

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

4 Elisenda Sánchez-Costa ^{a*}, Rafael Poyatos ^{a,c*}, Santiago Sabaté ^{a,b}

5 ^a CREAM, Cerdanyola del Vallès 08193, Spain

6 ^b Departament d'Ecologia, Universitat de Barcelona (UB), 08028 Barcelona, Spain

7 ^c Corresponding author: r.poyatos@creaf.uab.es

8 E-mail addresses: e.sanchez@creaf.uab.es (E.Sánchez-Costa), r.poyatos@creaf.uab.es

9 (R.Poyatos), santi.sabate@ub.edu (S.Sabaté)

10 * These authors contributed equally to this work and share first co-authorship.

This is the author's version of a work that was accepted for publication in Agricultural and Forest Meteorology. Changes resulting from the publishing process, such as peer review, editing, corrections, structural formatting, and other quality control mechanisms may not be reflected in this document. Changes may have been made to this work since it was submitted for publication. A definitive version was subsequently published in Sánchez Costa, E. et al. "Contrasting growth and water use strategies in four co-occurring Mediterranean tree species revealed by concurrent measurements of sap flow and stem diameter variations" in Agricultural and Forest Meteorology, vol. 207 (July 2015), p. 24-37. DOI 10.1016/j.agrformet.2015.03.012

11 **Abstract**

12 Drought limits tree water use and growth of Mediterranean trees. However, growth and
13 water use strategies are rarely addressed simultaneously across species and drought
14 conditions. Here, we investigate the link between stem diameter variations and sap flow
15 in four co-existing Mediterranean trees (*Pinus halepensis* Mill., *Quercus pubescens*
16 Willd., *Quercus ilex* L. and *Arbutus unedo* L.), under relatively wet (2011) and dry
17 (2012) conditions. Continuous stem diameter variations were converted to basal area
18 increment (BAI) and de-trended to estimate tree water deficit (ΔW), an indicator of stem
19 hydration. *P. halepensis* and *Q. pubescens* showed the most and the least conservative
20 sap flow density (J_S) regulation under drought, respectively, with *Q. ilex* and *A.unedo*
21 showing intermediate drought responses. All species, except *A. unedo*, showed some
22 between-year variability in the environmental control of J_S . Seasonal stem shrinkage in
23 response to drought (i.e. increasing ΔW) and subsequent trunk rehydration after rainfall
24 (i.e. decreasing ΔW) occurred in all species. Vapour pressure deficit (VPD) and soil
25 moisture (θ) interacted to determine seasonal variation in ΔW . Interestingly, in the dry
26 year, 2012, more species-specific differences were found in the responses of ΔW to θ
27 and VPD. Across species, J_S and ΔW began to decline at similar soil moisture thresholds,
28 underpinning the tight link between J_S and ΔW under varying drought conditions.
29 Annual BAI decreased proportionally more than tree-level transpiration (J_T) between
30 the wet (2011) and the dry (2012) year, hence growth-based WUE ($WUE_{BAI} = BAI/J_T$)
31 decreased for all species, albeit less acutely for *P. halepensis*. Overall, despite their
32 contrasting leaf habit and wood type, the studied Mediterranean tree species show
33 coordinated responses of transpiration, water storage dynamics and growth-based WUE
34 which allow them to cope with seasonal and interannual drought.

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

37 **1. Introduction**

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

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

59 Likewise, drought responses of stem radial increment across Mediterranean tree species
60 are also varied. After growth initiation in spring, summer drought slows down stem
61 increments in most species. Cell division and enlargement and carbohydrate availability
62 are reduced with increasing water stress (Zweifel et al. 2006), but drought sensitivity of
63 these processes is species-dependent (Sanz-Pérez et al. 2009). As a result, some
64 Mediterranean species enter a state of cambium quiescence in summer (Vieira et al.
65 2013) while others can keep growing, albeit at very small rates (Cherubini et al. 2003).
66 Radial stem increments following autumn rains are mostly related to stem rehydration,
67 but wood formation has also been shown in some Mediterranean species in early
68 autumn (Camarero et al. 2010).

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

84 Productivity and water use show different sensitivities to water availability, the former
85 being more sensitive to water deficits (Hsiao 1973). This relative variability is
86 conveniently encapsulated in water use efficiency (WUE), the ratio between
87 productivity and water use (Jones 1992), where productivity can be expressed in terms
88 of basal area increment (BAI) (Bréda and Granier 1996) or biomass production
89 (Forrester et al. 2010). Isotopic- and gas exchange-based WUE measurements have
90 indeed shown contrasted species-specific variation related to drought in Mediterranean
91 forests (Ferrio et al. 2003), but a limited interannual variation (Damesin et al. 1998).
92 However, neither of these measurements integrates both, the whole-plant level and the
93 annual timescale, the relevant ecological scales to address patterns in forest resource use
94 efficiency (Binkley 2004). The response of growth-based WUE to drought across
95 species may be used to study the relative sensitivities of transpiration and growth to
96 water deficits in different ecological contexts (McCarthy et al. 2011, Morán-López et al.
97 2014, Smith and Sperry 2014).

98 Here, we monitored seasonal sap flow and stem radius variations for almost two years
99 in four tree species growing in a Mediterranean forest: the winter-deciduous sub-
100 Mediterranean *Quercus pubescens* Willd., two evergreen sclerophyllous species
101 (*Quercus ilex* L. and *Arbutus unedo* L.) and *Pinus halepensis* Mill., an early
102 successional, drought-adapted pine. The main aim of this study is twofold: (1) to assess
103 interspecific drought responses of sap flow, BAI and ΔW under relatively wet (2011)
104 and dry (2012) conditions and (2) to study the coordination of growth and water use
105 strategies in this ecological context using growth-based WUE. Pines often display a
106 more conservative water use compared to co-occurring deciduous oaks (Poyatos et al.,
107 2008; Zweifel et al., 2007), hence we hypothesized that (1a) *P. halepensis* would show
108 the strongest reductions of sap flow and ΔW in response to drought (at the seasonal and

109 annual scales), in contrast with *Q. pubescens*; for both, sap flow and ΔW , the
110 sclerophyllous *Q. ilex* and *A. unedo* would show intermediate responses. Given the tight
111 link between transpiration and ΔW (Zweifel et al., 2007), we also hypothesize a close
112 correspondence between the soil moisture controls on both sap flow and ΔW across
113 species and years (1b). Moreover, because of its drought-adapted character and its high
114 priority for stem growth (Sanz-Pérez et al., 2009) we postulated that *P. halepensis*
115 would show the highest BAI and the lowest BAI reduction in the dry year. We also
116 expected that, given its preference for mesic habitats in the region (De Dios et al. 2009),
117 *Q. pubescens* would show the higher BAI reduction under drought. Because of the
118 different relative sensitivity of radial growth and water use in response to drought (e.g.
119 Hsiao, 1973), we hypothesized that (3) annual BAI would decrease proportionally more
120 than water use in the dry year of 2012, compared to 2011 across all species (i.e.
121 WUE_{BAI} would decline). Finally, we hypothesized (4) that *P. halepensis*, because of its
122 strict stomatal control, and *Q. pubescens*, because of its shorter leafy period, would
123 display higher annual WUE_{BAI} compared to *A. unedo* and *Q. ilex*.

124 **2. Materials and Methods**

125 *2.1. Study site, plot characteristics and environmental monitoring*

126 Field measurements were conducted in the Can Balasc experimental site (41° 25' 51.56''
127 N, 2° 04' 25'' E, 270 m a.s.l.) located in the coastal massif of Collserola (NE Spain).
128 Climate is typically Mediterranean with warm, dry summers and mild winters. Mean
129 annual precipitation and temperature (1951-2010) are 608 mm and 15.2 °C, according
130 to a spatially-explicit climatic database (Ninyerola et al. 2007a, Ninyerola et al. 2007b).
131 Soils are predominantly developed above lithological strata of shales and granite
132 (Espelta et al. 2008) and are *ca.* 50 cm deep; according to the USDA textural soil

133 classification (Cosby et al. 1984), the soil type is sandy-loam. The study plot is located
134 in a 0.7 ha stand area, dominated by holm oak (*Quercus ilex* L.), accompanied by
135 pubescent oak (*Quercus pubescens* Mill.) and strawberry tree (*Arbutus unedo* L.). Some
136 scattered Aleppo pines (*Pinus halepensis* Mill.) are also present, growing above the
137 main canopy (Table 1). The understory is a dense stratum mainly consisting of *Pistacia*
138 *lentiscus*, *Erica arborea* L., *Phillyrea latifolia* L., *Rhamnus alaternus*, *Cistus* pp,
139 *Crataegus monogyna*, *Bupleurum fruticosum* and other less abundant species. A more
140 detailed description of the stand's recent history can be found in Sperlich et al. (2014).

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

153 2.2. Sap flow measurements

154 In September 2010, we installed sap flow sensors in trees selected to cover the range of
155 diameter classes, except the smallest trees (<10 cm), which may be problematic for sap
156 flow measurements and have the lowest contribution to stand transpiration (*Q. ilex* $n=7$,

157 *Q. pubescens* $n=7$, *A. unedo* $n=4$ and *P. halepensis* $n=3$). In 2012, the number of
158 operative sensors was reduced due to probe failure (*Q. ilex* $n=5$, *Q. pubescens* $n=4$, *A.*
159 *unedo* $n=3$ and *P. halepensis* $n=3$). The measurement period for sap flow (and stem
160 radial variations) spanned from February 2011 (DOY 50) until the end of the year 2012
161 (DOY 365).

162 Stem sap flow was monitored with constant thermal dissipation sensors constructed in
163 our own laboratories according to Granier (1985, 1987). These two probes were
164 installed at a height of 1.20 m, with a vertical separation of ca. 12 cm between them. To
165 minimise the influence of natural temperature gradients in the stem, the installation was
166 carried out in the north face side of each tree and isolated with aluminium-covered
167 material to avoid direct solar radiation. Temperature differences (dT) were recorded at
168 30 s intervals and stored as 15 min average in a data logger (CR1000, Campbell
169 Scientific, Inc.). The monitored trees had estimated sapwood depths of 42-45 mm for
170 *A.unedo*, 44-48 mm for *P.halepensis*, 35-40 mm for *Q.pubescens*, and 47-69 mm for
171 *Q.ilex*. Although this range of sapwood depths reduced the risk of underestimating sap
172 flow due to the contact of the probe with non-conducting xylem, steep gradients in sap
173 flow density within the probe length can also cause underestimation of average sap flow
174 density (Clearwater et al 1999). Hence, we installed short sensors (10 mm) in all tree
175 species except Aleppo pine (20 mm), which does not display a steep radial variation of
176 sap flow within the outer ~20 mm of xylem (Cohen et al. 2008).

177 Natural temperature gradients were measured over 137 days to determine that the upper
178 (95 %) and lower (5 %) quantiles were 0.3 ± 0.02 and 0.2 ± 0.02 °C (across-trees mean
179 \pm SE), suggesting only a minor effect on sap flow measurements (Do and Rocheteau
180 2002). Nevertheless, we accounted for the effect of natural temperature gradients by

181 first modelling them as a function of environmental variables (including lagged
182 variables) for each sensor. We then used these tree-specific models (across-trees
183 average $R^2 = 0.44$) to predict natural temperature gradients in the stem and corrected the
184 raw dT signal; corrected sap flow density was 3.5 ± 1.1 % (across-trees mean \pm SE)
185 larger than the uncorrected values. For a robust dT_{\max} estimation (i.e. dT under zero
186 flow) we selected the highest dT of the previous night, only if the average of the
187 minimum evaporative demand was less than 0.05 kPa during 2 hours and the coefficient
188 of variation of the four highest dT values was less than 0.5 %. When these conditions
189 were not met, dT_{\max} was linearly interpolated from nearby days (Oishi et al. 2008).

190 Sap flow density per unit sapwood area (J_S) (kg m^{-2} sapwood s^{-1}), was calculated
191 following the original calibration derived empirically by Granier (1985, 1987),
192 multiplied by a radial correction coefficient (C_r) to account for the spatial variation of
193 sap flow along the xylem radius. C_r was obtained for each species from published
194 values of generic radial patterns of sap flow (Table 1) (Cohen et al. 2008, Poyatos et al.
195 2008, Mereu et al. 2009, Aguadé et al. 2011). Instantaneous values of J_S were then
196 averaged daily for each monitored tree. Missing data due to occasional sensor failure
197 (17 ± 4 % of individual tree data) was gap-filled using linear regressions with other
198 sensors, choosing the one displaying the best fit, according to R^2 (range between 0.7 and
199 0.9).

200 Whole-tree sap flow rates (J_T) (kg s^{-1}) were obtained by multiplying J_S by sapwood area
201 (A_S) (m^2). As we could not core the trees with sap flow sensors due to the long-term
202 nature of the experimental set-up, sapwood area was estimated from a linear regression
203 between stem basal area (A_B) and A_S obtained in the bibliography for the same tree
204 species within the same region (Martínez-Vilalta et al. 2003, Gracia et al. 2004, Poyatos

205 et al. 2007, Aguadé et al. 2011). These estimations were validated using visual
206 measurements based on wood translucency in fresh disks obtained in a nearby area *ca.* 8
207 km from the plot (Can Catà, Collserola Natural Park); we found an excellent agreement
208 between literature-derived estimations and field measurements (see supplementary
209 Figure S1).

210 2.3. Basal area increment, tree water deficit and growth-based water use efficiency

211 Automatic band dendrometers (DRL26, EMS Brno, Czech Republic), which measure
212 the linear displacement of a stainless steel band embraced around the trunk, were used
213 to monitor stem circumference variation continuously. Displacement has an accuracy of
214 1 μm over an adjusted range of 60 mm. Dendrometers were installed at height of about
215 1.30 m, above the sap flow sensors. Outer bark was removed before the installation of
216 the instrument. Almost all trees with sap flow probes had a dendrometer installed (*Q.*
217 *ilex* $n=6$, *Q. pubescens* $n=6$, *A. unedo* $n=4$ and *P. halepensis* $n=3$), recording data every
218 15 min. Dendrometer data were converted to stem diameter variations and to basal area
219 increment (BAI) (cm^2). We also calculated the BAI of each monitored tree relative to its
220 basal area at the beginning of 2011 (BAI/ A_B).

221 Dendrometer time series were de-trended in order to extract growth-independent
222 diameter fluctuations caused by changes in sapwood and bark water content as a result
223 of the daily and seasonal dynamics of stored water in the transpiration stream (Zweifel
224 et al. 2005, Drew et al. 2011). Tree water deficit (ΔW) was calculated as the difference
225 between the constant growth line and stem actual diameter variations and provides an
226 index of whole-tree water status (see supplementary Figure S3). Here we assume that,
227 having defined ΔW as a ‘deficit’ relative to an optimal hydrated state ($\Delta W = 0$), the
228 value of ΔW takes increasingly positive values as drought-stress increases, consistent

229 with Zweifel et al. (2005). As we focused on the seasonal variation in ΔW , not the daily
230 cycles, here we report daily-averaged values.

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

237 2.4. Data analysis

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

$$244 \quad J_S = b \cdot \ln(\text{VPD}) + a \quad (1)$$

245 Where a is the sap flow when VPD is equal to 1 kPa and the slope b represents absolute
246 J_S sensitivity to VPD. In this analysis, two individuals of *Q. pubescens* were not used
247 due to lack of fit. In order to capture the VPD response without other variables col-
248 limiting sap flow, we only included days with solar radiation $> 50 \text{ W m}^{-2}$ and $\theta > 0.15$
249 $\text{cm}^2 \text{ cm}^{-2}$. We also calculated the ratio between parameters b and a (b/a) as a measure of
250 relative sensitivity to VPD, in an analogous way to the well-known stomatal model by
251 Oren et al. 1999.

252 The response of J_S to θ was analysed using a three-parameter sigmoid function, based
253 on similar functional responses reported elsewhere (Duursma et al. 2008, Poyatos et al.
254 2013):

$$255 \quad J_S = \frac{J_{S,Asym}}{1 + \exp[(\theta_{mid} - \theta)/\theta_{scal}]} \quad (2)$$

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

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

267 Model selection for J_S and ΔW responses was based on the minimisation of the Akaike
268 Information Criterion (AIC); models within 2 units of AIC were considered equivalent
269 and, in this case, we retained the more parsimonious one (i.e. the one with less
270 parameters). We graphically inspected residual plots and implemented appropriate
271 variance structures to minimise heteroscedasticity in the residuals (varPower structure in
272 nlme/lme functions). In sap flow models, day of the year (DOY) was used as a
273 continuous time covariate (corCAR1 in function nlme/lme functions). We assessed the
274 statistical significance of fixed effects using Wald t -tests. For all statistical tests,

275 significance was accepted at $P < 0.05$. We calculated pseudo- R^2 values for linear mixed
276 models, based on a likelihood ratio test between the target model and a null (intercept-
277 only) model, as implemented in the R-package MuMIn (Bartoń 2014).

278 3. Results

279 3.1. Seasonal course of environmental variables and sap flow

280 Over the studied period, meteorology was typically Mediterranean (Figure 1a). For
281 2011 and 2012, the mean annual air temperature was similar to the climatic mean value
282 of 15.2 °C (1951-2010) but annual precipitation in 2011 (804 mm) was 32 % higher
283 than the climatic average, whereas in 2012 it was 21 % lower (479 mm) (Figure 1c). In
284 particular, the 2012 winter period presented 90 % less precipitation (25 mm) than the
285 same period of 2011 (254 mm) and 36 % less compared to the climatic average. Low
286 values of θ were achieved in both summer periods (ca. 0.12 cm³ cm⁻³), but in 2012 these
287 coincided with higher values of VPD (Figure 1a, d); mean daily VPD during summer
288 2011 was lower than in 2012 (0.9 and 1.2 kPa, respectively) (Figure 1a).

289 The seasonal patterns of sap flow showed high J_S rates during spring across species for
290 both years, and drought-related reductions in J_S beginning in August 2011 and June
291 2012, respectively (Figure 2). Autumn rainfall and the consequent rise in θ , helped to
292 recover sap flow rates (Figure 2), except for *Q. pubescens* which reduced J_S coinciding
293 with leaf senescence and maintained some residual sap flow during the leafless winter
294 period. During winter, *A. unedo* and *Q. ilex* were the species with highest values of J_S .
295 Spring J_S values were lowest for *P. halepensis* in both years and highest for *Q.*
296 *pubescens* in 2011 and for *Q. ilex* in 2012 (see supplementary Table S2 and Figure 2). *Q.*
297 *pubescens* displayed a lower J_S drop from spring to summer (10 % in 2011 and 20 % in
298 2012) compared to the rest of species (25 – 40 % in 2011 and 50 – 75 % in 2012), and

299 was able to maintain the highest summer J_S values. No significant differences in J_S for a
300 given seasonal period were found between years for either *A. unedo* or *Q. ilex* (see
301 supplementary Table S2). As for tree-level sap flow, *Q. ilex* showed higher J_T values
302 than the rest of species, while *Q. pubescens*, in general, displayed the lowest values.
303 Intermediate J_T values were found for *A. unedo* and *P. halepensis* (see supplementary
304 Table S2 and Figure 2).

305 3.2. Environmental responses of sap flow across species and years

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

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

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

325 3.3. Basal area increment across species and years

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

338 In 2011, *Q. pubescens* was the species with the highest values of annual BAI/A_B
339 followed by *P. halepensis* (Table 3 and Figure 4b). Nevertheless, for 2012, significant
340 differences among species were found, being *Q. pubescens* and *P. halepensis* the
341 species with the highest values of BAI/A_B (Table 3 and Figure 4b). In 2012, most
342 species showed significantly lower values than in 2011 (Table 3) and even some trees
343 presented a negligible annual BAI (see supplementary Table S3). BAI reductions in
344 2012 compared to 2011 were around 90 % for *Q. ilex* and *A. unedo*, and 60 % for *P.*
345 *halepensis*, but they were non-significant for *Q. pubescens*.

346 3.4. Environmental controls on ΔW

347 The seasonal course of daily ΔW was similar for all the species over the two study years
348 (Figure 4c). The higher values of ΔW were observed during summer and autumn,
349 coinciding with a decline in θ and the increase of VPD, although moderate values (~0.2-
350 0.3 mm) were also observed during wintertime. The longest period with sustained high
351 values of ΔW occurred in 2012, the intense drought year. In general, evergreen
352 sclerophyllous species presented the highest values of ΔW (Figure 4c).

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

368 3.5. Relationship between sap flow and ΔW

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

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

378 3.6. Growth-based water use efficiency

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

388 4. Discussion

389 4.1. Sap flow: seasonal course and environmental controls

390 Seasonal variability in sap flow differed across species, and it was mainly associated
391 with their leaf habit and response to drought. Deciduous *Q. pubescens* presented a
392 residual sap flow during the leafless period, which could be attributed to transpiration
393 through the bark (e.g. Stöhr and Lösch 2004) and to the fact that one *Q. pubescens* tree
394 kept its leaves functional all year round. Remarkably, winter sap flow was generally

395 higher than in summer for all three evergreen species (see supplementary Table S2),
396 particularly *Q. ilex* and *A. unedo*.

397 Responses of sap flow to water supply and demand varied across species and most
398 inter-annual variability was observed for *Quercus* species, which displayed the highest
399 J_S , but showed opposite species-specific patterns with drought intensity. In the dry year
400 (2012), *Q. ilex* increased $J_{S,Asym}$ and parameter a , because it displayed the highest fluxes
401 in in late winter and spring, in response to frequent rainfall which maintained soil water
402 availability during these periods (Figure 1c, d). In contrast, both $J_{S,Asym}$ and parameter a
403 decreased in 2012 for *Q. pubescens*. Reduced precipitation during late autumn and early
404 winter 2012 could have precluded the recharge of deep soil water, which is a preferred
405 water source for the deciduous *Q. pubescens* (Valentini et al. 1992), causing a reduction
406 in maximum sap flow rates.

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

419 showed a similar θ_{mid} value compared to *Q. ilex*, but presented a steeper reduction in J_S
420 with lower θ (Table 2 and Figure 3), consistent with mixed drought responses observed
421 for these two sclerophyllous species (Martínez-Vilalta et al. 2003, Mereu et al. 2009).

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

441 4.2. Seasonal BAI in Mediterranean tree species

442 *P. halepensis* showed considerably higher BAI rates than the rest of the species (Figure
443 4a), as expected for an early successional pine (hypothesis 2). However, in relative
444 terms (i.e. BAI/A_B), *Q. pubescens* showed slightly higher stem increment than *P.*
445 *halepensis*, whereas *Q. ilex* and *A. unedo*, again, showed similar dynamics (Figure 4b).
446 In 2012, all species reduced their BAI, but surprisingly, BAI was particularly reduced
447 for *Q. ilex* and *A. unedo* (Table 3). Our results, thus, only partially support hypothesis 2,
448 as we expected that drought-related decreases in BAI would be strongest for the sub-
449 Mediterranean *Q. pubescens*.

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

458 The stem contraction phase during the summer was longer in 2012 compared to 2011
459 (Figure 4b), and also longer than the *ca.* 3 months observed for *Pinus pinaster* (Vieira et
460 al. 2013). Overall, the seasonal dynamics of BAI/A_B in summer 2012 appeared to be
461 highly influenced by rainfall pulses; following a relatively long summer drought, most
462 of the stem diameter recovery observed in autumn was probably water-related. However,
463 late season growth has been reported for *Q. ilex* and *P. halepensis* (Campelo et al. 2007,
464 Camarero et al. 2010; Nicault et al., 2001), although it may be less likely for *A. unedo*
465 (De Lillis and Fontanella 1992) and *Q. pubescens* (Zweifel et al. 2007). Indeed, growth

466 curves extracted for ΔW calculation, which have been reported to be closely related to
467 the actual accumulation of new wood cells (Zweifel et al. 2007), suggest that detectable
468 growth only occurred for *P. halepensis* (see supplementary Figure S5). Direct
469 measurements of intrannual growth (i.e. repeated micro-coring or pinning) would be
470 needed to confirm these patterns.

471 4.3. Environmental control of dendrometer-based tree water deficit across 472 Mediterranean tree species

473 Maximum daily values of ΔW were 0.2 - 0.5 mm for all trees, a similar range to that
474 observed by Zweifel et al. (2005) for *Q. pubescens* (0.4 - 0.5 mm), but much lower than
475 the values > 1 mm observed for the drought-resistant *Callitris intratropica* (Drew et al.
476 2011). The species ranking of ΔW was: *A. unedo* (semi ring-porous) > *Q. ilex* (diffuse
477 porous) > *P. halepensis* (conifer) > *Q. pubescens* (ring-porous). Hence, the variability in
478 the magnitude of ΔW was not clearly associated with wood type. Given the tight
479 relationship between leaf water potential and ΔW (Drew et al. 2011), the observed
480 higher values for the two evergreen sclerophylls would suggest that they underwent
481 higher stress conditions (i.e. lower water potentials) compared to *Q. pubescens* and *P.*
482 *halepensis*. Simultaneous monitoring of leaf water potentials and ΔW would be needed
483 to test for likely species-specific differences in the association between these two
484 variables (Oberhuber et al. 2014).

485 Water supply (θ) and demand (VPD) interacted to determine the variation in ΔW , as
486 reported by Zweifel et al. (2005), despite that a recent study in a water-limited forest
487 only reported additive effects of VPD and θ (Drew et al. 2011). We observed that higher
488 ΔW values were reached at similar conditions of water supply and demand in 2012 (dry
489 year) compared to 2011 (wet year). These results imply that other factors, related to

490 unmeasured physiological processes (i.e. stomatal control) or environmental factors (i.e.
491 soil moisture at deeper soil layers) could be driving the observed shifts in ΔW between
492 years. With regard to species-specific differences, *A. unedo* and *Q. ilex* (in 2012)
493 showed the steepest increases in ΔW with decreasing θ , and, interestingly *A. unedo* also
494 showed the steepest reductions in J_S with θ . We did not observe a higher sensitivity to
495 drought in ΔW for *P. halepensis*, as hypothesized (hypothesis 1a). In general, across
496 species, the θ levels at which ΔW and J_S began to decline were similar. Hence, the θ
497 threshold for sap flow reduction seems to be related to the soil water availability where
498 the tree shows only partial refilling of its water reserves (Köcher et al. 2013).
499 Furthermore, our results show that a given increment in VPD causes a higher increase in
500 ΔW under dry soil conditions, supporting the view that water is withdrawn more
501 strongly from the tree's internal storage as the soil dries (Zweifel et al. 2005).

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

515 4.4. Drought-related variation in growth-based water use efficiency across
516 Mediterranean tree species

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

530 With respect to interspecific patterns, in 2011, *P. halepensis* and *Q. pubescens* achieved
531 the highest WUE_{BAI} through opposite functional strategies (hypothesis 4): strict (*P.*
532 *halepensis*) vs moderate (*Q. pubescens*) physiological control of transpiration in
533 response to drought and evergreen (*P. halepensis*) vs winter-deciduous (*Q. pubescens*)
534 leaf habit (see also McCarthy et al. 2011). However, in 2012 *P. halepensis* was clearly
535 the species with the higher WUE_{BAI} in accordance with its high preferential allocation
536 to aboveground growth (Sanz-Pérez et al. 2009) and its capacity to thrive in dry habitats
537 (Maseyk et al. 2008). Across years, *Q. ilex* and *A. unedo* showed similar and
538 consistently lower WUE_{BAI} values compared to *P. halepensis* and *Q. pubescens*. This

539 comparatively lower WUE_{BAI} in the two evergreen sclerophyllous species may be
540 explained by (1) an increased C allocation to roots or increased fine root turnover
541 (López et al. 1998), (2) enhanced carbohydrate storage or (3) higher respiratory costs
542 (Sanz-Pérez et al. 2009).

543 4.5. Concluding remarks

544 Tree species with contrasting leaf habit, wood type and stomatal behaviour have shown
545 coordinated drought responses of sap flow, water storage dynamics and growth-based
546 WUE which allowed them to co-exist in the studied Mediterranean forest. However
547 some species-specific variability in these responses may directly impact stand dynamics
548 and composition, especially under the projected increases in aridity for the
549 Mediterranean region (e.g. Collins et al. 2013). The comparatively stronger stomatal
550 control displayed by *P. halepensis* probably allowed this species to avoid substantial
551 leaf shedding in August 2012, when mostly *Q. pubescens* and *A. unedo* but also *Q. ilex*,
552 to a lesser extent, were affected (Sperlich et al. in press). Indeed, *Q. pubescens* is
553 especially vulnerable to hydraulic failure and subsequent leaf desiccation during intense
554 summer droughts, but it may also show a rapid canopy recovery in the following year
555 relying on carbohydrate reserves. Both *Q. pubescens* and *P. halepensis* maintained
556 comparatively higher WUE_{BAI} in a dry year by a combination of different physiological
557 (stomatal control) and structural (leaf habit, relative allocation to aboveground growth)
558 mechanisms. In contrast, *Q. ilex* and *A. unedo* showed a relatively high physiological
559 sensitivity to drought, which was somehow unexpected given the wide presence of both
560 species in Mediterranean forests. Nevertheless, their sustained transpiration outside the
561 main growing season probably indicates that they may take advantage of year-round
562 photosynthetic activity. Moreover, they may be more competitive and resilient in the

563 long-term if their low WUE_{BAI} results from a higher relative allocation to roots and/or
564 carbohydrate storage. In fact, the current low *P. halepensis* density and the
565 predominance of *Q. ilex* may be revealing the ongoing ecological succession in the
566 stand after the cessation of management practices during the 20th century (Sperlich et al.
567 2014).

568 **Acknowledgements**

569 This study was made possible thanks to the projects CLIMOAK CGL2008-04847-C02-
570 02, Consolider-Ingenio MONTES CSD2008-00040 and MEDFORESTREAM
571 CGL2011-30590-C02-01 (all funded by MICINN-MINECO, Spain), 2009 SGR 247
572 (AGAUR, Catalonia) and GREENCYCLES II 238366 (EU). E.S-C. was supported by
573 the program PTA and R.P. by the ‘Juan de la Cierva’ fellowship JCI-2010-08186 (both
574 MICINN-MINECO). The authors are very grateful to the Collserola Natural Park for
575 allowing us to conduct research in the Can Balasc forest. Field and laboratory assistance
576 by M. Fernández and M. Hernanz is greatly appreciated. We also want to thank J.M.
577 Espelta, R. Ogaya, J. Vayreda, L. Aguiillaume, D. Sperlich, C.T. Chang, C. Romeu, F.
578 Llimona, S. Cahill, Q. Calomardo and L. Cabañeros for their help during various stages
579 of this study. M. Ninyerola and M. Batalla (Unitat de Botànica, UAB) provided the
580 climatic database (CGL 2006-01293, MICINN). The comments of two anonymous
581 reviewers greatly improved the manuscript.

582 **References**

- 583 Aguadé D, Martínez-Vilalta J, Poyatos R (2011) Water relations of Scots Pine at its dry
584 limit: effects of crown condition and competition by co-occurring Holm oak.
585 Master's thesis, Universitat Autònoma de Barcelona.
- 586 Baldocchi DD, Ma S, Rambal S, Misson L, Ourcival JM, Limousin JM, Pereira J,
587 Papale D (2009) On the differential advantages of evergreenness and
588 deciduousness in mediterranean oak woodlands: a flux perspective. *Ecol Appl*
589 20:1583–1597.
- 590 Barbeta A, Mejía-Chang M, Ogaya R, Voltas J, Dawson TE, Peñuelas J (2014) The
591 combined effects of a long-term experimental drought and an extreme drought on
592 the use of plant-water sources in a Mediterranean forest. *Glob Change Biol.*
593 21:1213–1225.
- 594 Bartoń K (2014) MuMIn: multi-model inference. R package, version 1.10.5.
- 595 Binkley D, Stape JL, Ryan MG (2004) Thinking about efficiency of resource use in
596 forests. *Forest Ecol Manag* 193:5–16.
- 597 Blondel J, Aronson J (eds) (1999) *Biology and wildlife of the Mediterranean region.*
598 Oxford University Press.
- 599 Borghetti M, Cinnirella S, Magnani F, Saracino A (1998) Impact of long-term drought
600 on xylem embolism and growth in *Pinus halepensis* Mill. *Trees* 12:187–195.
- 601 Bréda N, Granier A (1996) Intra- and interannual variations of transpiration, leaf area
602 index and radial growth of a sessile oak stand (*Quercus petraea*). *Ann For Sci*
603 53:521–536.
- 604 Camarero JJ, Olano JM, Parras A (2010) Plastic bimodal xylogenesis in conifers from
605 continental Mediterranean climates. *New Phytol* 185:471–480.

606 Campelo F, Gutiérrez E, Ribas M, Nabais C, Freitas H (2007) Relationships between
607 climate and double rings in *Quercus ilex* from northeast Spain. *Can J Forest Res*
608 37:1915–1923.

609 Carnicer J, Coll M, Ninyerola M, Pons X, Sánchez G, Peñuelas J (2011) Widespread
610 crown condition decline, food web disruption, and amplified tree mortality with
611 increased climate change-type drought. *PNAS* 108:1474–1478.

612 Cherubini P, Gartner BL, Tognetti R, Bräker OU, Schoch W, Innes JL (2003)
613 Identification, measurement and interpretation of tree rings in woody species from
614 mediterranean climates. *Biol Rev* 78:119–148.

615 Clearwater MJ, Meinzer FC, Andrade JL, Goldstein G, Holbrook NM (1999) Potential
616 errors in measurement of nonuniform sap flow using heat dissipation probes. *Tree*
617 *physiol* 19:681–687.

618 Cohen Y, Cohen S, Cantuarias-Aviles T, Schiller G (2008) Variations in the radial
619 gradient of sap velocity in trunks of forest and fruit trees. *Plant soil* 305:49–59.

620 Collins M, Knutti R, Arblaster J, Dufresne JL, Fichefet T, Friedlingstein P, Gao X,
621 Gutowski WJ, Johns T, Krinner G, Shongwe M, Tebaldi C, Weaver AJ, Wehner
622 M (2013) Long-term climate change: projections, commitments and irreversibility.
623 In: *climate change 2013: The physical science basis. Contribution of working*
624 *group I to the fifth assessment report of the Intergovernmental Panel on Climate*
625 *Change*. Stocker TF, Qin D, Plattner GK, Tignor M, Allen SK, Boschung J,
626 Nauels A, Xia Y, Bex V, Midgley PM (eds). Cambridge University Press,
627 Cambridge, United Kingdom and New York, NY, USA.

628 Cosby BJ, Hornberger GM, Clapp RB, Ginn TR (1984) A Statistical exploration of the
629 relationships of soil moisture characteristics to the physical properties of soils.
630 *Water Resour Res* 20:682–690.

631 Damesin C, Rambal S, Joffre R (1998) Co-occurrence of trees with different leaf habit:
632 A functional approach on Mediterranean oaks. *Acta Oecol* 19:195–204.

633 De Dios RS de, Benito-Garzón M, Sainz-Ollero H (2009) Present and future extension
634 of the Iberian submediterranean territories as determined from the distribution of
635 marcescent oaks. *Plant Ecol* 204:189–205.

636 De Lillis M, Fontanella A (1992) Comparative phenology and growth in different
637 species of the Mediterranean maquis of central Italy. *Vegetatio* 99-100:83–96.

638 Do F, Rocheteau a (2002) Influence of natural temperature gradients on measurements
639 of xylem sap flow with thermal dissipation probes. 1. Field observations and
640 possible remedies. *Tree physiol* 22:641–8.

641 Drew DM, Richards AE, Downes GM, Cook GD, Baker P (2011) The development of
642 seasonal tree water deficit in *Callitris intratropica*. *Tree Physiol* 31:953–964.

643 Duursma RA, Kolari P, Perämäki M, Nikinmaa E, Hari P, Delzon S, Loustau D,
644 Ilvesniemi H, Pumpanen J, Mäkelä A (2008) Predicting the decline in daily
645 maximum transpiration rate of two pine stands during drought based on constant
646 minimum leaf water potential and plant hydraulic conductance. *Tree Physiol*
647 28:265–276.

648 Espelta JM, Cortés P, Molowny-Horas R, Sánchez-Humanes B, Retana J (2008)
649 Masting mediated by summer drought reduces acorn predation in Mediterranean
650 oak forests. *Ecology* 89:805–817.

651 Ferrio JP, Florit A, Vega A, Serrano L, Voltas J (2003) $\Delta^{13}\text{C}$ and tree-ring width reflect
652 different drought responses in *Quercus ilex* and *Pinus halepensis*. *Oecologia*
653 137:512–518.

654 Forrester DI, Theiveyanathan S, Collopy JJ, Marcar NE (2010) Enhanced water use
655 efficiency in a mixed *Eucalyptus globulus* and *Acacia mearnsii* plantation. *Forest*
656 *Ecol Manag* 259:1761–1770.

657 Gracia C, Burriel J, Ibàñez J, Mata T, Vayreda J (eds) (2004) *Inventari Ecològic i*
658 *Forestal de Catalunya. Volum 10.* CREAF, Bellaterra.

659 Granier A (1985) Une nouvelle méthode pour la mesure du flux de sève brute dans le
660 tronc des arbres. *Ann Sci Forest* 42:193–200.

661 Granier A (1987) Evaluation of transpiration in a Douglas-fir stand by means of sap
662 flow measurements. *Tree Physiol* 3:309–20.

663 Gratani L, Ghia E (2002) Adaptive strategy at the leaf level of *Arbutus unedo* L. to cope
664 with Mediterranean climate. *Flora* 197:275–284.

665 Hsiao TC (1973) Plant responses to water stress. *Annu Rev Plant Physiol* 24:519–570.

666 Jones H (ed) (1992) *Plants and microclimate: a quantitative approach to environmental*
667 *plant physiology.* Cambridge University Press, Cambridge, UK.

668 Köcher P, Horna V, Leuschner C (2013) Stem water storage in five coexisting
669 temperate broad-leaved tree species: significance, temporal dynamics and
670 dependence on tree functional traits. *Tree Physiol* 33:817–832.

671 Lindner M, Fitzgerald JB, Zimmermann NE, Reyer C, Delzon S, van der Maaten E,
672 Schelhaas MJ, Lasch P, Eggers J, van der Maaten-Theunissen M, Suckow F,
673 Psomas A, Poulter B, Hanewinkel M (2014) Climate change and European forests:
674 What do we know, what are the uncertainties, and what are the implications for
675 forest management? *J Environ manage* 146: 69–83.

676 López B, Sabaté S, Gracia C (1998) Fine roots dynamics in a Mediterranean forest:
677 effects of drought and stem density. *Tree Physiol* 18:601–606.

678 Martínez-Vilalta J, Mangirón M, Ogaya R, Sauret M, Serrano L, Peñuelas J, Piñol J
679 (2003) Sap flow of three co-occurring Mediterranean woody species under
680 varying atmospheric and soil water conditions. *Tree Physiol* 23:747–758.

681 Maseyk KS, Lin T, Rotenberg E, Grünzweig JM, Schwartz A, Yakir D (2008)
682 Physiology–phenology interactions in a productive semi-arid pine forest. *New*
683 *Phytol* 178:603–616.

684 McCarthy HR, Pataki DE, Jenerette GD (2011) Plant water-use efficiency as a metric of
685 urban ecosystem services. *Ecol Appl* 21:3115–3127.

686 Meinzer FC, Woodruff DR, Eissenstat DM, Lin HS, Adams TS, McCulloh KA (2013)
687 Above- and belowground controls on water use by trees of different wood types in
688 an eastern US deciduous forest. *Tree Physiol* 33:345–356.

689 Mereu S, Salvatori E, Fusaro L, Gerosa G, Muys B, Manes F (2009) An integrated
690 approach shows different use of water resources from Mediterranean maquis
691 species in a coastal dune ecosystem. *Biogeosci. Discuss.* 6:2599–2610.

692 Morán-López T, Poyatos R, Llorens P, Sabaté S (2014) Effects of past growth trends
693 and current water use strategies on Scots pine and pubescent oak drought
694 sensitivity. *Eur J Forest Res* 133:369–382.

695 Nicault, A., Rathgeber, C., Tessier, L. & Thomas, A. (2001) Observations sur la mise en
696 place du cerne chez le pin d'Alep (*Pinus halepensis* Mill.) : confrontation entre les
697 mesures de croissance radiale, de densité et les facteurs climatiques. *Ann For Sci*,
698 58:769-784.

699 Ninyerola M, Pons X, Roure JM (2007a) Objective air temperature mapping for the
700 Iberian Peninsula using spatial interpolation and GIS. *Int J Climatol* 27:1231–
701 1242.

702 Ninyerola M, Pons X, Roure JM (2007b) Monthly precipitation mapping of the Iberian
703 Peninsula using spatial interpolation tools implemented in a Geographic
704 Information System. *Theor Appl Climatol* 89:195–209.

705 Oberhuber W, Kofler W, Schuster R, Wieser G (2014) Environmental effects on stem
706 water deficit in co-occurring conifers exposed to soil dryness. *Int J Biometeorol*
707 1–10.

708 Ogaya R, Peñuelas J, Martínez-Vilalta J, Mangirón M (2003) Effect of drought on
709 diameter increment of *Quercus ilex*, *Phillyrea latifolia*, and *Arbutus unedo* in a
710 holm oak forest of NE Spain. *Forest Ecol Manag* 180:175–184.

711 Ogaya R, Barbeta A, Başnou C, Peñuelas J (2014) Satellite data as indicators of tree
712 biomass growth and forest dieback in a Mediterranean holm oak forest. *Ann For*
713 *Sci* 72:135-144.

714 Oishi AC, Oren R, Stoy PC (2008) Estimating components of forest evapotranspiration:
715 A footprint approach for scaling sap flux measurements. *Agr Forest Meteorol*
716 148:1719–1732.

717 Oren R, Sperry JS, Katul GG, Pataki DE, Ewers BE, Phillips N, Schäfer KVR (1999)
718 Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to
719 vapour pressure deficit. *Plant Cell Environ* 22:1515–1526.

720 Peñuelas J, Lloret F, Montoya R (2001) Severe drought effects on Mediterranean
721 woody flora in Spain. *Forest Sci* 47:214–218.

722 Pinheiro JC, Bates DM (2000) *Mixed-effects models in S and S-PLUS*. Springer Verlag.

723 Poyatos R, Llorens P, Gallart F (2005) Transpiration of montane *Pinus sylvestris* L. and
724 *Quercus pubescens* Willd. forest stands measured with sap flow sensors in NE
725 Spain. *Hydrol Earth Syst Sc* 2:1011–1046.

726 Poyatos R, Čermák J, Llorens P (2007) Variation in the radial patterns of sap flux
727 density in Pubescent Oak (*Quercus Pubescens*) and its implications for tree and
728 stand transpiration measurements. *Tree Physiol* 27:537–548.

729 Poyatos R, Llorens P, Piñol J, Rubio C (2008) Response of Scots pine (*Pinus sylvestris*
730 L.) and pubescent oak (*Quercus pubescens* Willd.) to soil and atmospheric water
731 deficits under Mediterranean mountain climate. *Ann For Sci* 65:306–306.

732 Poyatos R, Aguadé D, Galiano L, Mencuccini M, Martínez-Vilalta J (2013) Drought-
733 induced defoliation and long periods of near-zero gas exchange play a key role in
734 accentuating metabolic decline of Scots pine. *New Phytol* 200:388–401.

735 R Development Core Team (2010) R: A language and environment for statistical
736 computing. R Foundation for Statistical Computing Vienna Austria.

737 Romane F, Terradas J (eds) (1992) *Quercus ilex* ecosystems: function, dynamics and
738 management. *Vegetatio* 99/100. Kluwer Academic Publishers, Dordrecht.

739 Sanz-Pérez V, Castro-Díez P, Joffre R (2009) Seasonal carbon storage and growth in
740 Mediterranean tree seedlings under different water conditions. *Tree Physiol*
741 29:1105–1116.

742 Seibt U, Rajabi A, Griffiths H, Berry JA (2008) Carbon isotopes and water use
743 efficiency: sense and sensitivity. *Oecologia* 155:441–454.

744 Smith DD, Sperry JS (2014) Coordination between water transport capacity, biomass
745 growth, metabolic scaling and species stature in co-occurring shrub and tree
746 species. *Plant Cell Environ.* doi: 10.1111/pce.12408.

747 Sperlich D, Chang CT, Peñuelas J, Gracia C, Sabaté S (2014) Foliar photochemical
748 processes and carbon metabolism under favourable and adverse winter conditions
749 in a Mediterranean mixed forest, Catalonia (Spain). *Biogeosci* 11:5657–5674.

750 Sperlich D, Chang CT, Peñuelas J, Gracia C, Sabaté S (in press) Effects of seasonal
751 drought on foliar photosynthetic and morphological traits in a Mediterranean
752 mixed forest. *Tree Physiol*.

753 Stöhr A, Lösch R (2004) Xylem sap flow and drought stress of *Fraxinus excelsior*
754 saplings. *Tree Physiol* 24:169–180.

755 Tognetti R, Longobucco A, Miglietta F, Raschi A (1998) Transpiration and stomatal
756 behaviour of *Quercus ilex* plants during the summer in a Mediterranean carbon
757 dioxide spring. *Plant Cell Environ* 21:613–622.

758 Valentini R, Mugnozza GS, Ehleringer JR (1992) Hydrogen and carbon isotope ratios
759 of selected species of a Mediterranean macchia ecosystem. *Funct Ecol* 6:627–631.

760 Vieira J, Rossi S, Campelo F, Freitas H, Nabais C (2013) Seasonal and daily cycles of
761 stem radial variation of *Pinus pinaster* in a drought-prone environment. *Agr*
762 *Forest Meteorol* 180:173–181.

763 Warren JM, Meinzer FC, Brooks JR, Domec JC (2005) Vertical stratification of soil
764 water storage and release dynamics in Pacific Northwest coniferous forests. *Agr*
765 *Forest Meteorol* 130:39–58.

766 Zweifel R, Häsler R (2001) Dynamics of water storage in mature subalpine *Picea abies*:
767 temporal and spatial patterns of change in stem radius. *Tree Physiol* 21:561–569.

768 Zweifel R, Zimmermann L, Newbery DM (2005) Modeling tree water deficit from
769 microclimate: an approach to quantifying drought stress. *Tree Physiol* 25:147–156.

770 Zweifel R, Zimmermann L, Zeugin F, Newbery DM (2006) Intra-annual radial growth
771 and water relations of trees: implications towards a growth mechanism. *J Exp Bot*
772 57:1445–1459.

773 Zweifel R, Steppe K, Sterck FJ (2007) Stomatal regulation by microclimate and tree
774 water relations: interpreting ecophysiological field data with a hydraulic plant
775 model. *J Exp Bot* 58:2113–2131.

776

Accepted manuscript

777 **Figure captions**

778 **Figure 1.** Seasonal course of: (a) daily mean water vapour pressure deficit (VPD) (black
779 dots) and air temperature (grey dots), (b) daily mean solar radiation, (c) daily total gross
780 precipitation and (d) daily mean volumetric soil water availability over the top 30 cm of
781 soil (θ) (solid line) and daily volumetric soil water availability for each sensor (n=5)
782 (dot line). Labels on the x axis represent year in month/year format (i.e. January 2011 is
783 1/2011).

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

789 **Figure 3.** Responses of sap flow density (J_s) to (a) volumetric soil water availability (θ)
790 (data selected when $VPD > 0.5$ kPa and solar radiation > 150 W m⁻²) for each species in
791 2011 and (b) 2012, (c) responses to vapour pressure deficit (VPD) (data selected when
792 $\theta > 0.15$ cm³ cm⁻³ and solar radiation > 50 W m⁻²) in 2011 and (d) 2012. *Q. ilex* (grey
793 triangle and grey solid line), *Q. pubescens* (black diamond and black solid line), *A.*
794 *unedo* (black empty circle and black dashed line) and *P. halepensis* (grey cross and grey
795 dashed line). Average daily values for each species are shown.

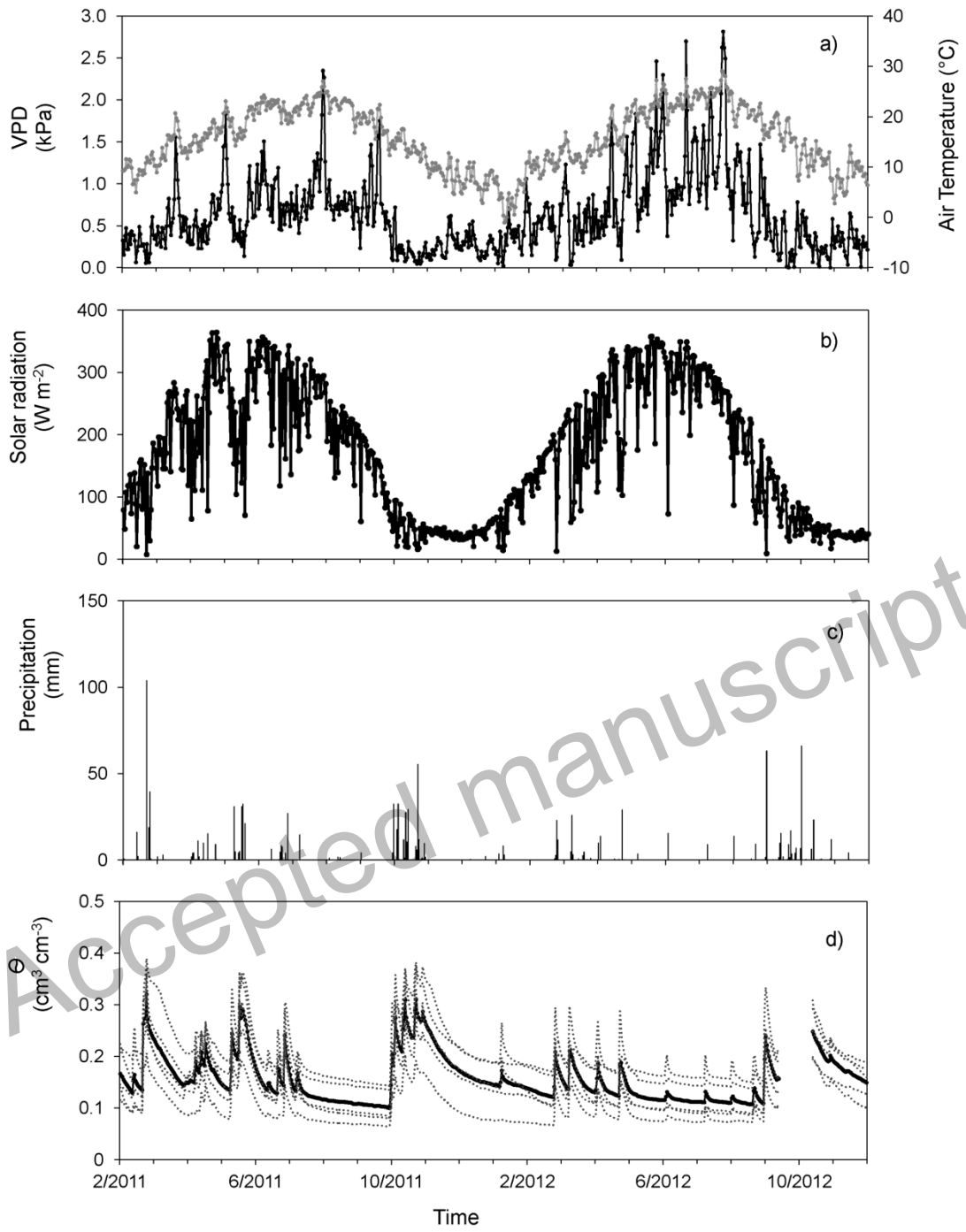
796 **Figure 4.** Seasonal course of (a) mean basal area increment (BAI), (b) BAI of each tree
797 relative to its basal area at the beginning of 2011 (BAI/ A_B) and (c) tree water deficit
798 (ΔW) over the study period for: *Q. ilex* (grey line), *Q. pubescens* (black line), *A. unedo*

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

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

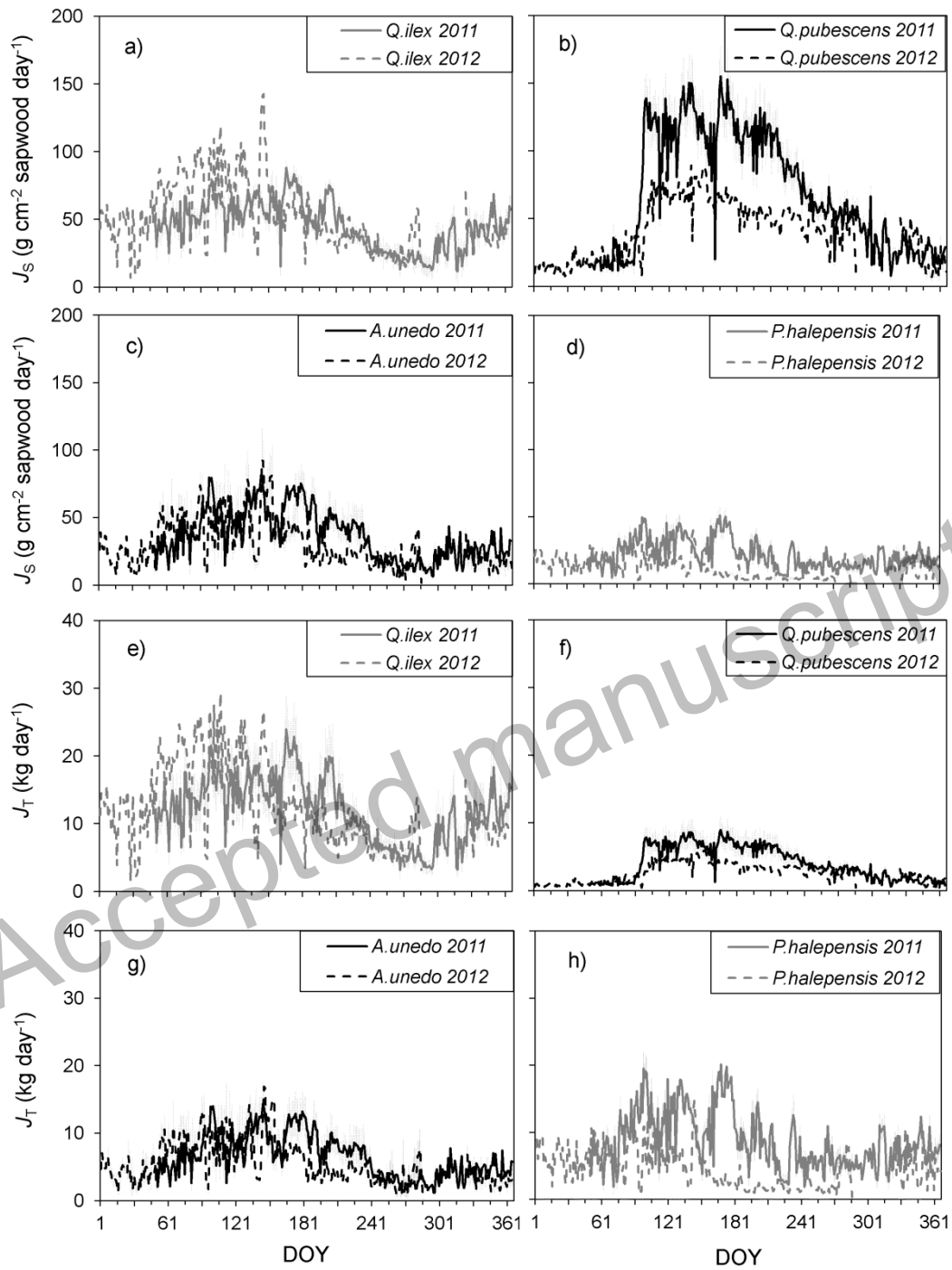
808 **Figure 6.** Modelled responses of tree water deficit (ΔW) to volumetric soil water
809 availability (θ) at different values of vapour pressure deficit (VPD) (0.5, 1.0, 2.0 and 2.5
810 kPa) for each species, according to model in Table 4. Panels on the left column depict
811 results for 2011 and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

812 **Figure 7.** Responses of sap flow density (J_s) to tree water deficit (ΔW) (data selected
813 when VPD>0.5 kPa and solar radiation>150 W m⁻²) for each species in (a) 2011 and (b)
814 2012. *Q. ilex* (grey triangle and grey solid line), *Q. pubescens* (black diamond and black
815 solid line), *A. unedo* (black empty circle and black dashed line) and *P. halepensis* (grey
816 cross and grey dashed line). Average daily values for each species are shown.



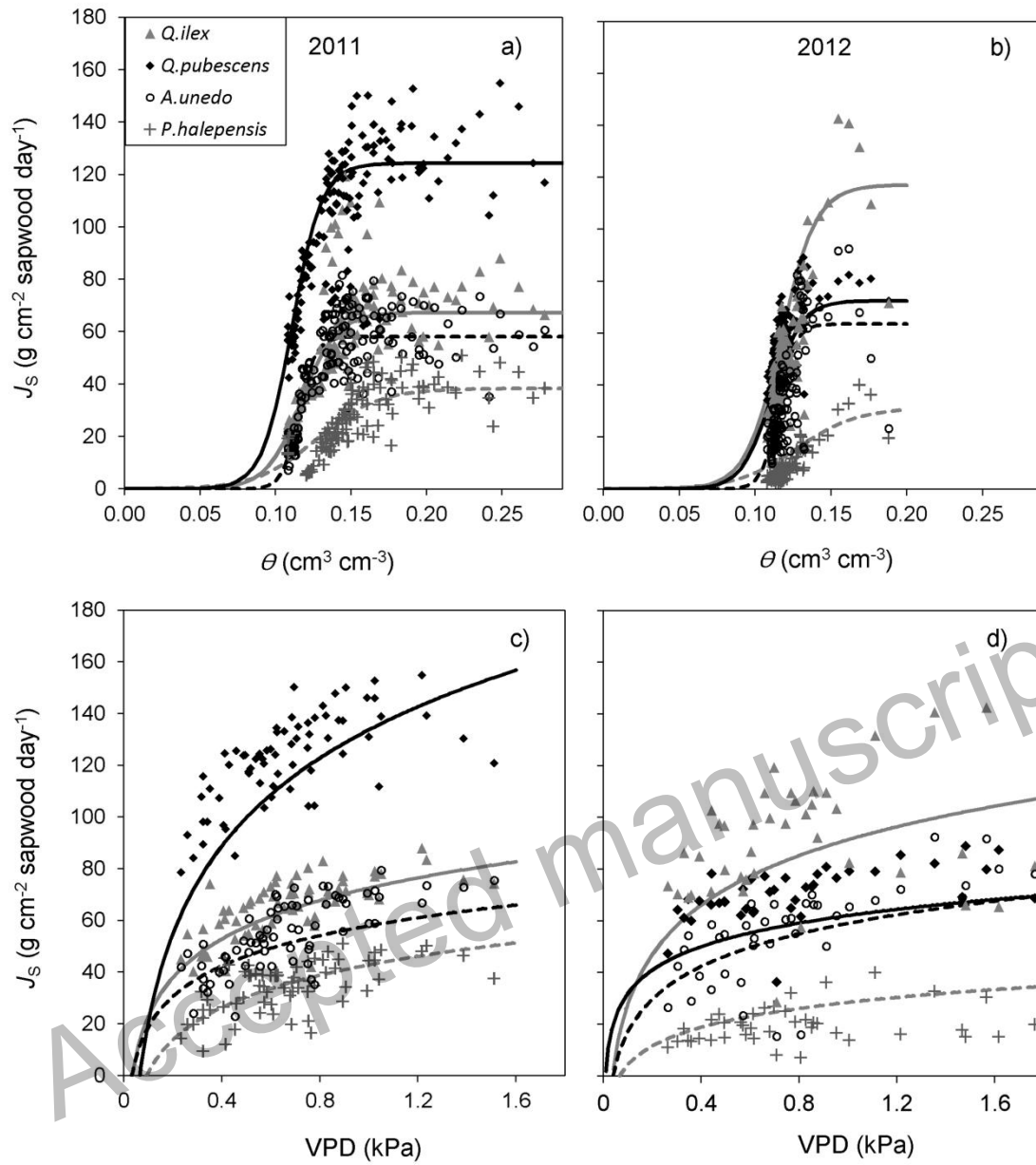
817

818 **Figure 1.**



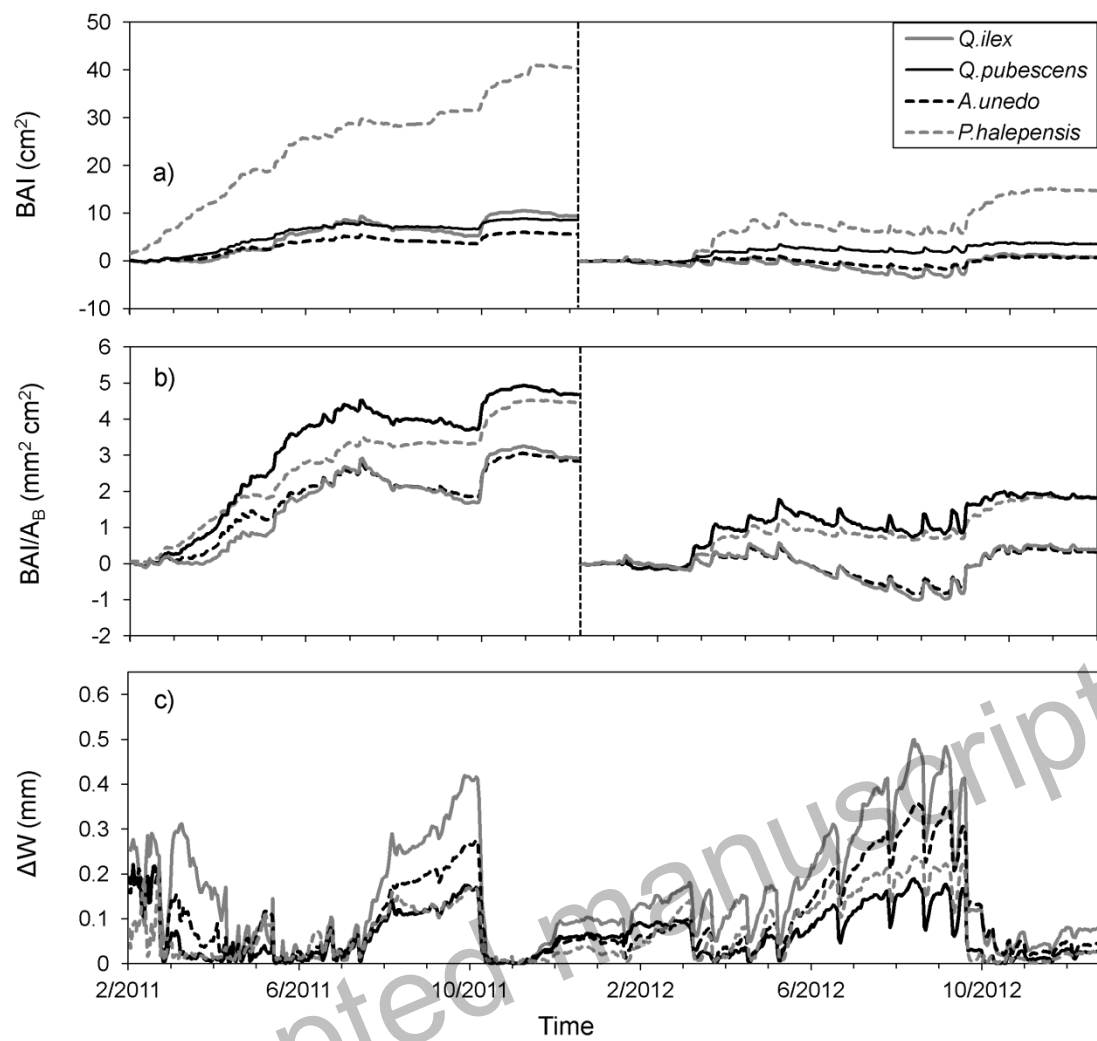
820

821 **Figure 2.**



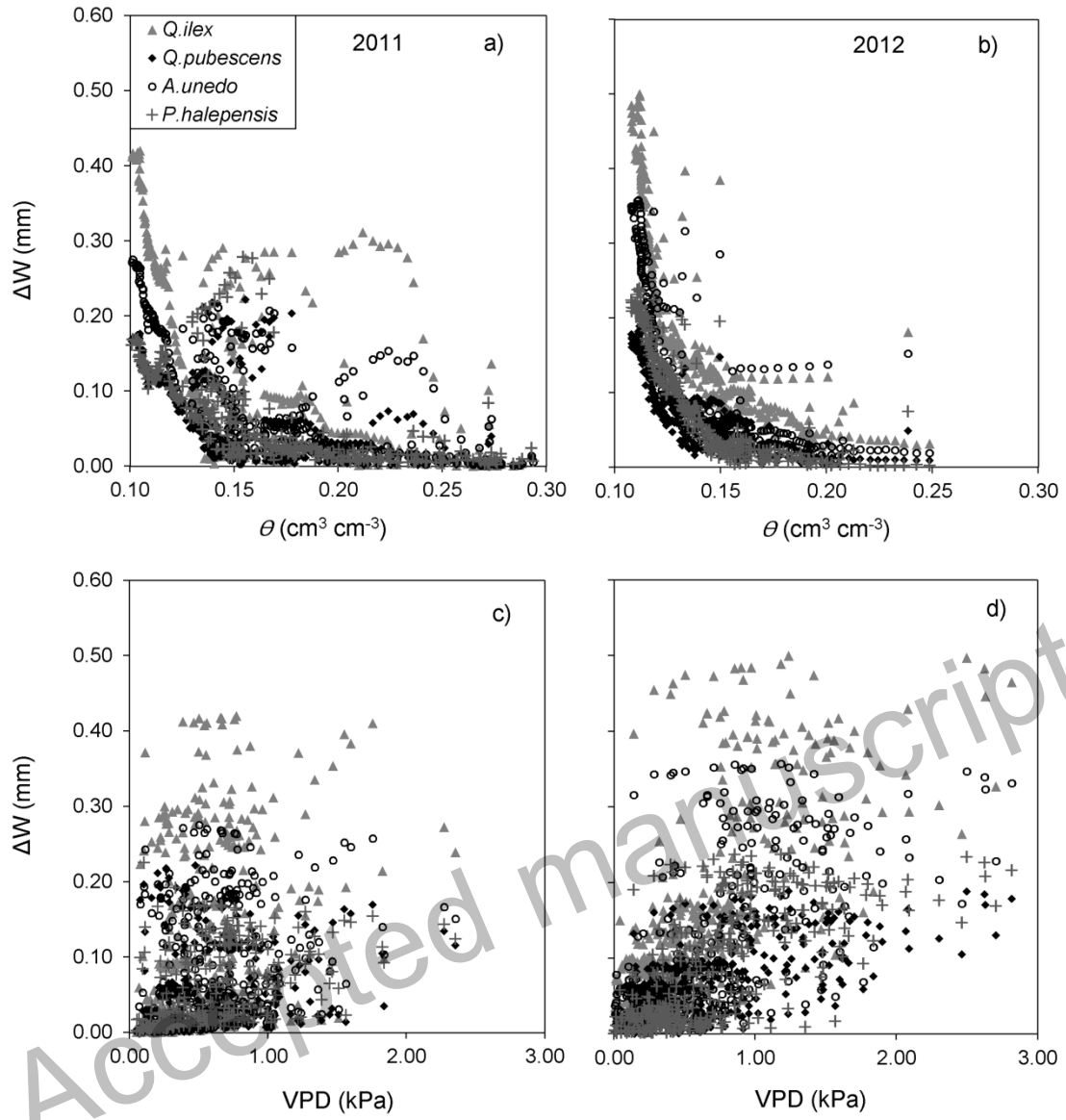
822

823 **Figure 3.**



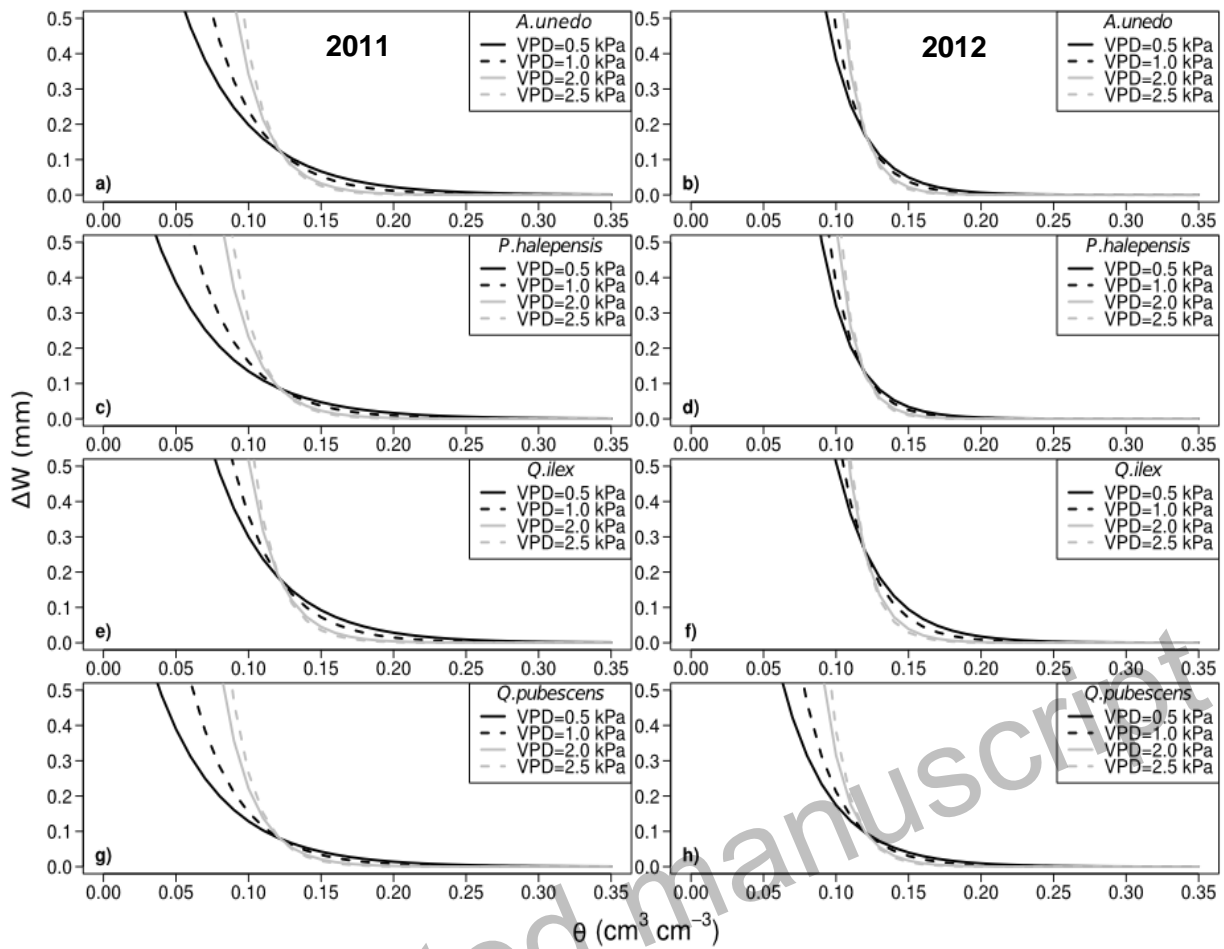
824

825 **Figure 4.**



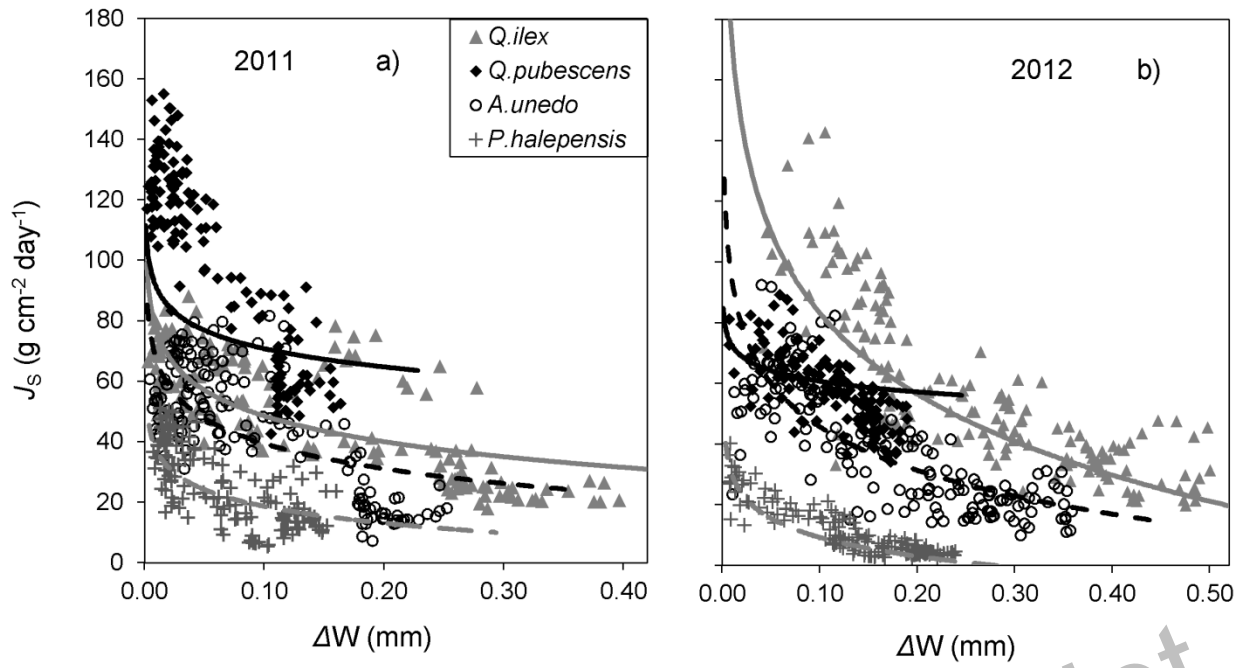
826

827 **Figure 5.**



828

829 **Figure 6.**



830

831 **Figure 7.**

Accepted manuscript

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

	<i>Q. ilex</i>	<i>Q. pubescens</i>	<i>A. unedo</i>	<i>P. halepensis</i>	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	-

837

838 ^a Mean height of all the monitored trees ($n=7$, $n=7$, $n=4$ and $n=3$ respectively)

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

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

843 ^d Data adapted from Aguadé et al. 2011, Cohen et al. 2008, Poyatos et al. 2008 and
 844 Mereu et al. 2009.

845 **Table 2.** Parameter values estimated of the nonlinear mixed models relating species sap
 846 flow per unit sapwood area (J_S) with volumetric soil water availability (θ) and vapour
 847 pressure deficit (VPD) for 2011 and 2012. Different letter represents statistically
 848 significant differences between species for a given parameter and year ($P<0.05$). Bold
 849 numbers represent statistically significant differences between years for a given
 850 parameter and species ($P<0.05$). The parameters have been extracted from the following
 851 equations (see main text for more details): $J_S = b \cdot \ln(\text{VPD}) + a$ and

$$852 \quad J_S = \frac{J_{S, \text{Asym}}}{1 + \exp[(\theta_{\text{mid}} - \theta) / \theta_{\text{scal}}]}$$

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

853

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

		<i>Q. ilex</i>	<i>Q. pubescens</i>	<i>A. unedo</i>	<i>P. halepensis</i>
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 ₂ O ⁻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

862

863 **Table 4.** Summary statistics for the linear mixed models relating tree water deficit (ΔW)
864 with species, vapour pressure deficit (VPD) and volumetric soil water availability (θ)
865 for 2011 and 2012. *A. unedo* was used as the reference level. Bold numbers represent
866 statistically significant results ($P < 0.05$). R^2_{LR} is a likelihood-based pseudo- R^2 (cf. Data
867 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	
	<i>P. halepensis</i>	-0.469	0.235	20.000	-1.997	0.060	
	<i>Q. ilex</i>	0.585	0.189	20.000	3.091	0.006	
	<i>Q. pubescens</i>	-0.402	0.209	20.000	-1.925	0.069	
	VPD : θ	-16.849	1.079	5371.000	-15.617	0.000	
	θ : <i>P. halepensis</i>	0.819	1.205	5371.000	0.680	0.497	
	θ : <i>Q. ilex</i>	-1.718	0.945	5371.000	-1.817	0.069	
	θ : <i>Q. pubescens</i>	-0.321	1.077	5371.000	-0.298	0.766	
	2012	(Intercept)	1.981	0.154	5902.000	12.844	
VPD		2.310	0.081	5902.000	28.625	0.000	
θ		-31.380	0.810	5902.000	-38.740	0.000	
<i>P. halepensis</i>		0.264	0.222	19.000	1.189	0.249	
<i>Q. ilex</i>		-0.412	0.172	19.000	-2.391	0.027	
<i>Q. pubescens</i>		-1.934	0.204	19.000	-9.490	0.000	
VPD : θ		-19.116	0.691	5902.000	-27.659	0.000	
VPD : <i>P. halepensis</i>		-0.044	0.026	5902.000	-1.685	0.092	
VPD : <i>Q. ilex</i>		-0.035	0.017	5902.000	-2.094	0.036	
VPD : <i>Q. pubescens</i>		-0.004	0.027	5902.000	-0.150	0.881	
θ : <i>P. halepensis</i>		-4.220	1.153	5902.000	-3.659	0.000	
θ : <i>Q. ilex</i>		7.150	0.805	5902.000	8.883	0.000	
θ : <i>Q. pubescens</i>		11.460	1.028	5902.000	11.146	0.000	

868

869

870 **Table 5.** Summary statistics for the linear mixed models relating species tree water
 871 deficit (ΔW) with sap flow density (J_s) for 2011 and 2012. *A. unedo* was used as the
 872 reference level. Bold numbers represent statistically significant results ($P < 0.05$). R^2_{LR} is
 873 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	
	<i>P. halepensis</i>	-11.558	18.860	15	-0.613	0.549	
	<i>Q. ilex</i>	8.544	15.936	15	0.536	0.600	
	<i>Q. pubescens</i>	38.931	16.022	15	2.430	0.028	
	logΔW:<i>P. halepensis</i>	4.014	0.811	2884	4.948	0.000	
	log ΔW : <i>Q. ilex</i>	-0.254	0738	2884	-0.344	0.731	
	logΔW:<i>Q. pubescens</i>	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	
	<i>P. halepensis</i>	-9.355	12.341	7	-0.758	0.473	
	<i>Q. ilex</i>	-3.345	10.495	7	-0.319	0.759	
	<i>Q. pubescens</i>	51.121	13.005	7	3.931	0.006	
	logΔW:<i>P. halepensis</i>	11.807	0.988	1745	11.947	0.000	
	logΔW:<i>Q. ilex</i>	-17.715	1.638	1745	-10.812	0.000	
	logΔW:<i>Q. pubescens</i>	15.705	1.810	1745	8.675	0.000	

874