting found no species-specific differences in the seasonal variation of plant water sources (Barbeta et al. 2014). In addition, despite this availability of water at deeper soil layers, tree transpiration regulation may still be related to θ in the uppermost soil, where most fine-root biomass is located (Warren et al. 2005, Duursma et al. 2008).

4.2. Seasonal BAI in Mediterranean tree species

P. halepensis showed considerably higher BAI rates than the rest of the species (Figure 4a), as expected for an early successional pine (hypothesis 2). However, in relative terms (i.e. BAI/A_B), *Q. pubescens* showed slightly higher stem increment than *P. halepensis*, whereas *Q. ilex* and *A. unedo*, again, showed similar dynamics (Figure 4b). In 2012, all species reduced their BAI, but surprisingly, BAI was particularly reduced for *Q. ilex* and *A. unedo* (Table 3). Our results, thus, only partially support hypothesis 2, as we expected that drought-related decreases in BAI would be strongest for the sub-Mediterranean *Q. pubescens*.

The seasonal BAI curve of all species in 2011 clearly showed stem hydration and growth in spring and early summer, a contraction phase due to depletion of stored water during the summer (concurrent with increases in ΔW; Figure 4b, c) and stem rehydration after autumn rainfall. However, in 2012, a long winter period with negligible or even negative BAI was followed by very small stem increments in spring. For *A. unedo*, we did not observe a clear stem increment phase, which may be indicative that radial growth was nearly suppressed, in line with studies showing a high drought sensitivity of *A. unedo* radial growth (Cherubini et al. 2003, Ogaya et al. 2003).

The stem contraction phase during the summer was longer in 2012 compared to 2011 (Figure 4b), and also longer than the *ca.* 3 months observed for *Pinus pinaster* (Vieira et al. 2013). Overall, the seasonal dynamics of BAI/A_B in summer 2012 appeared to be highly influenced by rainfall pulses; following a relatively long summer drought, most of the stem diameter recovery observed in autumn was probably water-related. However, late season growth has been reported for *Q. ilex* and *P. halepensis* (Campelo et al. 2007, Camarero et al. 2010; Nicault et al., 2001), although it may be less likely for *A. unedo* (De Lillis and Fontanella 1992) and *Q. pubescens* (Zweifel et al. 2007). Indeed, growth curves extracted for ΔW calculation, which have been reported to be closely related to the actual accumulation of new wood cells (Zweifel et al. 2007), suggest that detectable growth only occurred for *P. halepensis* (see supplementary Figure S5). Direct measurements of intrannual growth (i.e. repeated micro-coring or pinning) would be needed to confirm these patterns.

4.3. Environmental control of dendrometer-based tree water deficit across Mediterranean tree species

Maximum daily values of ΔW were 0.2 - 0.5 mm for all trees, a similar range to that observed by Zweifel et al. (2005) for *Q.pubescens* (0.4 - 0.5 mm), but much lower than the values > 1 mm observed for the drought-resistant *Callitris intratropica* (Drew et al. 2011). The species ranking of ΔW was: *A. unedo* (semi ring-porous) > *Q. ilex* (diffuse porous) > *P. halepensis* (conifer) > *Q. pubescens* (ring-porous). Hence, the variability in the magnitude of ΔW was not clearly associated with wood type. Given the tight relationship between leaf water potential and ΔW (Drew et al. 2011), the observed higher values for the two evergreen sclerophylls would suggest that they underwent higher stress conditions (i.e. lower water potentials) compared to *Q. pubescens* and *P. halepensis*. Simultaneous monitoring of leaf water potentials and ΔW would be needed to test for likely species-specific differences in the association between these two variables (Oberhuber et al. 2014).

Water supply (θ) and demand (VPD) interacted to determine the variation in ΔW, as reported by Zweifel et al. (2005), despite that a recent study in a water-limited forest only reported additive effects of VPD and θ (Drew et al. 2011). We observed that higher ΔW values were reached at similar conditions of water supply and demand in 2012 (dry year) compared to 2011 (wet year). These results imply that other factors, related to unmeasured physiological processes (i.e. stomatal control) or environmental factors (i.e. soil moisture at deeper soil layers) could be driving the observed shifts in ΔW between years. With regard to species-specific differences, *A. unedo* and *Q. ilex* (in 2012) showed the steepest increases in ΔW with decreasing θ, and, interestingly *A. unedo* also showed the steepest reductions in J_S with θ. We did not observe a higher sensitivity to drought in ΔW for *P. halepensis*, as hypothesized (hypothesis 1a). In general, across species, the θ levels at which ΔW and J_S began to decline were similar. Hence, the θ threshold for sap flow reduction seems to be related to the soil water availability where the tree shows only partial refilling of its water reserves (Köcher et al. 2013). Furthermore, our results show that a given increment in VPD causes a higher increase in ΔW under dry soil conditions, supporting the view that water is withdrawn more strongly from the tree's internal storage as the soil dries (Zweifel et al. 2005).

We observed a strong nonlinear decrease of J_S and ΔW with θ at similar θ thresholds (compare Figure 3a, b with Figure 5a, b), as proposed in hypothesis 1b. All species showed a remarkably similar relationship between J_S and ΔW in 2011, but not in 2012. *Q. pubescens*, especially in 2012, managed to maintain a comparatively higher J_S at a given ΔW, as previously observed in a temperate forest (Zweifel et al. 2007). For the rest of species, more intense drought conditions in 2012 caused a steeper relationship between J_S and ΔW. Hence, the nonlinear decrease of J_S with increasing ΔW and the strong coupling of both variables with drying soil demonstrate the linkage between transpiration regulation and tree water storage dynamics. However, J_S and ΔW could be temporally decoupled during relatively wet conditions; for example, for *Q. ilex*, ΔW showed some decline with decreasing θ at values larger than 0.15 cm^3 cm^{-3} (Figure 5a, b; Figure 6e, f), while J_S for this species remained relatively unchanged at such θ levels (Figure 3a, b).

4.4. Drought-related variation in growth-based water use efficiency across Mediterranean tree species

The studied Mediterranean forest displays a high functional diversity of strategies with respect to growth and water use, and thus a wide range of WUE_{BAI}. Annual BAI was more reduced than water use in a dry year (2012) as compared to a wet year (2011), consistent with our hypothesis 3. Given the inverse relationship between WUE and VPD (e.g. Seibt et al. 2008), higher VPD in 2012 (0.68 kPa) vs 2011 (0.55 kPa) would be responsible for a 24 % lower WUE_{BAI} in 2012. However, we found stronger declines for all species, except for *P. halepensis*, suggesting that VPD effects alone could not explain WUE_{BAI} variation. This decrease in WUE_{BAI} with drought may seem counterintuitive if we consider the link between instantaneous, leaf-level photosynthesis and transpiration. However, a decrease in WUE_{BAI} with drought is consistent with a positive association between forest resource use efficiency and resource intensity use, when assessed at large spatiotemporal scales (whole-tree, annual measurements) (Binkley et al. 2004).

With respect to interspecific patterns, in 2011, *P. halepensis* and *Q. pubescens* achieved the highest WUE_{BAI} through opposite functional strategies (hypothesis 4): strict (*P. halepensis*) vs moderate (*Q. pubescens*) physiological control of transpiration in response to drought and evergreen (*P. halepensis*) vs winter-deciduous (*Q. pubescens*) leaf habit (see also McCarthy et al. 2011). However, in 2012 *P. halepensis* was clearly the species with the higher WUE_{BAI} in accordance with its high preferential allocation to aboveground growth (Sanz-Pérez et al. 2009) and its capacity to thrive in dry habitats (Maseyk et al. 2008). Across years, *Q. ilex* and *A. unedo* showed similar and consistently lower WUE_{BAI} values compared to *P. halepensis* and *Q. pubescens*. This comparatively lower WUE_{BAI} in the two evergreen sclerophyllous species may be explained by (1) an increased C allocation to roots or increased fine root turnover (López et al. 1998), (2) enhanced carbohydrate storage or (3) higher respiratory costs (Sanz-Pérez et al. 2009).

4.5. Concluding remarks

Tree species with contrasting leaf habit, wood type and stomatal behaviour have shown coordinated drought responses of sap flow, water storage dynamics and growth-based WUE which allowed them to co-exist in the studied Mediterranean forest. However some species-specific variability in these responses may directly impact stand dynamics and composition, especially under the projected increases in aridity for the Mediterranean region (e.g. Collins et al. 2013). The comparatively stronger stomatal control displayed by *P. halepensis* probably allowed this species to avoid substantial leaf shedding in August 2012, when mostly *Q. pubescens* and *A. unedo* but also *Q. ilex*, to a lesser extent, were affected (Sperlich et al. in press). Indeed, *Q. pubescens* is especially vulnerable to hydraulic failure and subsequent leaf desiccation during intense summer droughts, but it may also show a rapid canopy recovery in the following year relying on carbohydrate reserves. Both *Q. pubescens* and *P. halepensis* maintained comparatively higher WUE_{BAI} in a dry year by a combination of different physiological (stomatal control) and structural (leaf habit, relative allocation to aboveground growth) mechanisms. In contrast, *Q. ilex* and *A.unedo* showed a relatively high physiological sensitivity to drought, which was somehow unexpected given the wide presence of both species in Mediterranean forests. Nevertheless, their sustained transpiration outside the main growing season probably indicates that they may take advantage of year-round photosynthetic activity. Moreover, they may be more competitive and resilient in the long-term if their low WUE_{BAI} results from a higher relative allocation to roots and/or carbohydrate storage. In fact, the current low *P. halepensis* density and the predominance of *Q. ilex* may be revealing the ongoing ecological succession in the stand after the cessation of management practices during the 20th century (Sperlich et al. 2014).

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Figure captions

Figure 1. Seasonal course of: (a) daily mean water vapour pressure deficit (VPD) (black dots) and air temperature (grey dots), (b) daily mean solar radiation, (c) daily total gross precipitation and (d) daily mean volumetric soil water availability over the top 30 cm of soil (θ) (solid line) and daily volumetric soil water availability for each sensor (n=5) (dot line). Labels on the x axis represent year in month/year format (i.e. January 2011 is 1/2011).

Figure 2. Seasonal course of daily sap flow over the study period across trees mean sap flow per unit sapwood area (J_S) for (a) *Q.ilex*, (b) *Q.pubescens*, (c) *A.unedo* and (d) *P.halepensis*; and sap flow per tree (J_T) for (e) *Q.ilex*, (f) *Q.pubescens*, (g) *A.unedo* and (h) *P.halepensis*. For all the panels 2011 values are shown in line and 2012 values in dash line. Labels on the x axis represent day of the year (DOY).

Figure 3. Responses of sap flow density (*J*s) to (a) volumetric soil water availability (θ) (data selected when VPD>0.5 kPa and solar radiation>150 W m^{-2}) for each species in 2011 and (b) 2012, (c) responses to vapour pressure deficit (VPD) (data selected when θ>0.15 cm^2 cm^{-2} and solar radiation>50 W m^{-2}) in 2011 and (d) 2012. *Q. ilex* (grey triangle and grey solid line), *Q. pubescens* (black diamond and black solid line), *A. unedo* (black empty circle and black dashed line) and *P. halepensis* (grey cross and grey dashed line). Average daily values for each species are shown.

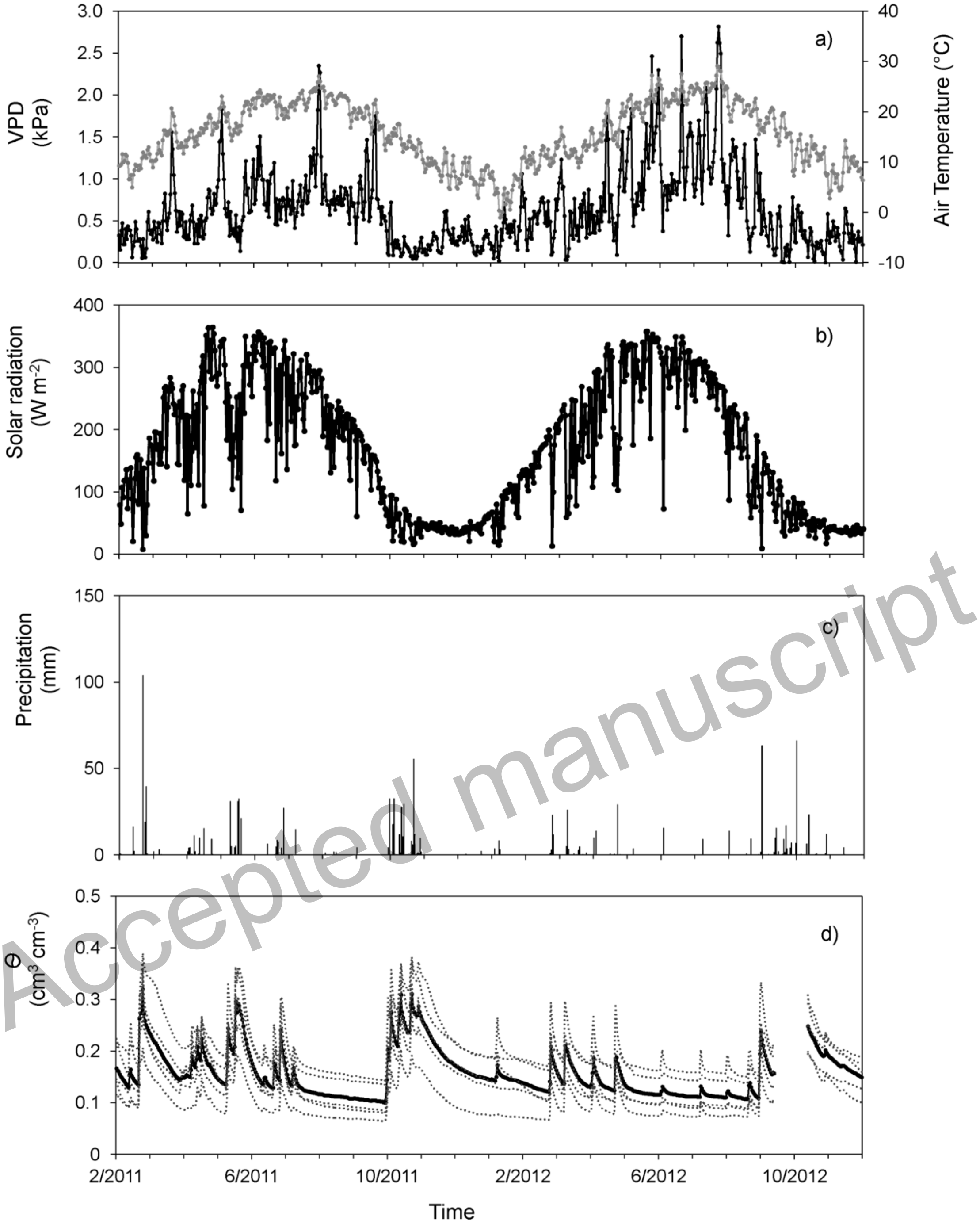
Figure 4. Seasonal course of (a) mean basal area increment (BAI), (b) BAI of each tree relative to its basal area at the beginning of 2011 (BAI/A_B) and (c) tree water deficit (ΔW) over the study period for: *Q. ilex* (grey line), *Q. pubescens* (black line), *A. unedo*

(black dashed line) and *P. halepensis* (grey short dash line). Labels on the x axis represent year in month/year format (i.e. February 2011 is 2/2011). BAI curves in panels (a) and (b) are reset to zero at the beginning of 2012.

Figure 5. Responses of tree water deficit (Δ*W*) to (a) volumetric soil water availiability (*θ*) (data selected when VPD>0.5 kPa and solar radiation>150 W m^{-2}) for each species in 2011 and (b) 2012, (c) responses to vapour pressure deficit (VPD) (data selected when solar radiation>50 W m^{-2}) in 2011 and (d) 2012. *Q. ilex* (grey triangle), *Q. pubescens* (black diamond), *A. unedo* (black empty circle) and *P. halepensis* (grey cross). Average daily values for each species are shown.

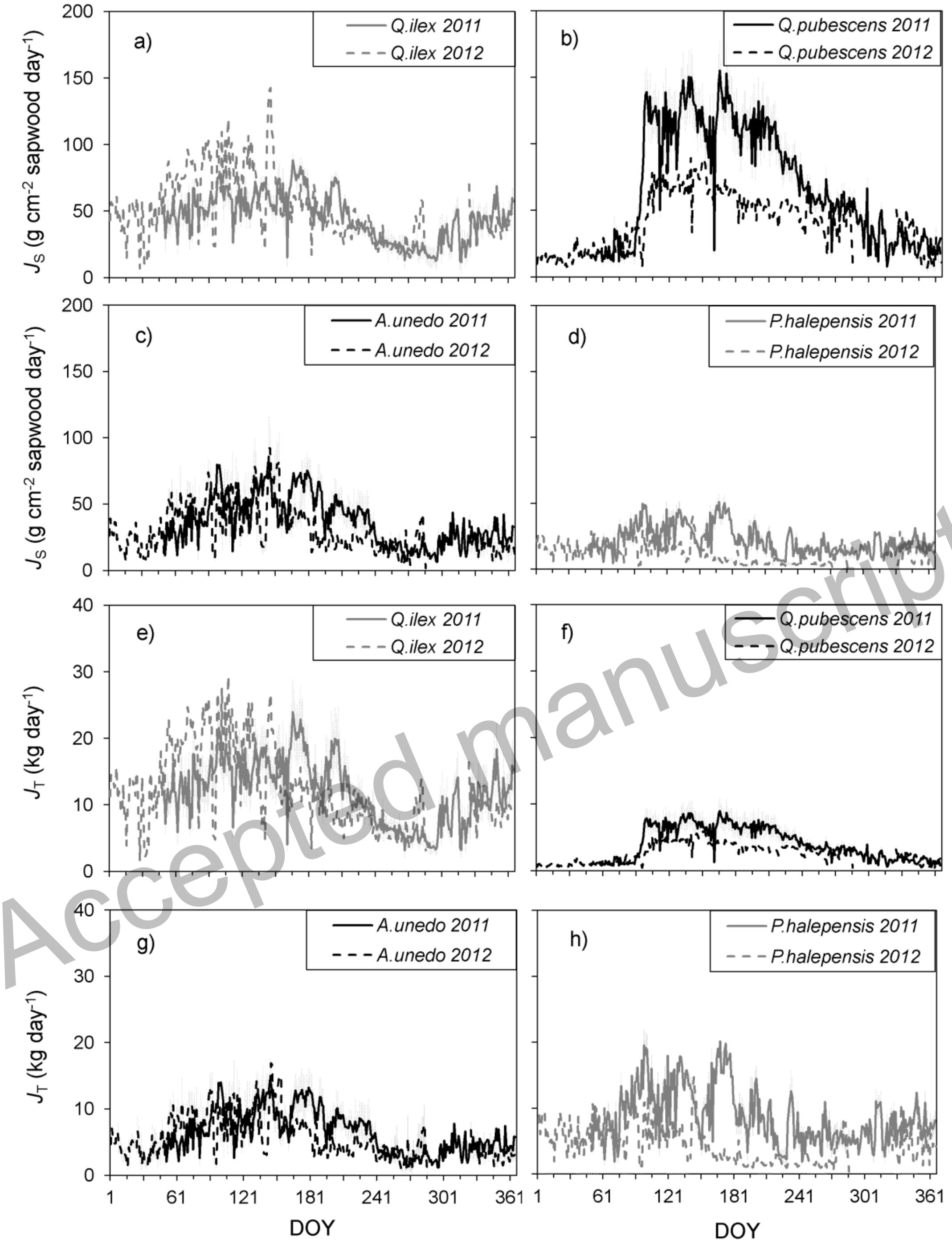
Figure 6. Modelled responses of tree water deficit (Δ*W*) to volumetric soil water availability (*θ*) at different values of vapour pressure deficit (VPD) (0.5, 1.0, 2.0 and 2.5 kPa) for each species, according to model in Table 4. Panels on the left column depict results for 2011 and panels on the right, for 2012.

Figure 7. Responses of sap flow density (*J*s) to tree water deficit (Δ*W*) (data selected when VPD>0.5 kPa and solar radiation>150 W m^{-2}) for each species in (a) 2011 and (b) 2012. *Q. ilex* (grey triangle and grey solid line), *Q. pubescens* (black diamond and black solid line), *A. unedo* (black empty circle and black dashed line) and *P. halepensis* (grey cross and grey dashed line). Average daily values for each species are shown.

817 

818 **Figure 1.**

819



820

821 **Figure 2.**

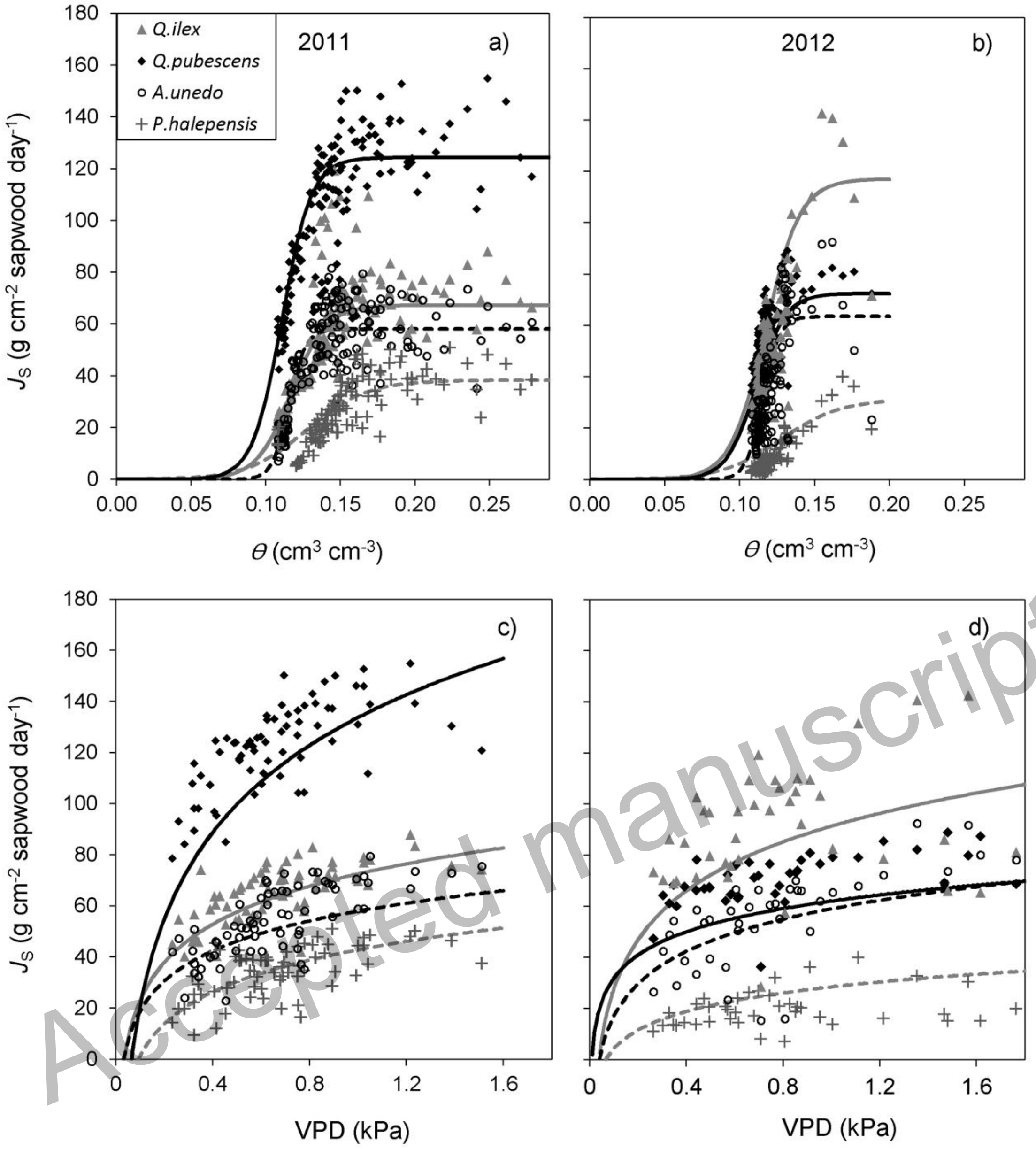
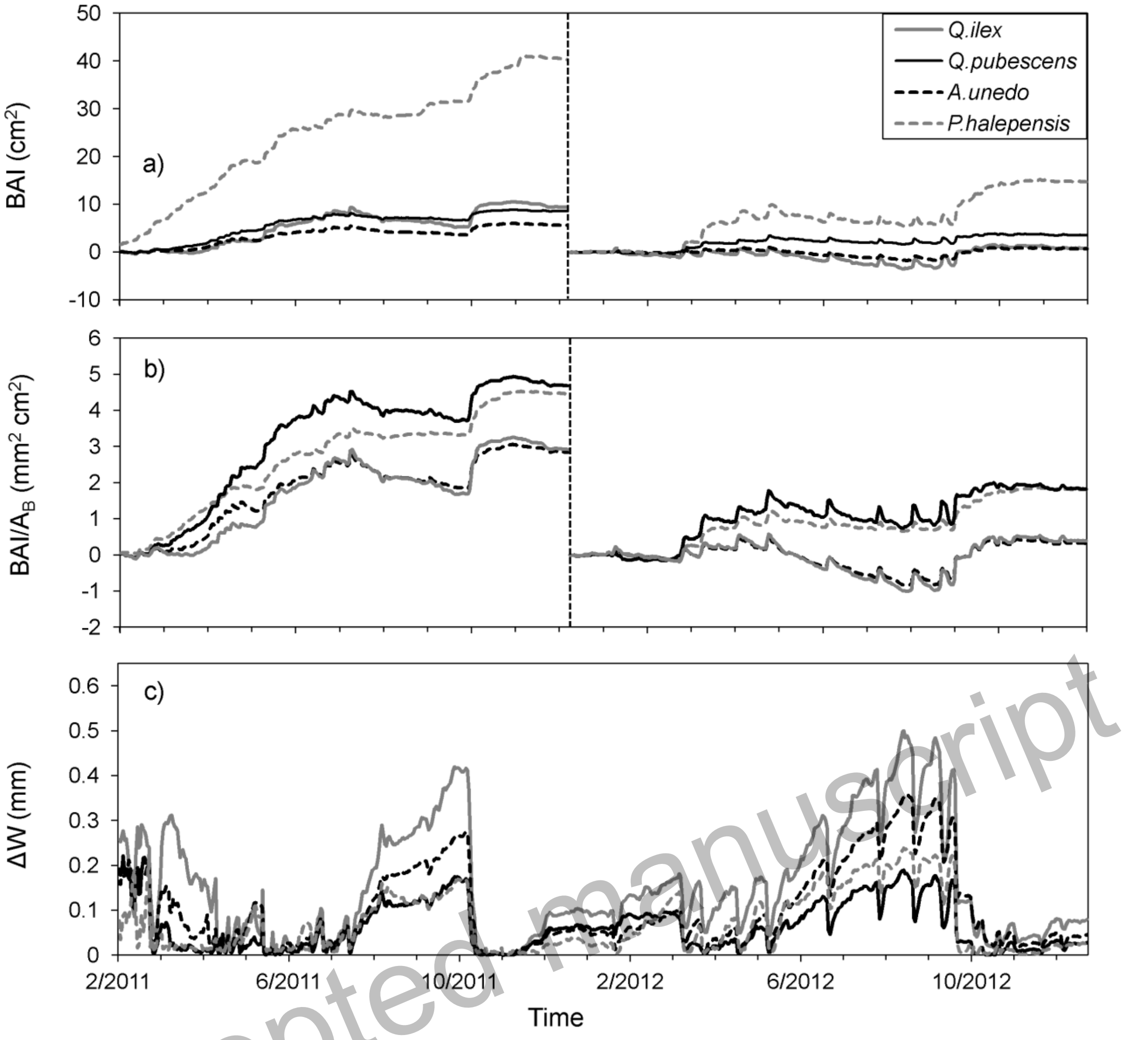

Q.ilex
Q.pubescens
A.unedo
P.halepensis
2011
a)
2012
b)
c)
d)
J_S (g cm^{-2} sapwood day^{-1})
θ (cm^3 cm^{-3})
VPD (kPa)
0
20
40
60
80
100
120
140
160
180
0.00
0.05
0.10
0.15
0.20
0.25
0.4
0.8
1.2
1.6

Figure 3.



824

825 **Figure 4.**

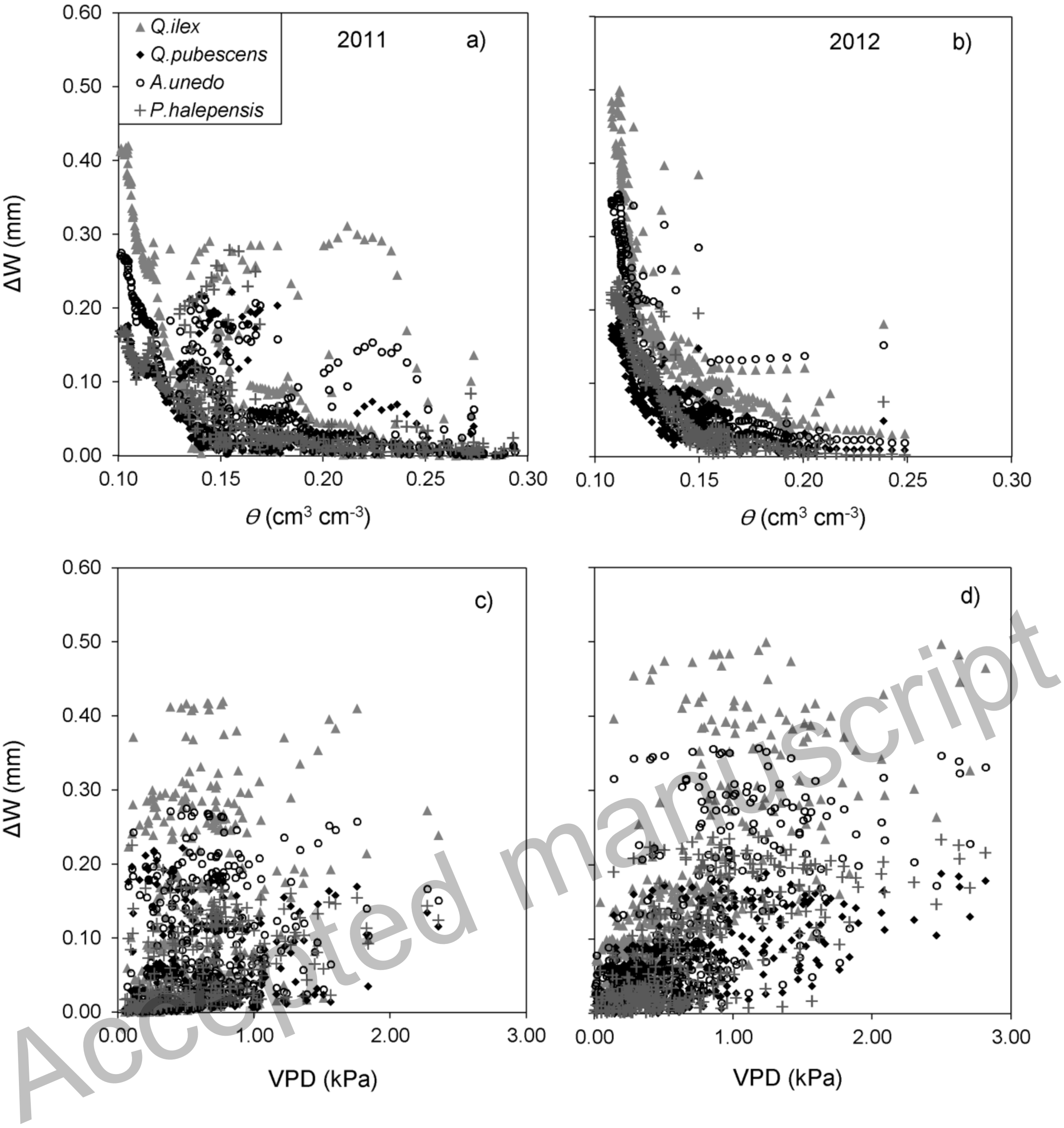

▲ Q.ilex
◆ Q.pubescens
○ A.unedo
+ P.halepensis
2011
a)
2012
b)
c)
d)
ΔW (mm)
θ (cm³ cm⁻³)
VPD (kPa)
0.00
0.10
0.20
0.30
0.40
0.50
0.60
0.10
0.15
0.20
0.25
0.30
1.00
2.00
3.00

Figure 5.

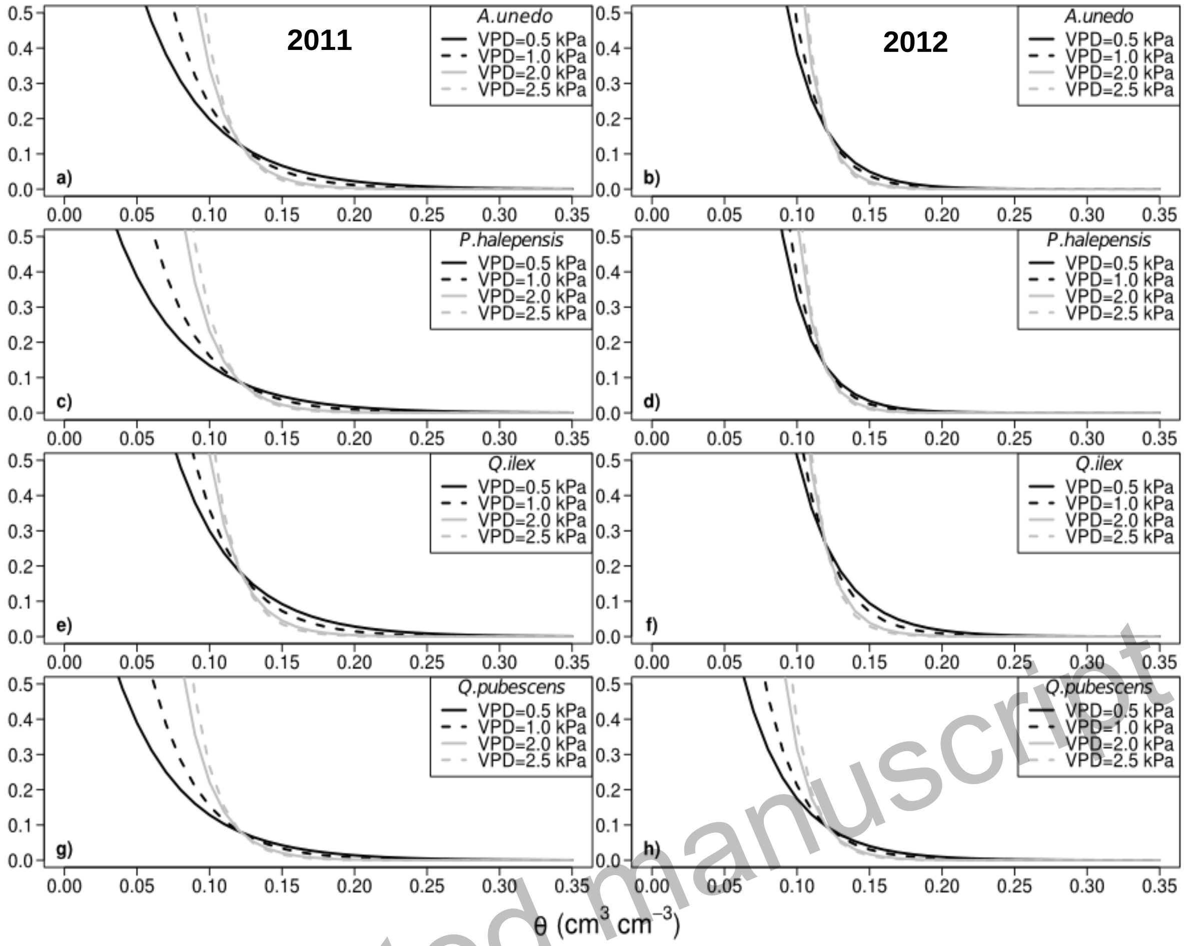
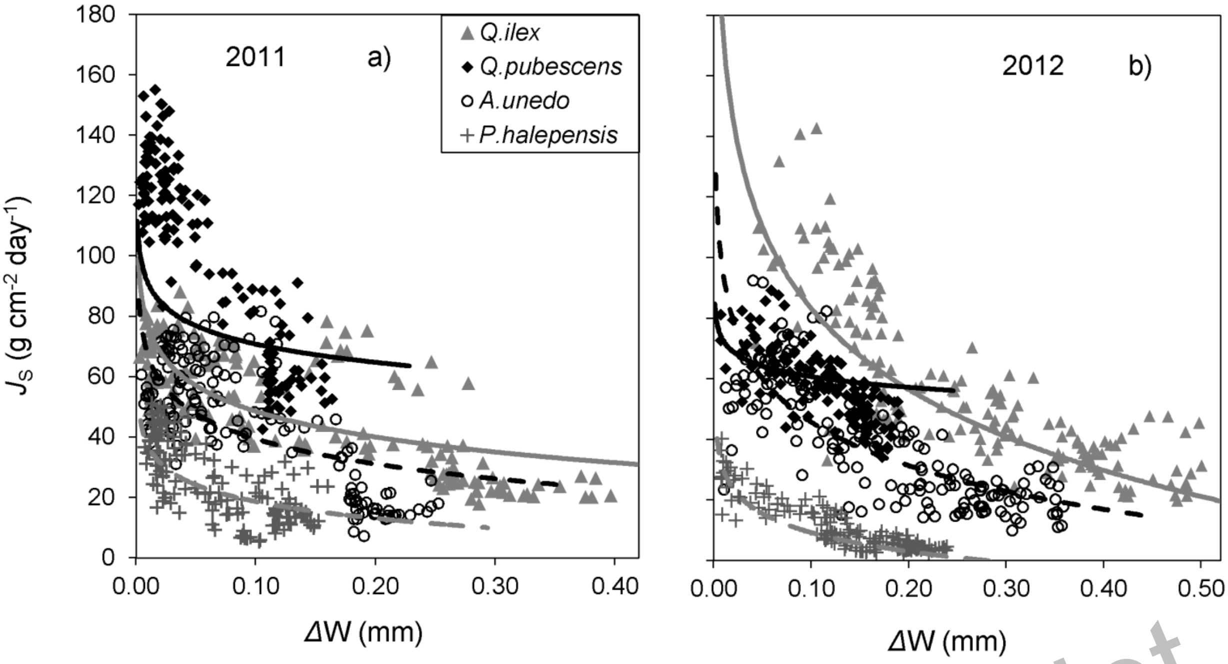

2011
2012
A.unedo
P.halepensis
Q.ilex
Q.pubescens
VPD=0.5 kPa
VPD=1.0 kPa
VPD=2.0 kPa
VPD=2.5 kPa
a)
b)
c)
d)
e)
f)
g)
h)
ΔW (mm)
θ (cm3 cm−3)
0.0
0.1
0.2
0.3
0.4
0.5
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35

Figure 6.



2011
a)
2012
b)
Q.ilex
Q.pubescens
A.unedo
P.halepensis
J_S (g cm^{-2} day^{-1})
ΔW (mm)
0
20
40
60
80
100
120
140
160
180
0.00
0.10
0.20
0.30
0.40
0.50

Figure 7.

Table 1. Main stand characteristics for each tree species. All data are reported at the stand scale except mean height, which is the average height of the monitored trees. Abbreviations: Mean DBH: Mean diameter at breast height; A_B: Basal area; A_S: Sapwood area; LAI: Leaf area index; A_L/A_S: Leaf to sapwood area ratio; Cr: Radial correction coefficient.

	Q. ilex	*Q. pubescens*	*A. unedo*	*P. halepensis*	Total
Density (stems ha^{-1})	1150	150	76	53	1429
Mean height (m)[a]	10.2 ± 0.6	9.6 ± 0.3	8.1 ± 0.3	17.1 ± 0.4	10.8 ± 0.6
Mean DBH (cm)	11.9 ± 0.7	12.0 ± 0.6	9.6 ± 0.5	33.7 ± 1.4	12.6 ± 0.2
A_B (m^2 ha^{-1})	14.9	1.9	0.6	5.2	22.6
A_S (m^2 ha^{-1})[b]	11.5	0.8	0.5	2.2	15.1
A_S/A_B	0.8	0.4	0.9	0.4	0.7
LAI (m^2 m^{-2})[c]	2.5	0.3	0.1	0.3	3.3
A_L/A_S (m^2 cm^{-2})	0.2 ± 0.1	0.4 ± 0.1	0.3 ± 0.0	0.1 ± 0.0	-
C_r[d]	0.5	0.7	1.0	0.7	-

[a] Mean height of all the monitored trees (*n*=7, *n*=7, *n*=4 and *n*=3 respectively)

[b] Data from this study and estimated according to Aguadé et al. 2011, Martínez-Vilalta et al. 2003 and Poyatos et al. 2007.

[c] Based on allometric equations from the Ecological and Forest Inventory of Catalonia (IEFC) for Collserola Natural Park (Gracia et al. 2004).

[d] Data adapted from Aguadé et al. 2011, Cohen et al. 2008, Poyatos et al. 2008 and Mereu et al. 2009.

Table 2. Parameter values estimated of the nonlinear mixed models relating species sap flow per unit sapwood area (J_{S}) with volumetric soil water availability (θ) and vapour pressure deficit (VPD) for 2011 and 2012. Different letter represents statistically significant differences between species for a given parameter and year ($P<0.05$). Bold numbers represent statistically significant differences between years for a given parameter and species ($P<0.05$). The parameters have been extracted from the following equations (see main text for more details): $J_{\mathrm{S}} = b \cdot \ln(\mathrm{VPD}) + a$ and $J_{\mathrm{S}} = \frac{J_{\mathrm{S,Asym}}}{1+\exp[(\theta_{\mathrm{mid}}-\theta)/\theta_{\mathrm{scal}}]}$

		Q. ilex	*Q. pubescens*	*A. unedo*	*P. halepensis*
$J_{\mathrm{S,\ Asym}}$	2011	**67.26 ± 7.16$^{\mathbf{a}}$**	**124.30 ± 8.41$^{\mathbf{b}}$**	58.17 ± 9.33^{ac}	38.35 ± 11.00^{c}
(g cm^{-2} day^{-1})	2012	**118.20 ± 10.12$^{\mathbf{a}}$**	**71.33 ± 12.77$^{\mathbf{b}}$**	63.04 ± 12.78^{b}	31.50 ± 13.09^{c}
θ_{mid}	2011	0.117 ± 0.002^{a}	0.111 ± 0.002^{b}	0.115 ± 0.002^{ab}	0.127 ± 0.005^{c}
(cm^{3} cm^{-3})	2012	0.123 ± 0.003^{a}	0.109 ± 0.004^{b}	0.118 ± 0.004^{ab}	0.133 ± 0.005^{c}
θ_{scal}	2011	0.012 ± 0.001^{ac}	0.010 ± 0.001^{a}	0.005 ± 0.001^{b}	**0.020 ± 0.005$^{\mathbf{c}}$**
(cm^{3} cm^{-3})	2012	0.011 ± 0.001^{a}	0.007 ± 0.001^{b}	0.007 ± 0.001^{b}	**0.010 ± 0.002$^{\mathbf{ab}}$**
a	2011	**72.65 ± 6.31$^{\mathbf{a}}$**	**133.84 ± 7.58$^{\mathbf{b}}$**	58.05 ± 8.39^{ac}	42.93 ± 9.72^{c}
	2012	**91.49 ± 6.86$^{\mathbf{a}}$**	**62.13 ± 8.36$^{\mathbf{b}}$**	59.14 ± 9.67^{b}	28.53 ± 9.66^{c}
b	2011	**21.54 ± 1.32$^{\mathbf{a}}$**	**49.04 ± 1.63$^{\mathbf{b}}$**	16.99 ± 1.81^{c}	**18.00 ± 2.00$^{\mathbf{ac}}$**
	2012	**27.56 ± 1.28$^{\mathbf{a}}$**	**13.07 ± 1.53$^{\mathbf{b}}$**	18.19 ± 1.77^{c}	**10.45 ± 1.77$^{\mathbf{b}}$**
b/a	2011	0.30	0.37	0.29	0.42
	2012	0.30	0.21	0.31	0.37

Table 3. Main averaged parameters of growth production and water use for each tree species and year. Different letter represents statistically significant differences between species for a given parameter and year ($P<0.05$). Bold numbers represent statistically significant differences between years for a given parameter and species ($P<0.05$). Abbreviations: J_T: total tree transpiration; BAI: basal area increment; BAI/A_B: relative basal area increment; AGC: aboveground carbon production; WUE_{BAI}: water use efficiency calculated according to basal area increment; WUE_{AGC}: water use efficiency calculated according to aboveground carbon production.

		Q. ilex	*Q. pubescens*	*A. unedo*	*P. halepensis*
Total J_T (m^{3} year^{-1})	2011	4.22 ± 0.77^{a}	1.35 ± 0.28^{b}	2.06 ± 0.50^{b}	2.76 ± 0.48^{ab}
	2012	4.74 ± 0.93^{a}	1.00 ± 0.08^{b}	1.87 ± 0.57^{b}	1.50 ± 0.47^{b}
BAI (cm^{2} year^{-1})	2011	**9.64 ± 0.93^{a}**	8.34 ± 1.39^{a}	**5.62 ± 1.35^{a}**	**39.55 ± 5.67^{b}**
	2012	**1.11 ± 0.32^{a}**	3.54 ± 1.81^{a}	**0.70 ± 0.36^{a}**	**14.73 ± 3.16^{b}**
BAI/A_B (mm^{2} cm^{-2} year^{-1})	2011	**2.92 ± 0.43^{a}**	4.66 ± 0.81^{a}	**2.85 ± 0.64^{a}**	**4.56 ± 0.80^{a}**
	2012	**0.37 ± 0.16^{a}**	1.82 ± 0.24^{b}	**0.32 ± 0.17^{a}**	**1.81 ± 0.25^{b}**
AGC (kg C year^{-1})*	2011	**2.49 ± 0.26^{a}**	1.79 ± 0.33^{a}	**1.25 ± 0.30^{a}**	**7.77 ± 1.10^{b}**
	2012	**0.29 ± 0.08^{a}**	0.79 ± 0.45^{a}	**0.16 ± 0.08^{a}**	**2.94 ± 0.66^{b}**
WUE_{BAI} (cm^{2} m^{-3} year^{-1})	2011	**2.53 ± 0.3^{a}**	8.86 ± 3.57^{ab}	**3.51 ± 1.23^{a}**	**14.60 ± 1.41^{b}**
	2012	**0.26 ± 0.08^{a}**	3.40 ± 1.53^{b}	**0.51 ± 0.37^{a}**	**10.16 ± 1.05^{c}**
WUE_{AGC} (g C kg H_2O^{-1} year^{-1})	2011	**0.65 ± 0.07^{a}**	1.83 ± 0.69^{ab}	**0.78 ± 0.27^{a}**	**2.85 ± 0.24^{b}**
	2012	**0.07 ± 0.02^{a}**	0.76 ± 0.39^{b}	**0.12 ± 0.09^{a}**	**2.02 ± 0.19^{c}**

Table 4. Summary statistics for the linear mixed models relating tree water deficit (ΔW) with species, vapour pressure deficit (VPD) and volumetric soil water availability (θ) for 2011 and 2012. *A. unedo* was used as the reference level. Bold numbers represent statistically significant results ($P<0.05$). R^2_{LR} is a likelihood-based pseudo-R^2 (cf. Data analysis).

Year	Model term	Estimate	SE	Df	t	*P*	R^2_{LR}
2011	**(Intercept)**	**-0.455**	**0.182**	**5371.000**	**-2.505**	**0.012**	0.643
	VPD	**2.048**	**0.138**	**5371.000**	**14.887**	**0.000**	
	θ	**-13.441**	**1.001**	**5371.000**	**-13.425**	**0.000**	
	P. halepensis	-0.469	0.235	20.000	-1.997	0.060	
	Q. ilex	**0.585**	**0.189**	**20.000**	**3.091**	**0.006**	
	Q. pubescens	-0.402	0.209	20.000	-1.925	0.069	
	VPD : θ	**-16.849**	**1.079**	**5371.000**	**-15.617**	**0.000**	
	θ : *P. halepensis*	0.819	1.205	5371.000	0.680	0.497	
	θ : *Q. ilex*	-1.718	0.945	5371.000	-1.817	0.069	
	θ : *Q. pubescens*	-0.321	1.077	5371.000	-0.298	0.766	
2012	**(Intercept)**	**1.981**	**0.154**	**5902.000**	**12.844**	**0.000**	0.936
	VPD	**2.310**	**0.081**	**5902.000**	**28.625**	**0.000**	
	θ	**-31.380**	**0.810**	**5902.000**	**-38.740**	**0.000**	
	P. halepensis	0.264	0.222	19.000	1.189	0.249	
	Q. ilex	**-0.412**	**0.172**	**19.000**	**-2.391**	**0.027**	
	Q. pubescens	**-1.934**	**0.204**	**19.000**	**-9.490**	**0.000**	
	VPD : θ	**-19.116**	**0.691**	**5902.000**	**-27.659**	**0.000**	
	VPD : *P. halepensis*	-0.044	0.026	5902.000	-1.685	0.092	
	VPD : *Q.ilex*	**-0.035**	**0.017**	**5902.000**	**-2.094**	**0.036**	
	VPD : *Q.pubescens*	-0.004	0.027	5902.000	-0.150	0.881	
	θ : *P. halepensis*	**-4.220**	**1.153**	**5902.000**	**-3.659**	**0.000**	
	θ : *Q. ilex*	**7.150**	**0.805**	**5902.000**	**8.883**	**0.000**	
	θ : *Q. pubescens*	**11.460**	**1.028**	**5902.000**	**11.146**	**0.000**	

Table 5. Summary statistics for the linear mixed models relating species tree water deficit (ΔW) with sap flow density (J_S) for 2011 and 2012. *A. unedo* was used as the reference level. Bold numbers represent statistically significant results (P<0.05). R^2_{LR} is a pseudo-R^2 based on a likelihood ratio test (cf. Data analysis).

Year	Model term	Estimate	SE	df	T	P	R^2_{LR}
2011	(Intercept)	11.751	12.351	2884	0.951	0.342	0.921
	logΔW	**-12.037**	**0.571**	**2884**	**-21.097**	**0.000**	
	P. halepensis	-11.558	18.860	15	-0.613	0.549	
	Q. ilex	**8.544**	**15.936**	**15**	**0.536**	**0.600**	
	Q. pubescens	**38.931**	**16.022**	**15**	**2.430**	**0.028**	
	logΔW:*P. halepensis*	**4.014**	**0.811**	**2884**	**4.948**	**0.000**	
	logΔW:*Q. ilex*	-0.254	0738	2884	-0.344	0.731	
	logΔW:*Q. pubescens*	**3.277**	**0.805**	**2884**	**4.070**	**0.000**	
2012	(Intercept)	-2.110	7.850	1745	-0.269	0.788	0.987
	log ΔW	**-20.816**	**0.851**	**1745**	**-24.470**	**0.000**	
	P. halepensis	-9.355	12.341	7	-0.758	0.473	
	Q. ilex	-3.345	10.495	7	-0.319	0.759	
	Q. pubescens	**51.121**	**13.005**	**7**	**3.931**	**0.006**	
	logΔW:*P. halepensis*	**11.807**	**0.988**	**1745**	**11.947**	**0.000**	
	logΔW:*Q. ilex*	**-17.715**	**1.638**	**1745**	**-10.812**	**0.000**	
	logΔW:*Q. pubescens*	**15.705**	**1.810**	**1745**	**8.675**	**0.000**	