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1 The combined effects of a long-term experimental drought and an extreme drought on  
2 the use of plant-water sources in a Mediterranean forest

3 Running head: Effects of drought on plant-water sources

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27 Mediterranean forest, climate change, extreme drought, water-use strategies, *Arbutus*  
28 *unedo*, *Quercus ilex*, *Phillyrea latifolia*.

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31

32 **Abstract**

33 Vegetation in water-limited ecosystems relies strongly on access to deep water reserves  
34 to withstand dry periods. Most of these ecosystems have shallow soils over deep  
35 groundwater reserves. Understanding the functioning and functional plasticity of  
36 species-specific root systems and the patterns of or differences in the use of water  
37 sources under more frequent or intense droughts is therefore necessary to properly  
38 predict the responses of seasonally dry ecosystems to future climate. We used stable  
39 isotopes to investigate the seasonal patterns of water uptake by a sclerophyll forest on  
40 sloped terrain with shallow soils. We assessed the effect of a long-term experimental  
41 drought (12 years) and the added impact of an extreme natural drought that produced  
42 widespread tree mortality and crown defoliation. The dominant species, *Quercus ilex*,  
43 *Arbutus unedo* and *Phillyrea latifolia*, all have dimorphic root systems enabling them to  
44 access different water sources in space and time. The plants extracted water mainly  
45 from the soil in the cold and wet seasons but increased their use of groundwater during  
46 the summer drought. Interestingly, the plants subjected to the long-term experimental  
47 drought shifted water uptake toward deeper (10-35 cm) soil layers during the wet season  
48 and reduced groundwater uptake in summer, indicating plasticity in the functional  
49 distribution of fine roots that dampened the effect of our experimental drought over the  
50 long term. An extreme drought in 2011, however, further reduced the contribution of  
51 deep soil layers and groundwater to transpiration, which resulted in greater crown  
52 defoliation in the drought-affected plants. The present study suggests that extreme  
53 droughts aggravate moderate but persistent drier conditions (simulated by our  
54 manipulation) and may lead to the depletion of water from groundwater reservoirs and  
55 weathered bedrock, threatening the preservation of these Mediterranean ecosystems in  
56 their current structures and compositions.

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## 61 **Introduction**

62 The consequences of anthropogenic climatic change in the Mediterranean Basin include  
63 the ongoing increases in temperature coupled to a very likely notable reduction in  
64 precipitation in summer and spring for the coming decades (Christensen *et al.*, 2007).  
65 Some Mediterranean forests have already adjusted and in some cases even adapted to  
66 seasonal drought and an irregular precipitation regime, but unprecedented duration,  
67 intensity and seasonality of future droughts predicted by general circulation models  
68 (GCMs) could have strong impacts on the vegetation and therefore the structure and  
69 function of ecosystems that are beyond the tolerance of most plants. Indeed, the  
70 numbers of documented drought-induced tree mortalities and episodes of forest decline  
71 in this region are growing (Peñuelas *et al.*, 2000, 2013; Galiano *et al.*, 2012). These  
72 events may lead to community shifts (Mueller *et al.*, 2005) and may cascade to affect  
73 nutrient cycling, microclimate and/or hydrology (Anderegg *et al.*, 2013a). The  
74 distribution of tree mortality, however, tends to be patchy across landscapes, indicating  
75 that certain individuals or populations are more predisposed to death (Suarez *et al.*,  
76 2004). This disparity in the responses to climate is partly driven by the interspecific  
77 differences in the ability to cope with water stress and warm temperatures (Breshears *et*  
78 *al.*, 2009; Allen *et al.*, 2010; Carnicer *et al.*, 2013a) but also by site characteristics  
79 (Lloret *et al.*, 2004). Detailed knowledge of the diversity of different responses and  
80 plant strategies is necessary for understanding the mechanisms behind tree mortality and  
81 for improving predictions of future forest declines or community shifts.

82 The experimental manipulation of precipitation is useful for studying the effects  
83 of drought on forest declines (Wu *et al.*, 2011). Such experiments in Mediterranean  
84 forests have helped to identify the physiological, morphological, structural (Ogaya &  
85 Peñuelas, 2006; Limousin *et al.*, 2010) and temporal (Barbeta *et al.*, 2013; Martin-  
86 Stpaul *et al.*, 2013) changes induced by drought. The projected increase in frequency of  
87 extreme droughts may imply a carry-over effect of multiple droughts, where plant  
88 resilience could be at risk (Anderegg *et al.*, 2012), but more counter-intuitively,  
89 structural changes caused by droughts seem to progressively enhance plant resistance  
90 (Lloret *et al.*, 2012; Barbeta *et al.*, 2013). Consequently, long-term experiments are  
91 desirable both to account for the accumulative effect of multiple droughts or to avoid  
92 overestimating the effects of drought on vegetation (Leuzinger *et al.*, 2011).

93           The use of water by plants has been well studied in temperate ecosystems, but  
94 we still have limited knowledge about a wide range of processes, on scales of leaves to  
95 entire landscapes, within many water-limited ecosystems (Zeppel, 2013). The effects of  
96 increasing drought on the patterns of use of underground water in Mediterranean trees  
97 has not been extensively studied, although recent studies have characterized seasonal  
98 patterns of water uptake in some *Quercus* species (Kurz-Besson *et al.*, 2014; David *et*  
99 *al.*, 2007; Nadezhdina *et al.*, 2007). The stable-isotope ( $\delta^{18}\text{O}$  and  $\delta^2\text{H}$ ) composition of  
100 water is a powerful tool for tracing the movement of water underground (Dawson *et al.*,  
101 2002). Isotopic fractionation does not occur during water absorption by roots  
102 (Ehleringer & Dawson, 1992; but see Lin and Sternberg, 1993 for exceptions), so the  
103 isotopic signature of xylem water can be used to determine a plant's source of water at a  
104 given moment. Pools of underground water can have different isotopic signatures due to  
105 differences in the original water sources (precipitation at different times of the year or  
106 from different source areas), and evaporation during and after rains can markedly  
107 change the isotopic composition of the soil water (Allison and Barnes 1992). Gradients  
108 in the compositions of H or O isotopes of the remaining soil in seasonally dry  
109 environments can also develop, with water in the surface layers becoming more  
110 enriched (leading to more positive  $\delta$  values), and water in the deeper layers becoming  
111 more depleted, in the heavy isotopes (Allison, 1982). Additionally, groundwater  
112 extracted from water tables or bedrock fractures can often have distinct signatures,  
113 reflecting the isotopic composition of rainwater during either wet or cold seasons, when  
114 these pools are refilled by infiltration with little evaporation (Brooks *et al.*, 2009).  
115 Isotopic signatures may also reflect the biased or weighted average of annual inputs of  
116 precipitation (Ehleringer & Dawson, 1992), the subsurface fractionation caused by  
117 water interacting with charged clays (Oerter *et al.*, 2014) or unique redox chemical  
118 evolution (Oshun *et al.*, 2014). These differences in isotopic signatures have been  
119 successfully used to determine the sources of water of vegetation in the Mediterranean  
120 Basin (David *et al.*, 2007; West *et al.*, 2012) and other biomes (Eggemeyer *et al.*, 2009;  
121 Kukowski *et al.*, 2013). Some studies have applied these techniques in short-term  
122 experimental droughts or under extreme natural droughts (Schwinning *et al.*, 2005; West  
123 *et al.*, 2012; Anderegg *et al.*, 2013b; Kukowski *et al.*, 2013), but little is known about  
124 the accumulative effect of long-term experimental drought on the isotopic compositions  
125 and sources of the water used by plants.

126           Some species in seasonally dry climates depend on access to groundwater for  
127 withstanding periods without precipitation (Dawson and Pate 1996; Kurz-Besson *et al.*,  
128 2014; David *et al.*, 2007; Eggemeyer *et al.*, 2009; Rossatto *et al.*, 2012; Zeppel, 2013;  
129 Oshun *et al.*, 2014). Forests commonly occur on mountainsides in Mediterranean  
130 climatic zones (Carnicer *et al.*, 2013b) where soils are shallow and roots do not reach  
131 the water table but may extract water stored in weathered bedrock (Witty *et al.*, 2003).  
132 This situation could be common among many forests in other biomes, because water  
133 tables are deeper than 10 m in an estimated 44.8% of terrestrial ecosystems (Fan *et al.*,  
134 2013), while the mean maximum rooting depth is approximately 7 m for trees and 5 m  
135 for shrubs (Canadell *et al.*, 1996). Nonetheless, the depth of root systems in sympatric  
136 species in Mediterranean ecosystems may differ and sometimes co-vary with other traits  
137 such as hydraulic safety margins or photosynthetic activity under water stress (West *et*  
138 *al.*, 2012). These characteristics define a species' water-use strategy as more isohydric  
139 or more anisohydric (Tardieu & Simonneau, 1998; Mcdowell *et al.*, 2008). Increasing  
140 evaporative demand, together with longer, more intense, more frequent and aseasonal  
141 droughts, are likely to reduce groundwater reserves (Eckhardt & Ulbrich, 2003), so the  
142 effects on vegetation would highly depend on these water-use strategies; the more  
143 isohydric phreatophytic species (West *et al.*, 2012) would be more vulnerable to carbon  
144 starvation caused by early stomatal closure, and anisohydric species would have a  
145 higher risk of hydraulic failure (Mcdowell *et al.*, 2008). Ecophysiological processes of  
146 acclimation (Matesanz & Valladares, 2013) and structural changes forced by previous  
147 droughts (Lloret *et al.*, 2012; Barbeta *et al.*, 2013), however, may mitigate the negative  
148 effects of drought.

149           We present the results of an ecohydrological study applying water stable-isotope  
150 techniques in a long-term experimental drought system established in 1998. A forest  
151 dominated by Holm oaks (*Quercus ilex* L.) was subjected to a 15% reduction in soil  
152 moisture (matching GCM predictions for the Mediterranean Basin (Christensen *et al.*,  
153 2007)) that caused a drastic suppression of growth in the dominant species *Q. ilex* and  
154 *Arbutus unedo* L. and an increase in mortality rates in *Q. ilex* but not *Phillyrea latifolia*  
155 L. (Ogaya *et al.* 2007). The effect size of the drought treatment, however, was dampened  
156 over time (Barbeta *et al.* 2013). The characterization of seasonal changes in plant-water  
157 sources is crucial for understanding the mechanisms underlying these species-specific  
158 responses to drought. Moreover, an extreme drought during the study period enabled us

159 to investigate the causes of drought-induced mortality in this Holm oak forest. This  
160 study asked the following questions: (i) what are/were the sources of water for each  
161 plant species, and do they change over time? (ii) did the sources of water change after  
162 12 years of experimental drought? (iii) does constant or excessive use of deeper water  
163 sources lead to the progressive depletion of groundwater under drought? (iv) how are  
164 water sources related to species-specific drought responses? and (v) is drought-induced  
165 mortality linked to changes in usage of particular water sources?

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## 184 **Materials and methods**

### 185 *Experimental site*

186 The experimental site was established in 1998 at the Prades Holm oak forest in southern  
187 Catalonia (northeastern Iberian Peninsula) (41°21'N, 1°2'E) at 930 m a.s.l. on a south-  
188 facing slope (25% slope). The forest has a very dense multi-stem crown (18 366 stems  
189 ha<sup>-1</sup>) dominated by *Q. ilex* (3850 stems ha<sup>-1</sup> and 50 Mg ha<sup>-1</sup>), *P. latifolia* (12 683 stems  
190 ha<sup>-1</sup> and 29 Mg ha<sup>-1</sup>) and *A. unedo* (667 stems ha<sup>-1</sup> and 9 Mg ha<sup>-1</sup>), accompanied by  
191 other Mediterranean woody species that do not reach the upper canopy (e.g. *Erica*  
192 *arborea* L., *Juniperus oxycedrus* L. and *Cistus albidus* L.) and the occasional isolated  
193 deciduous tree species (e.g. *Sorbus torminalis* L. Crantz and *Acer monspessulanum* L.).  
194 The canopy in the study plots did not exceed 4 m. This forest has been managed as a  
195 coppice for centuries but has not been significantly disturbed in the last 70 years.

196 The climate is typically Mediterranean. Since the beginning of the experiment  
197 (1998), the mean annual temperature has been 12.2 °C and the mean annual  
198 precipitation has been 610 mm. Holm oak forests can occur at sites with a mean annual  
199 precipitation as low as 400-450 mm (Terradas, 1999). The annual and seasonal  
200 distribution of precipitation is irregular, with annual precipitation ranging from 376 to  
201 926 mm in the 12 years of the experiment. Spring and autumn are the wettest seasons,  
202 and summer droughts usually last three months, during which precipitation is ~10% of  
203 the annual total and coincides with the highest temperatures. Winters are relatively cold.  
204 January is the coldest month (mean temperature of 4.4 °C), and the mean daily  
205 temperature is below 0 °C an average of eight days per winter. The soil is a Dystric  
206 Cambisol over Paleozoic schist and has a mean depth of ~35 cm. The mean annual  
207 precipitation is higher than that in the driest distributional limit of *Q. ilex*, but the  
208 topographic characteristics of the study site represent relatively xeric conditions due to  
209 the shallow soils and steep terrain.

210 The experimental system consisted of four 150-m<sup>2</sup> plots delimited at the same  
211 altitude along the slope. Half the plots (randomly selected) received the drought  
212 treatment, and the other half faced natural conditions. Precipitation was partially  
213 excluded from the plots of the drought treatment by PVC strips suspended 0.5-0.8 m  
214 above the soil and covering approximately 30% of the plot surfaces. A ditch 0.8 m in  
215 depth was excavated along the entire top edge of the plots to intercept runoff water. The



216 water intercepted by the strips and ditches was conducted around the plots, below their  
217 bottom edges. The strips were installed below the canopy and thus did not intercept  
218 light. Litter falling on the plastic strips was regularly transferred below them to ensure  
219 that differences in the content of soil nutrients among treatments and control plots were  
220 attributable only to the availability of water for the decomposition of this litter.

#### 221 *Sampling and environmental monitoring*

222 The field work was initially planned for spring 2010 to winter 2011, with one sampling  
223 campaign each season. The extreme drought in the summer of 2011 offered the  
224 possibility of an extra campaign to monitor plant performance under intense water  
225 stress. In each of these campaigns, samples of xylem, bulk-soil and spring water were  
226 collected at midday (between 1100 and 1400). For the samples of xylem water, 3-4  
227 sunlit twigs per tree were cut, the bark and phloem were removed to prevent  
228 interference from the isotopes in the water of the leaves and the twigs were then  
229 transferred to borosilicate glass vials with PTFE/silicone septa tops (National Scientific  
230 Company, Rockwood, USA). The vials were sealed with parafilm and stored in a  
231 portable cooler to prevent evaporation. In all four plots, the same five dominant  
232 individuals of *A. unedo*, *Q. ilex* and *P. latifolia* were sampled in each campaign. The  
233 samples of bulk soil were extracted with a soil corer from two layers (0-10 and 10-35  
234 cm). The soil samples were also immediately stored in the same type of glass vials as  
235 the xylem samples, sealed with parafilm and stored in a portable cooler. All samples  
236 were refrigerated until processing and analysis. Five locations were randomly selected  
237 in the control plots for soil sampling. In the drought plots, five locations under the  
238 plastics strips and five locations not under the strips were selected to control for  
239 potentially different amounts of evaporation. Samples of spring water were collected  
240 from a nearby fountain (natural spring); the isotopic signature of this water should be  
241 comparable to that of the groundwater. The experimental site is high on a ridge on schist  
242 bedrock, so the groundwater may remain in rock fractures for a period of time after  
243 infiltration from the surface but without forming a water table.

244 We also measured the midday foliar water potential in each field campaign with  
245 a pressure chamber (PMS Instruments, Corvallis, USA) in the same plots and species  
246 where the water samples were collected and in dominant individuals that reached the  
247 upper canopy. Ten randomly selected dominant individuals per plot and species were

248 sampled. The selected trees had no significant mechanical damage. Soil moisture was  
249 measured each campaign by time-domain reflectometry (Tektronix 1502C, Beaverton,  
250 USA) (Zegelin *et al.*, 1989; Gray & Spies, 1995). Three stainless-steel cylindrical rods,  
251 25 cm long, were vertically installed in the upper 25 cm of the soil at four randomly  
252 selected locations in each plot. The time-domain reflectometer was manually attached to  
253 the ends of the rods for each measurement. An automatic meteorological station  
254 installed between the plots monitored temperature, photosynthetically active radiation,  
255 air humidity and precipitation every 30 min. Both the Standardized Precipitation and  
256 Evapotranspiration Index (SPEI) at different timescales (Vicente-Serrano *et al.*, 2013)  
257 and the mortality rates were calculated for the study plots using the same methodology  
258 described by Barbeta *et al.* (2013). Additionally, a visual evaluation of crown  
259 defoliation estimated the effect of the extreme drought in 2011. Defoliation was defined  
260 as the percentage of leaf loss in the assessable crown, using a sliding scale of 10%.

#### 261 *Isotopic analyses*

262 The water in the soil and xylem samples was extracted by cryogenic vacuum distillation  
263 following West *et al.* (2006). The extraction system consisted of 10 extraction tubes  
264 connected with Ultra-Torr™ fittings (Swagelok Company, Solon, USA) to 10 U-shaped  
265 collection tubes specifically designed for this system. The extraction tubes were  
266 submerged in a pot containing mineral oil maintained at 110 °C, and the collection tubes  
267 were submerged in liquid nitrogen to freeze/capture the extracted water vapor for  
268 isotopic analysis. The extraction system was connected to a vacuum pump (model RV3;  
269 Edwards, Bolton, UK). The isotopic compositions ( $\delta^{18}\text{O}$  and  $\delta^2\text{H}$ ) of the distilled water  
270 samples were determined using isotope ratio infrared spectroscopy (IRIS) with a Picarro  
271 L2120-i Analyzer (Picarro Inc., Santa Clara, USA). Residual organic compounds in the  
272 distilled water can interfere with the analyses of plant and soil samples conducted with  
273 IRIS technology (West *et al.*, 2010, 2011). The ChemCorrect™ post-processing  
274 software from Picarro, though, can determine the degree of contamination of each  
275 sample, and Picarro also offers a post-test correction for the isotopic composition of  
276 contaminated samples. To test the reliability of IRIS and therefore our data, we analyzed  
277 a subset of plant and soil samples (104, including samples from other studies) using  
278 isotope ratio mass spectrometry (IRMS), which is not affected by organic compounds. A  
279 detailed description of the methodology of IRMS and IRIS analyses can be found in  
280 West *et al.* (2011) and Goldsmith *et al.* (2012) for both  $\delta^{18}\text{O}$  and  $\delta^2\text{H}$ . We then

281 compared the isotopic compositions obtained by IRIS and IRMS and their post-  
282 processing corrections and confirmed that IRIS was highly reliable for our samples. The  
283 discrepancies between the two methods remained below the instrumental errors.  
284 Nonetheless, we discarded those samples with very high concentrations of organic  
285 compounds. The isotope ratios in this study are expressed as:

$$286 \quad \delta^{18}\text{O} \text{ or } \delta^2\text{H} = ((R_{\text{sample}} - R_{\text{standard}}) - 1)$$

287 where  $R_{\text{sample}}$  and  $R_{\text{standard}}$  are the heavy/light isotope ratios ( $^2\text{H}/\text{H}$  and  $^{18}\text{O}/^{16}\text{O}$ ) of the  
288 sample and the standard (VSMOW, Vienna Standard Mean Ocean Water), respectively.  
289 The water extractions and isotopic analyses were conducted at the Department of Crop  
290 and Forest Sciences (University of Lleida, Catalonia, Spain) and at the Center for Stable  
291 Isotope Biogeochemistry (University of California, Berkeley, USA).

#### 292 *Determining the sources of plant water and statistical analyses*

293 The isotopic compositions of the xylem water and its potential sources can be directly  
294 compared by plotting both isotopes together (Goldsmith *et al.*, 2012) but also by using  
295 the *siar* (stable isotope analysis in R) package in R (Parnell *et al.*, 2010). These  
296 Bayesian mixing models estimate the most likely proportion of plant water taken up  
297 from each source, which is a suitable approach in our study because three different  
298 monitored sources contributed simultaneously to plant-water use. We applied these  
299 models to our data to infer the relative contribution of each water source to the xylem  
300 water, producing simulations of plausible contributing values from each source using  
301 Markov chain Monte Carlo (MCMC) methods. Stable-isotope mixing models are  
302 widely applied to the study of food webs but can also be used for determining plant-  
303 water sources. Our model inputs were the isotopic composition ( $\delta^{18}\text{O}$  and  $\delta^2\text{H}$ ) and their  
304 standard errors for each potential source (shallow (0-10 cm) soil water, deep (10-35 cm)  
305 soil water and groundwater) and the isotopic compositions of the xylem water, which  
306 were assigned as the target values (“consumers” in Parnell *et al.* (2010)). We set the  
307 TEF (trophic enrichment factor) to 0, because of the absence of fractionation during  
308 water uptake from soil by roots (Ehleringer & Dawson, 1992), and set concentration  
309 dependence to 0. We ran 500 000 iterations and discarded the first 50 000. We ran a  
310 model for the isotopic values from each plant in each campaign with the isotopic values  
311 from the soil water of the corresponding plot. We thereby obtained the most likely

312 contribution (the mean of the posterior distribution of the MCMC simulation) of each  
313 source for every plant measurement. These relative contributions were then compared  
314 between seasons and species and between control and droughted individuals using  
315 analyses of variance (ANOVAs) with Tukey's HSD (honest significant difference) post-  
316 hoc tests. Differences in the midday foliar water potentials and stem mortality rates  
317 were also evaluated by ANOVAs and Tukey's HSD post-hoc tests. Soil moisture, soil  
318 isotopic signatures and crown defoliation were analyzed with generalized linear mixed  
319 models (GLMMs) of the MCMCglmm package in R (Hadfield, 2010) for including plot  
320 as a random factor. Furthermore, the MCMCglmm package allows fitting multi-  
321 response models, and we assessed the changes in soil-water isotopic composition fitting  
322 these multi-response models with  $\delta^{18}\text{O}$  and  $\delta^2\text{H}$  as dependent variables. We selected the  
323 model with the lowest DIC (deviance information criterion) when several combinations  
324 of independent factors and interactions were possible. All statistical analyses were  
325 conducted using R version 2.14.2 (R Core Development Team, 2012).

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## 338 **Results**

### 339 *Environmental data*

340 The study was carried out between 2010 and 2011. The first year was slightly cooler  
341 and wetter than the 1975-2011 average (11.0 vs 11.8 °C mean annual temperature and  
342 687 vs 663 mm annual precipitation), but 2011 was slightly warmer and drier than  
343 average (13.1 °C and 549 mm). More importantly, rainfall distribution throughout the  
344 year differed between the two years. The seasonality of rainfall was typical for this site  
345 in 2010, with a wet spring and autumn and a summer drought that lasted two months. In  
346 contrast, 2011 had a wet March but afterward was generally very dry, with little  
347 precipitation until the end of October. Total precipitation for 142 consecutive days was  
348 only 13 mm, without a single rainfall >3 mm, coinciding with the highest temperatures  
349 (Fig. 1). This period from April to September was the driest since 1975, as shown by the  
350 lowest September SPEI-6 and SPEI-3 for 1975-2011 (Figs. S1 and S2). The droughted  
351 plots during the study period had a significantly lower soil-water content than the  
352 control plots ( $17.32 \pm 1.56$  vs  $14.75 \pm 1.59\%$ ,  $pMCMC < 0.05$ ). Moreover, the droughted  
353 plots, which had been subjected to the treatment since 1998, had an average reduction of  
354  $14.9 \pm 1.1\%$  in total soil-water content ( $pMCMC < 0.01$ , for 1998-2011). Soil moisture  
355 ranged between 4.7 and 26.4% (v/v) during the period of study.

### 356 *Midday foliar water potential*

357 The plants in the drought treatment had significantly lower midday foliar water  
358 potentials ( $\Psi_{md}$ ) than the plants in the control plots ( $-3.1 \pm 0.29$  vs  $-2.8 \pm 0.28$  MPa,  
359  $F=5.43$ ,  $n=6$ ,  $p < 0.05$ ).  $\Psi_{md}$  differed significantly across seasons ( $F=144.99$ ,  $p < 0.001$ ),  
360 becoming more negative in the extreme drought in 2011 (Fig. 2), and species ( $F=49.94$ ,  
361  $p < 0.001$ ). The seasonal variation of  $\Psi_{md}$  also differed significantly among species, as  
362 shown by the interaction between species and seasonal factors ( $F=12.04$ ,  $p < 0.001$ ), and  
363 the effect of the drought treatment also varied across seasons ( $F=3.52$ ,  $p < 0.05$ ). Mean  
364  $\Psi_{md}$  was significantly lower in *P. latifolia* than in *Q. ilex* and *A. unedo* ( $-3.71 \pm 0.46$ , -  
365  $2.48 \pm 0.17$  and  $-2.74 \pm 0.28$  respectively,  $p < 0.001$ , Tukey's HSD test) but did not differ  
366 significantly between the latter two species.

367 *Isotopic composition of plant-water sources*

368  $\delta^{18}\text{O}$  and  $\delta^2\text{H}$  in the soil water varied with depth and season. Depth was negatively  
369 associated with  $\delta^{18}\text{O}$  and  $\delta^2\text{H}$ : the shallow (0-10 cm) soil layer was significantly more  
370 enriched in the heavier isotopes of O and H than the deep (10-35 cm) soil layer  
371 (posterior mean of the effect (p.m.e.)=-0.12,  $pMCMC<0.001$ ). The drought treatment  
372 did not affect  $\delta^{18}\text{O}$  and  $\delta^2\text{H}$  ( $pMCMC=0.51$ ). The values of  $\delta^{18}\text{O}$  and  $\delta^2\text{H}$  indicated the  
373 seasonal patterns, being more depleted in autumn and winter than in spring and both  
374 summers (winter p.m.e.=-0.84,  $pMCMC<0.01$ ; autumn p.m.e.=-1.19,  $pMCMC<0.001$ ;  
375 spring p.m.e.=2.04,  $pMCMC<0.001$ ; summer 2010 p.m.e.=1.68,  $pMCMC<0.001$ ; p.m.e.  
376 respect isotopic ratios of summer 2011). Soil-water isotopic levels were significantly  
377 more enriched in heavier isotopes under the plastic strips (p.m.e.=0.76,  
378  $pMCMC<0.001$ ). Water collected from a nearby spring, having an isotopic signature  
379 representative of the deeper water reserves, remained unchanged throughout the seasons  
380 ( $\delta^{18}\text{O}=-7.19\pm 0.14$  and  $\delta^2\text{H}=-47.34\pm 1.29$  ‰). Springwater samples fell along the local  
381 meteoric water line (Neal et al 1992) (Fig. 3), indicating that it did not evaporate during  
382 infiltration.

383 *Determination of plant-water sources*

384 The mixing model revealed that the canopy species in Prades forest took up water  
385 simultaneously from the three well-defined water pools; shallow soil (0-10 cm), deep  
386 soil (10-35 cm) and groundwater. The largest proportion was generally from shallow  
387 soil ( $38.7\pm 1.5\%$ ), followed by deep soil ( $31.23\pm 1.4\%$ ) and groundwater ( $30.10\pm 1.5\%$ ).  
388 Water uptake, however, strongly varied seasonally, as indicated both graphically (Fig.  
389 3) and in the output of the siar models. The statistical assessment of these seasonal  
390 shifts of plant-water sources is summarized in Table S1. The shallow soil layer  
391 contributed the most to water uptake in autumn and winter (Table S1, Fig. 4), with  
392 significantly higher proportions than in the spring and summer of 2010. The  
393 contribution of the shallow soil to water uptake during the abnormally dry summer in  
394 2011, although lower than in the cold seasons, was higher than in the spring and  
395 summer of 2010 (Table S1). Deep soil (10-35 cm) was the main source of water in the  
396 summer and spring of 2010, with lower relative contributions in cold seasons and in  
397 summer 2011 (Fig. 4, Table S2 for statistics). Groundwater was the main water source

398 in the summers of 2010 and 2011 ( $42.84 \pm 8.58$  and  $39.41 \pm 2.66\%$  respectively). The siar  
399 mixing models, however, attributed a contribution of approximately 25% of the total  
400 extracted water to this water pool, even in spring, autumn and winter when surface-soil  
401 water levels were high (Table S1, Fig. 4). The xylem samples to the upper left of the  
402 soil samples and near the LMWL in Fig. 3 (autumn and winter panels) indicate that in  
403 the cold seasons, the plants absorbed recent rainwater, which was not subject to isotopic  
404 enrichment by evaporation from the soil surface. The seasonal patterns of water use did  
405 not differ significantly among the three species (Fig. 5, Table S3).

406 The long-term experimental drought treatment significantly affected the depth  
407 from which water was taken up in all seasons except for spring 2010 (Fig. 4, Table S2).  
408 These effects consisted of differences in the relative contribution of the water sources in  
409 response to the drought treatment. The shallow (0-10 cm) soil layer contributed  
410 relatively more water to the xylems of the droughted individuals during the summer of  
411 2010 ( $33.83 \pm 4.47$  vs  $5.58 \pm 1.94\%$ ,  $F=46.41$ ,  $p<0.001$ , ANOVA; Table S2, Fig. 4). This  
412 shallow soil layer, though, contributed less water to the droughted individuals in winter  
413 ( $44.91 \pm 2.17$  vs  $59.71 \pm 4.06\%$ ,  $F=10.11$ ,  $p<0.01$ , ANOVA; Table S2, Fig. 4). In autumn,  
414 the deep (10-35 cm) soil layer contributed relatively more water to the droughted  
415 individuals than to the control individuals ( $32.54 \pm 1.57$  vs  $23.30 \pm 1.45\%$ ,  $F=17.68$ ,  
416  $p<0.001$ , ANOVA; Table 4, Fig. 4). During the extreme drought in the summer of 2011,  
417 the droughted individuals had reduced access to the deep water reserves (groundwater)  
418 relative to the control individuals ( $33.95 \pm 2.99$  vs  $44.64 \pm 4.13\%$ ,  $F=4.33$ ,  $p<0.05$ ,  
419 ANOVA; Table S2, Fig. 4). The proportion of groundwater uptake remained  $<30\%$   
420 when the soil-water content was  $>15\%$ . The soil-water content was  $<10\%$  in both  
421 summers, coinciding with an increase in the proportion of groundwater taken up by the  
422 plants. The increase, however, was higher in the control plants (Fig. 6).

#### 423 *Stem mortality rates and crown defoliation*

424 The extreme drought in the summer of 2011 caused a significant increase in stem  
425 mortality rates relative to 2010 ( $F=5.23$ ,  $p<0.05$ , ANOVA). Stem mortality rates were  
426 significantly higher in *Q. ilex* than in *P. latifolia* ( $F=7.79$ ,  $p<0.05$ , ANOVA; Fig. 7). *Q.*  
427 *ilex* had the second highest annual stem mortality rate in 2011 since the onset of the  
428 experiment in 1998, and *P. latifolia* had the third highest rate for the same period. *A.*  
429 *unedo* was not included in these analyses because of its low sample size. The

430 percentages of crown defoliation following the drought in 2011 were generally  
431 significantly higher in the drought treatments than in the control plots (p.m.e.=1.20,  
432  $pMCMC < 0.01$ , MCMCglmm; Fig. 8), except for *P. latifolia* (6.0% difference between  
433 treatments,  $p = 0.84$ , ANOVA with Tukey's-HSD post-hoc tests). Defoliation  
434 percentages for both *Q. ilex* and *A. unedo* analyzed separately, however, were  
435 significantly higher in the drought plots (19.5% difference between treatments for *A.*  
436 *unedo*,  $p < 0.01$ ; 20.5% difference between treatments for *Q. ilex*,  $p < 0.01$ ; ANOVA with  
437 Tukey's-HSD post-hoc tests; Fig. 8).

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454 **Discussion**

455 This study investigated the combined effects of a long-term (12 years) experimental  
456 drought and an extreme natural drought on the patterns of water uptake by a Holm oak  
457 forest growing on shallow soils over schist and so lacked access to a water table. The  
458 three species of trees studied have dimorphic root systems that enable access to different  
459 water sources in space and time but used water primarily from shallow soil layers but  
460 also water stored in the fractured schist. These findings are consistent with those of  
461 previous studies in other arid and semi-arid communities (Dawson & Pate, 1996; David  
462 *et al.*, 2013; Oshun *et al.*, 2014). Interestingly, the relative contribution of groundwater  
463 decreased in the drought treatment and during the extreme drought in 2011, suggesting  
464 that plant access to deeper groundwater pools had declined over time and in the extreme  
465 drought in 2011. This response was often coupled with a decrease in  $\Psi_{md}$ , hence  
466 suggesting that the plants were subjected to high levels of drought-induced water stress.  
467 Recent studies have demonstrated the important role of deep water sources in the  
468 response to extreme droughts and their links to tree mortality and species-specific  
469 water-use strategies (West *et al.*, 2012; Anderegg *et al.*, 2013b; Kukowski *et al.*, 2013),  
470 but the long timescale of this study allowed an assessment of the accumulative effect of  
471 experimental drought on root functioning and on the zones of water uptake that helped  
472 sustain this functioning.

473 During seasons in which soil-water content was  $>15\%$ , the soil-water pool (0-10  
474 and 10-35 cm soil layers combined) supported forest transpiration, with a contribution  
475 of at least 75% (Fig. 4). David *et al.* (2013) reported a contribution of soil water near  
476 100% in winter in a more mesic savannah containing *Q. suber* oaks. The vegetation on  
477 the steep and shallow soils of our study site thus appeared to require a contribution to  
478 transpiration from the deeper groundwater, even during wet seasons. Likewise, the  
479 highest transpiration rates occurred in summer in the more mesic sites (David *et al.*,  
480 2013), whereas stomatal conductance decreases in spring and summer in the Prades  
481 Holm oak forest (Peñuelas *et al.*, 1998; Ogaya & Peñuelas, 2003), suggesting that the  
482 groundwater reserves may not be able to meet the high evaporative demand. The use of  
483 groundwater, though, increased in both summers (Fig. 4), confirming that the allocation  
484 of growth to deep roots is an advantageous strategy for withstanding very dry periods

485 (Canadell *et al.*, 1996, 1999). The deeper (10-35 cm) soil horizon at our site supplied  
486 most of the water that plants used in the relatively wet spring of 2010. The similar  
487 isotopic signatures of the xylem waters in the spring and summer of 2010 (Fig. 3)  
488 suggest that rainwater from late winter and spring was used throughout the dry season.  
489 This finding is further supported by the highest relative contribution of the water from  
490 the deep (10-35 cm) soil horizon in the summer of 2010 (Fig. 4) and by correlations  
491 between drought indices and stem mortality (Barbeta *et al.*, 2013). The roots of *Q. ilex*  
492 can access bedrock fractures seeking moisture, especially in dry areas (Canadell *et al.*,  
493 1999). We also observed this capacity in the tall shrubs *A. unedo* and *P. latifolia*, in  
494 agreement with prior observations of woody Mediterranean species (Canadell & Zedler,  
495 1995; West *et al.*, 2012). In addition, the seasonal patterns of water uptake were  
496 consistent for the three plant species we studied (Fig. 5). This finding helps us to rule  
497 out the possibility of species-specific use of water sources, suggesting that the reported  
498 disparity in their physiological, morphological and demographic responses to drought  
499 (Martínez-Vilalta *et al.*, 2003; Ogaya & Peñuelas, 2006; Barbeta *et al.*, 2012, 2013)  
500 cannot be directly attributed to rooting depth or seasonal patterns of water uptake, as  
501 similarly found in South African fynbos (West *et al.*, 2012).

502         The seasonal patterns of water uptake varied greatly in the three species. The  
503 differences we observed in the use of water sources between the drought and control  
504 treatments could be a short-term response to the lower availability of water. The effect  
505 of the drought treatment on soil moisture, however, was much weaker than that of the  
506 seasonal variation. Because we did not detect differences in plant-water sources  
507 between autumn and winter despite the different environmental conditions (highlighted  
508 by contrasting plant-water status (Fig. 2)), the higher dependence of the droughted  
509 plants on water from the deep (10-35 cm) soil horizon (Fig. 4) does not represent a  
510 transient response (*sensu* Martin-Stpaul *et al.*, 2013) but a persistent shift in the vertical  
511 distribution of fine roots induced by our long-term experiment. Furthermore, short-term  
512 experimental drought may not affect the depth of water uptake in trembling aspens  
513 (Anderegg *et al.*, 2013b), although the water sources for this species varied little  
514 seasonally.

515 *Q. ilex* has less fine-root biomass in the top 10 cm of soil than in deeper layers  
516 (Canadell *et al.*, 1999; López *et al.*, 2001), arguably because the elevated soil

517 temperatures in summer in Mediterranean ecosystems can dehydrate or even kill fine  
518 roots. Consequently, the decrease in soil moisture induced by the drought treatment may  
519 have exacerbated this situation, favoring the production of fine roots in deeper soil  
520 layers. In contrast, the lower contribution of groundwater in droughted plants in the  
521 summer of 2011 relative to the summer of 2010 (Figs. 4 and 6) may be a direct  
522 consequence of a decreased recharge of the groundwater or water that resides within the  
523 bedrock fractures during rainy seasons. The capacity of plants to redistribute their fine  
524 roots within the soil profile, based on our results, is evidence of phenotypic plasticity in  
525 a key trait of the plant-water relationship (root functional distribution). Understanding  
526 the limits of species-specific plasticity for any trait or suite of traits is crucial for  
527 predicting the responses of species to environmental change (Matesanz & Valladares,  
528 2013; Moritz & Agudo, 2013). Together with ecosystem structural changes (Lloret *et*  
529 *al.*, 2012), species-specific responses are likely to help buffer plants against the negative  
530 effects of climate change. A dampening of the drought treatment has also been observed  
531 in our study system (Barbeta *et al.*, 2013; Rosas *et al.*, 2013); the effect of the drought  
532 treatment on tree growth tended to decrease over time. A shift in the distribution of fine  
533 roots would thus be another possible factor leading to a dampening pattern, along with  
534 other alterations such as reductions in foliar area (Ogaya & Peñuelas, 2006; Limousin *et*  
535 *al.*, 2009) and adjustments of xylem hydraulic properties (Martin-Stpaul *et al.*, 2013).

536         The vegetation faced average meteorological conditions in the summer of 2010,  
537 but April to September 2011 was extraordinarily dry (Poyatos *et al.*, 2013), increasing  
538 tree mortality in *Q. ilex* (Fig. 7) and inducing widespread crown defoliation, especially  
539 in *A. unedo* and *Q. ilex* (Ogaya *et al.*, 2014) (Fig. 8). The levels of soil moisture in the  
540 upper 25 cm, however, were not substantially different between the summers of 2010  
541 and 2011 (Fig. 1), and  $\Psi_{md}$  was more negative in the three species in 2011 (Fig. 3).  
542 Plants extracted significantly more water from the 10-35 cm soil horizon and less from  
543 the 0-10 cm soil horizon during the moderate drought of 2010 than during the drier  
544 summer of 2011 (Fig. 4), suggesting that the drought-induced forest decline may have  
545 been associated with the lower contributions of deep soil-water reserves to the uptake of  
546 water by the trees. The characteristics of the geological substrate (Lloret *et al.*, 2004),  
547 soil depth (Galiano *et al.*, 2012) and soil-water storage capacity may thus interact with  
548 extreme droughts to determine the patchy landscape of forest declines. Accordingly, the  
549 use of deep water reserves are likely required for the maintenance of transpiration and

550 carbon assimilation during droughts in Mediterranean oaks (Canadell *et al.*, 1996;  
551 David *et al.*, 2007; 2013). The more anisohydric *P. latifolia*, however, was less affected  
552 by the acute drought in 2011 (Fig. 7), and its  $\Psi_{md}$  and crown defoliation appeared to be  
553 insensitive to the drought treatment despite a similar depth of water uptake. We attribute  
554 this response to its higher resistance to xylem embolism (Martínez-Vilalta *et al.*, 2002),  
555 which allows this species to maintain carbon assimilation under water stress. The depth  
556 of water uptake in this community thus did not seem to co-vary across species with  
557 other hydraulic properties, such as xylem anatomy and stomatal regulation. Even though  
558 the depth of water uptake did not vary across species, the absolute quantity of water  
559 transpired by each species is likely to differ. The species-specific seasonal patterns of  
560 transpiration rates should be combined with the depth of water uptake to obtain a  
561 complete picture of species-specific water use. Moreover, some of the species studied  
562 may be able to move water through roots at different depths (hydraulic lift and  
563 downward siphoning), which could mask the impossibility of the roots of the other  
564 species to reach deep water reserves.

565         The lack of hydraulic niche segregation among the co-occurring species in this  
566 Holm oak forest contrasts with the findings of other recent studies in other  
567 Mediterranean systems (Araya *et al.*, 2011; Peñuelas *et al.*, 2011; West *et al.*, 2012). It  
568 implies that the three species could be competing for the same water resources in space.  
569 The seasonal resolution of our measurements, however, prevented us from assessing  
570 species-specific differences in the timing of water use. The projected increase in the  
571 recurrence of extreme droughts, though, could favor the more drought-resistant *P.*  
572 *latifolia* over *Q. ilex* and *A. unedo*. Changes in the distribution of fine roots, as  
573 suggested by our data, could buffer the species against environmental change to some  
574 extent, but we also found that an extreme drought could cause widespread defoliation  
575 and tree mortality in *Q. ilex* and *A. unedo* (Ogaya *et al.*, 2014) (Fig. 8), associated with a  
576 reduction in groundwater uptake by these species in the drought treatment. Long and  
577 intense periods of drought such as occurred during the summer of 2011 will thus likely  
578 threaten the preservation of this community in its current structure and composition, and  
579 these effects will presumably be amplified by a larger depletion of deep water reserves  
580 after several extreme droughts (see Schwinning, 2010).

581           The impact of recent climatic changes and particularly more acute and prolonged  
582 droughts on groundwater reserves is not well understood (Broolsma *et al.*, 2010;  
583 Anderegg *et al.*, 2013a; Schäfer *et al.*, 2013). The present study suggests that extreme  
584 drought and moderate but persistent drier conditions (simulated by our manipulation)  
585 may lead to the depletion of water reservoirs from groundwater and weathered bedrock  
586 in this system. Mortality and high defoliation levels may reduce canopy transpiration  
587 and interception, which could ultimately trigger an increase in groundwater recharge.  
588 Future studies should examine the ability of the impacts of future climate on vegetation  
589 to offset the effects of a decline in precipitation and an increase in surface evaporation  
590 on groundwater recharge.

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634 **References**

- 635 Allison GB (1982) The relationship between  $^{18}\text{O}$  and deuterium in water in sand  
636 columns undergoing evaporation. *Journal of Hydrology*, **55**, 163–169.
- 637 Anderegg WRL, Berry JA, Field CB (2012) Linking definitions, mechanisms, and  
638 modeling of drought-induced tree death. *Trends in Plant Science*, **17**, 693–700.
- 639 Anderegg WRL, Kane JM, Anderegg LDL (2013a) Consequences of widespread tree  
640 mortality triggered by drought and temperature stress. *Nature Climate Change*, **3**,  
641 30–36.
- 642 Anderegg LDL, Anderegg WRL, Abatzoglou J, Hausladen AM, Berry JA (2013b)  
643 Drought characteristics' role in widespread aspen forest mortality across Colorado,  
644 USA. *Global Change Biology*, **19**, 1526–37.
- 645 Araya YN, Silvertown J, Gowing DJ, McConway KJ, Linder HP, Midgley G (2011) A  
646 fundamental , eco-hydrological basis for niche segregation in plant communities.  
647 *New Phytologist*, **189**, 253–258.
- 648 Barbeta A, Ogaya R, Peñuelas J (2012) Comparative study of diurnal and nocturnal sap  
649 flow of *Quercus ilex* and *Phillyrea latifolia* in a Mediterranean holm oak forest in  
650 Prades (Catalonia , NE Spain). *Trees*, **26**, 1651–1659.
- 651 Barbeta A, Ogaya R, Peñuelas J (2013) Dampening effects of long-term experimental  
652 drought on growth and mortality rates of a Holm oak forest. *Global Change*  
653 *Biology*, **19**, 3133–44.
- 654 Breshears DD, Myers OB, Meyer CW *et al.* (2009) Tree die-off in response to global  
655 change-type drought: mortality insights from a decade of plant water potential  
656 measurements. *Frontiers in Ecology and the Environment*, **7**, 185–189.
- 657 Brolsma RJ, van Vliet MTH, Bierkens MFP (2010) Climate change impact on a  
658 groundwater-influenced hillslope ecosystem. *Water Resources Research*, **46**, 1–15.
- 659 Brooks JR, Barnard HR, Coulombe R, McDonnell JJ (2009) Ecohydrologic separation  
660 of water between trees and streams in a Mediterranean climate. *Nature Geoscience*,  
661 **3**, 100–104.
- 662 Canadell J, Zedler PH (1995) Underground structures of woody plants in Mediterranean  
663 ecosystems of Australia, California and Chile. In: *Ecology and Biogeography of*  
664 *Mediterranean Ecosystems in Chile, California and Australia* (eds Kalin Arroyo  
665 MT, Zedler PH, Fox MD), pp. 177–210. Springer New York.
- 666 Canadell J, Jackson RB, Ehleringer JB, Mooney H a., Sala OE, Schulze E-D (1996)  
667 Maximum rooting depth of vegetation types at the global scale. *Oecologia*, **108**,  
668 583–595.

- 669 Canadell J, Djema A, López B, Lloret F, Sabate S, Siscart D, Gracia CA (1999)  
670 Structure and dynamics of the root system. In: *Ecology of Mediterranean*  
671 *Evergreen Oak Forests* (eds Rodà F, Retana J, Gracia CA, Bellot J), pp. 47–59.  
672 Springer Berlin / Heidelberg.
- 673 Carnicer J, Barbeta A, Sperlich D, Coll M, Peñuelas J (2013a) Contrasting trait  
674 syndromes in angiosperms and conifers are associated with different responses of  
675 tree growth to temperature on a large scale. *Frontiers in plant science*, **4**, 409.
- 676 Carnicer J, Brotons L, Herrando S, Sol D (2013b) Improved empirical tests of area-  
677 heterogeneity tradeoffs. *Proceedings of the National Academy of Sciences of the*  
678 *United States of America*, **110**, E2858–60.
- 679 Christensen JH, Hewitson B, Busuioc A *et al.* (2007) Regional Climate Projections. In:  
680 *Climate Change 2007: The Physical Science Basis. Contribution of Working*  
681 *Group I to the Fourth Assessment Report of the Intergovernmental Panel on*  
682 *Climate Change* (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt  
683 KB, Tignor M, Miller HL). Cambridge University Press, Cambridge, UK. New  
684 York, USA.
- 685 David TS, Henriques MO, Kurz-Besson C *et al.* (2007a) Water-use strategies in two co-  
686 occurring Mediterranean evergreen oaks: surviving the summer drought. *Tree*  
687 *Physiology*, **27**, 793–803.
- 688 David TS, Henriques MO, Kurz-Besson C *et al.* (2007b) Water-use strategies in two co-  
689 occurring Mediterranean evergreen oaks: surviving the summer drought. *Tree*  
690 *Physiology*, **27**, 793–803.
- 691 David TS, Pinto CA, Nadezhdina N *et al.* (2013) Root functioning, tree water use and  
692 hydraulic redistribution in *Quercus suber* trees: A modeling approach based on root  
693 sap flow. *Forest Ecology and Management*, **307**, 136–146.
- 694 Dawson TE, Pate JS (1996) Seasonal water uptake and movement in root systems of  
695 Australian phraeatophytic plants of dimorphic root morphology: a stable isotope  
696 investigation. *Oecologia*, **107**, 13–20.
- 697 Dawson TE, Mambelli S, Plamboeck AH, Templer PH, Tu KP (2002) Stable Isotopes in  
698 Plant Ecology. *Annual Review of Ecology and Systematics*, **33**, 507–559.
- 699 Eckhardt K, Ulbrich U (2003) Potential impacts of climate change on groundwater  
700 recharge and streamflow in a central European low mountain range. *Journal of*  
701 *Hydrology*, **284**, 244–252.
- 702 Eggemeyer KD, Awada T, Harvey FE, Wedin DA, Zhou X, Zanner CW (2009)  
703 Seasonal changes in depth of water uptake for encroaching trees *Juniperus*  
704 *virginiana* and *Pinus ponderosa* and two dominant C4 grasses in a semiarid  
705 grassland. *Tree Physiology*, **29**, 157–69.
- 706 Ehleringer JR, Dawson TE (1992) Water uptake by plants: perspectives from stable  
707 isotope composition. *Plant Cell and Environment*, **15**, 1073–1082.



- 708 Fan Y, Li H, Miguez-Macho G (2013) Global patterns of groundwater table depth.  
709 *Science*, **339**, 940–3.
- 710 Filella I, Peñuelas J (2003) Partitioning of water and nitrogen in co-occurring  
711 Mediterranean woody shrub species of different evolutionary history. *Oecologia*,  
712 **137**, 51–61.
- 713 Galiano L, Martínez-Vilalta J, Sabaté S, Lloret F (2012) Determinants of drought  
714 effects on crown condition and their relationship with depletion of carbon reserves  
715 in a Mediterranean holm oak forest. *Tree Physiology*, **32**, 478–489.
- 716 Goldsmith GR, Muñoz-Villers LE, Holwerda F, McDonnell JJ, Asbjornsen H, Dawson  
717 TE (2012) Stable isotopes reveal linkages among ecohydrological processes in a  
718 seasonally dry tropical montane cloud forest. *Ecohydrology*, **5**, 779–790.
- 719 Gray AN, Spies TA (1995) Water content measurement in forest soils and decayed  
720 wood using time domain reflectometry. *Canadian Journal of Forest Research*, **25**,  
721 376–385.
- 722 Hadfield JD (2010) MCMC Methods for Multi-Response Generalized Linear Mixed  
723 Models: The MCMCglmm R Package. *Journal of Statistical Software*, **33**.
- 724 Kukowski KR, Schwinning S, Schwartz BF (2013) Hydraulic responses to extreme  
725 drought conditions in three co-dominant tree species in shallow soil over bedrock.  
726 *Oecologia*, **171**, 819–30.
- 727 Kurz-Besson C, Lobo-do-vale R, Rodrigues ML *et al.* (2014) Cork oak physiological  
728 responses to manipulated water availability in a Mediterranean woodland.  
729 *Agricultural and Forest Meteorology*, **184**, 230–242.
- 730 Leuzinger S, Luo Y, Beier C, Dieleman W, Vicca S, Körner C (2011) Do global change  
731 experiments overestimate impacts on terrestrial ecosystems? *Trends in Ecology &*  
732 *Evolution*, **26**, 236–41.
- 733 Limousin JM, Rambal S, Ourcival JM, Rocheteau A, Joffre R, Rodríguez-Cortina R  
734 (2009) Long-term transpiration change with rainfall decline in a Mediterranean  
735 *Quercus ilex* forest. *Global Change Biology*, **15**, 2163–2175.
- 736 Limousin J, Longepierre D, Huc R, Rambal S (2010) Change in hydraulic traits of  
737 Mediterranean *Quercus ilex* subjected to long-term throughfall exclusion, **30**,  
738 1026–1036.
- 739 Lin GH, Sternberg L da SL (1993) Hydrogen isotopic fractionation by plant roots  
740 during water uptake in coastal wetland plants. In: Stable isotopes and plant carbon-  
741 water relations. (eds Ehleringer JR, Hall AE, Farquhar GD). Department of  
742 Biology, University of Miami, Coral Gables, FL, 33124, USA.
- 743 Lloret F, Siscart D, Dalmases C (2004) Canopy recovery after drought dieback in holm-  
744 oak Mediterranean forests of Catalonia (NE Spain). *Global Change Biology*, **10**,  
745 2092–2099.

- 746 Lloret F, Escudero A, Iriondo JM, Martínez-Vilalta J, Valladares F (2012) Extreme  
747 climatic events and vegetation: the role of stabilizing processes. *Global Change*  
748 *Biology*, **18**, 797–805.
- 749 López B, Sabaté S, Gracia CA (2001) Annual and seasonal changes in fine root biomass  
750 of a *Quercus ilex* L. forest. *Plant and Soil*, 125–134.
- 751 Martínez-Vilalta J, Prat E, Oliveras I, Piñol J (2002) Xylem hydraulic properties of  
752 roots and stems of nine Mediterranean woody species. *Oecologia*, **133**, 19–29.
- 753 Martínez-Vilalta J, Mangirón M, Ogaya R, Sauret M, Serrano L, Peñuelas J, Piñol J  
754 (2003) Sap flow of three co-occurring Mediterranean woody species under varying  
755 atmospheric and soil water conditions. *Tree Physiology*, **23**, 747–58.
- 756 Martin-Stpaul NK, Limousin JM, Vogt-Schilb H, Rodríguez-Calcerrada J, Rambal S,  
757 Longepierre D, Misson L (2013) The temporal response to drought in a  
758 Mediterranean evergreen tree: comparing a regional precipitation gradient and a  
759 throughfall exclusion experiment. *Global Change Biology*, **19**, 2413–26.
- 760 Matesanz S, Valladares F (2013) Ecological and evolutionary responses of  
761 Mediterranean plants to global change. *Environmental and Experimental Botany*,  
762 **103**, 53-67.
- 763 Mcdowell N, Pockman WT, Allen CD *et al.* (2008) Mechanisms of plant survival and  
764 mortality during drought: why do some plants survive while others succumb to.
- 765 Moritz C, Agudo R (2013) The Future of Species Under Climate Change: Resilience or  
766 Decline? *Science*, **341**, 504–508.
- 767 Mueller RC, Scudder CM, Porter ME, Talbot Trotter R, Gehring C a., Whitham TG  
768 (2005) Differential tree mortality in response to severe drought: evidence for long-  
769 term vegetation shifts. *Journal of Ecology*, **93**, 1085–1093.
- 770 Nadezhdina N, Ferreira MI, Silva R, Pacheco CA (2007) Seasonal variation of water  
771 uptake of a *Quercus suber* tree in Central Portugal. *Plant and Soil*, **305**, 105–119.
- 772 Neal C, Neal M, Warrington A, Ávila A, Piñol J, Rodà F (1992) Stable hydrogen and  
773 oxygen isotope studies of rainfall and streamwaters for two contrasting holm oak  
774 areas of Catalonia , northeastern Spain. *Journal of Hydrology*, **140**, 163–178.
- 775 Oerter E, Finstad K, Schaefer J, Goldsmith GR, Dawson T, Amundson R (2014)  
776 Oxygen isotope fractionation effects in soil water via interaction with cations (Mg,  
777 Ca, K, Na) adsorbed to phyllosilicate clay minerals. *Journal of Hydrology*, **515**, 1–  
778 9.
- 779 Ogaya R, Barbeta A, Basnou C, Peñuelas (2014) Satellite data as indicators of tree  
780 biomass growth and forest dieback in a Mediterranean holm oak forest. *Annals of*  
781 *Forest Science*, 1-10.

- 782 Ogaya R, Peñuelas J (2003) Comparative field study of *Quercus ilex* and *Phillyrea*  
783 *latifolia*: photosynthetic response to experimental drought conditions.  
784 *Environmental and Experimental Botany*, **50**, 137–148.
- 785 Ogaya R, Peñuelas J (2006) Contrasting foliar responses to drought in *Quercus ilex* and  
786 *Phillyrea latifolia*. *Biologia Plantarum*, **50**, 373–382.
- 787 Oshun J, Dietrich WE, Dawson TE, Fung I (2014) Dynamic, structured heterogeneity of  
788 water isotopes inside hillslopes. *Nature GeoSciences*. Submitted.
- 789 Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable  
790 isotopes: coping with too much variation. *PloS one*, **5**, e9672.
- 791 Peñuelas J, Filella I, Llusia J, Siscart D, Piñol J (1998) Comparative field study of  
792 spring and summer leaf gas exchange and photobiology of the mediterranean trees  
793 *Quercus ilex* and *Phillyrea latifolia*. *Journal of experimental botany*, **49**, 229–238.
- 794 Peñuelas J, Filella I, Lloret F, Piñol J, Siscart D (2000) Effects of a severe drought on  
795 water and nitrogen use by *Quercus ilex* and *Phillyrea latifolia*. *Biologia Plantarum*,  
796 **43**, 47–53.
- 797 Peñuelas J, Terradas J, Lloret F (2011) Solving the conundrum of plant species  
798 coexistence: water in space and time matters most. *New Phytologist*, **189**, 5–8.
- 799 Peñuelas J, Sardans J, Estiarte M *et al.* (2013) Evidence of current impact of climate  
800 change on life: a walk from genes to the biosphere. *Global change biology*, **19**,  
801 2303–38.
- 802 Poyatos R, Aguadé D, Galiano L, Mencuccini M, Martínez-Vilalta J (2013) Drought-  
803 induced defoliation and long periods of near-zero gas exchange play a key role in  
804 accentuating metabolic decline of Scots pine. *New Phytologist*, **200**, 388–401.
- 805 R Core Development Team (2012) R: A language and environment for statistical  
806 computing. R Foundation for Statistical Computing. Vienna, Austria. ISBN 3-  
807 900051-07-0, URL: [www.r-project.org](http://www.r-project.org).
- 808 Rosas T, Galiano L, Ogaya R, Peñuelas J, Martínez-Vilalta J (2013) Dynamics of non-  
809 structural carbohydrates in three Mediterranean woody species following long-term  
810 experimental drought. *Frontiers in Plant Science*, **4**, 1–16.
- 811 Schäfer KVR, Renninger HJ, Clark KL, Medvigy D (2013) Hydrological responses to  
812 defoliation and drought of an upland oak / pine forest. *Hydrological Processes*.  
813 DOI: 10.1002/hyp.10104.
- 814 Schwinning S (2010) The ecohydrology of roots in rocks. *Ecohydrology*, **245**, 238–245.
- 815 Schwinning S, Starr BI, Ehleringer JR (2005) Summer and winter drought in a cold  
816 desert ecosystem (Colorado Plateau) part I: effects on soil water and plant water  
817 uptake. *Journal of Arid Environments*, **60**, 547–566.

- 818 Suarez ML, Ghermandi L, Kitzberger T (2004) Factors predisposing episodic drought-  
819 induced tree mortality in Nothofagus – site , climatic sensitivity and. *Journal of*  
820 *Ecology*, **92**, 954–966.
- 821 Tardieu F, Simonneau T (1998) Variability among species of stomatal control under  
822 fluctuating soil water status and evaporative demand: modelling isohydric and  
823 anisohydric behaviours *Franc. Journal of experimental botany*, **49**, 419–432.
- 824 Terradas J (1999) Holm Oak and Holm Oak Forests: An Introduction. In: *Ecology of*  
825 *Mediterranean Evergreen Oak Forests* (eds Rodà F, Retana J, Gracia C, Bellot J),  
826 pp. 3–14. Springer Berlin / Heidelberg, Berlin.
- 827 Vicente-Serrano SM, Gouveia C, Camarero JJ *et al.* (2013) Response of vegetation to  
828 drought time-scales across global land biomes. *Proceedings of the National*  
829 *Academy of Sciences of the United States of America*, **110**, 52–7.
- 830 West AG, Patrickson SJ, Ehleringer JR (2006) Water extraction times for plant and soil  
831 materials used in stable isotope analysis. *Rapid Communications in Mass*  
832 *Spectrometry*, **20**, 1317–1321.
- 833 West AG, Goldsmith GR, Brooks PD, Dawson TE (2010) Discrepancies between  
834 isotope ratio infrared spectroscopy and isotope ratio mass spectrometry for the  
835 stable isotope analysis of plant and soil waters. *Rapid Communications in Mass*  
836 *Spectrometry*, **24**, 1948–1954.
- 837 West AG, Goldsmith GR, Matimati I, Dawson TE (2011) Spectral analysis software  
838 improves confidence in plant and soil water stable isotope analyses performed by  
839 isotope ratio infrared spectroscopy (IRIS). *Rapid Communications in Mass*  
840 *Spectrometry*, **25**, 2268–74.
- 841 West AG, Dawson TE, February EC, Midgley GF, Bond WJ, Aston TL (2012) Diverse  
842 functional responses to drought in a Mediterranean-type shrubland in South Africa.  
843 *New Phytologist*, **195**, 396–407.
- 844 Witty JH, Graham RC, Hubbert KR, Doolittle JA, Wald JA (2003) Contributions of  
845 water supply from the weathered bedrock zone to forest soil quality. *Geoderma*,  
846 **114**, 389–400.
- 847 Wu Z, Dijkstra P, Koch GW, Peñuelas J, Hungate BA. (2011) Responses of terrestrial  
848 ecosystems to temperature and precipitation change: a meta-analysis of  
849 experimental manipulation. *Global Change Biology*, **17**, 927–942.
- 850 Zegelin SJ, White I, Jenkins DR (1989) Improved field probes for soil water content  
851 and electrical conductivity measurement using time domain reflectometry. *Water*  
852 *Resources Research*, **25**, 2367–2376.
- 853 Zeppel M (2013) Convergence of tree water use and hydraulic architecture in water-  
854 limited regions: a review and synthesis. *Ecohydrology*, **6**, 889–900.
- 855

856 **Figure legends**

857 **Fig. 1** Daily precipitation and mean temperatures during the study period (2010-2011).  
858 Soil moisture in the control and drought plots. The error bars are the standard errors of  
859 the means (n=2). Arrows indicate the sampling campaigns.

860 **Fig. 2** Seasonal variation in midday foliar water potentials of the three species for  
861 control (open circles) and droughted (closed circles) individuals. The droughted plants  
862 had significantly lower midday foliar water potentials ( $F=5.43$ ,  $p<0.05$ , ANOVA).  
863 Differences between seasons and species are described in the Results section.

864 **Fig. 3** Water isotopes for all samples of xylem (triangles), soil (circles) and spring  
865 (squares) water. All samples are plotted in the upper left panel, with the remaining  
866 panels corresponding to single seasons. The line in the panels is the local meteoric water  
867 line (LMWL), corresponding to  $\delta^2\text{H}=6.62+7.60*\delta^{18}\text{O}$  with  $R^2=96.03\%$ , obtained by a  
868 previous study in the same area (Neal *et al.*, 1992).

869 **Fig. 4** Mean contributions of plant-water sources for each season in the control and  
870 drought treatments obtained by six Bayesian mixing models. The error bars are the  
871 standard errors of the means. The asterisks denote significance levels for the  
872 comparisons between the control and drought treatments performed by ANOVAs and  
873 Tukey's HSD post-hoc tests (\*\* $p<0.001$ , \*\* $p<0.01$ , \* $p<0.05$ , (\*)  $p<0.1$ ).

874 **Fig. 5** Seasonal percentages of groundwater uptake in the three species for each season.  
875 The errors bars are the standard errors of the means.

876 **Fig. 6** Relationship between percentage of groundwater uptake and soil moisture in the  
877 two treatments. The Y-axis values are the mean seasonal proportions of groundwater  
878 uptake for each treatment, and the three species are pooled. The error bars are the  
879 standard errors of the means.

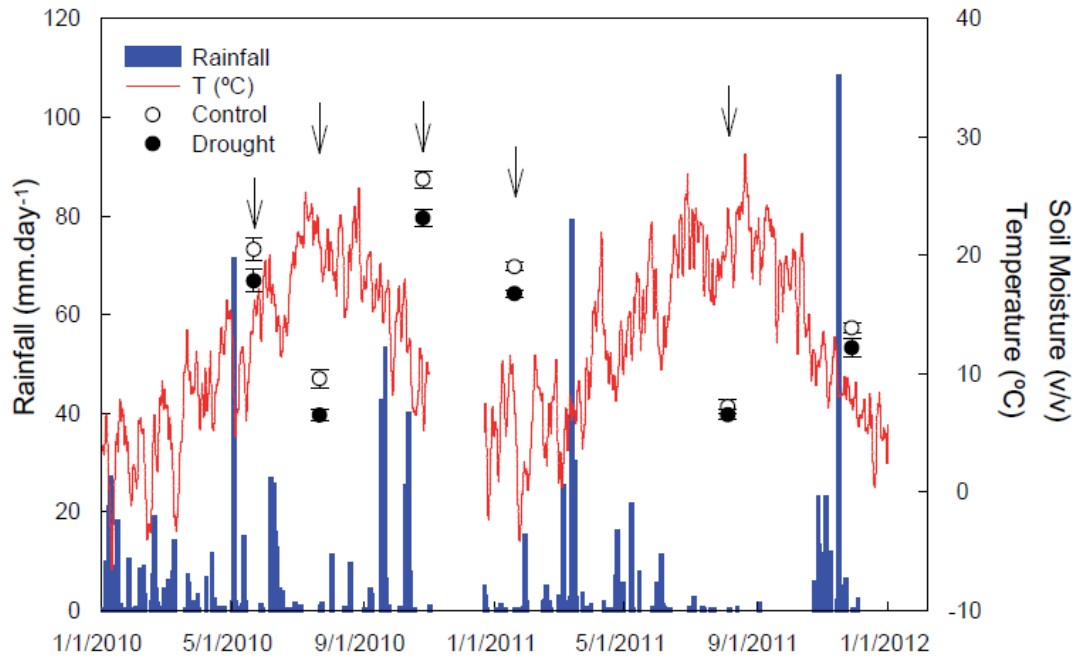
880 **Fig. 7** Stem mortality rates for *Quercus ilex* and *Phillyrea latifolia* (2010 and 2011)  
881 calculated for the plots where the isotope samples were collected. Different letters  
882 indicate significantly different stem mortality rates, which were assessed by ANOVAs  
883 ( $p<0.05$ ).

884 **Fig. 8** Crown defoliation (%) following the extreme drought in 2011 for each species  
885 and treatment for the plots where the isotope samples were collected. The error bars are  
886 the standard errors of the means (n=10). Different letters indicate significant differences  
887 between group percentages, assessed by ANOVAs with Tukey's HSD post-hoc tests.  
888 The differences between the treatments pooling all species together were assessed using  
889 generalized linear mixed models (MCMCglmm) with plot as a random factor.

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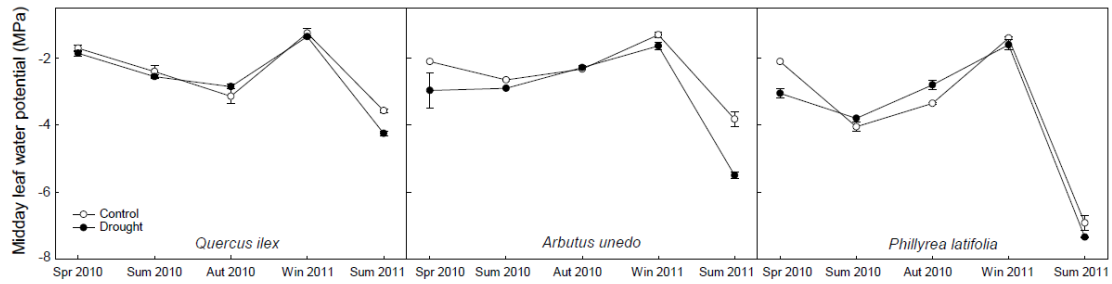
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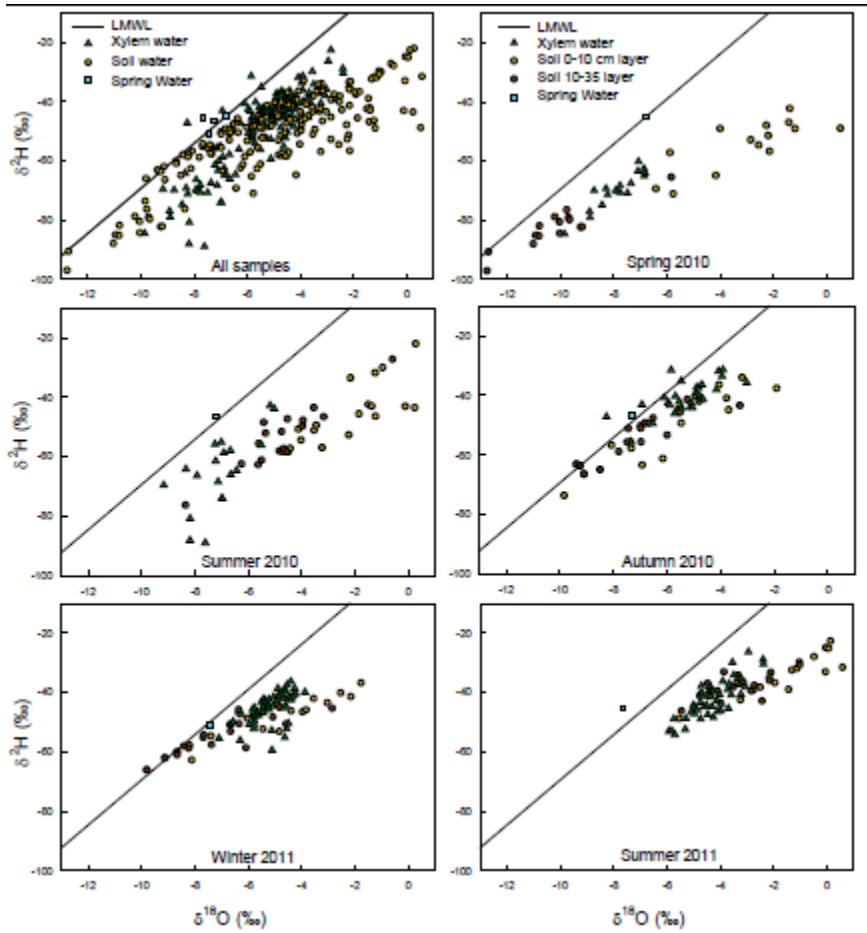
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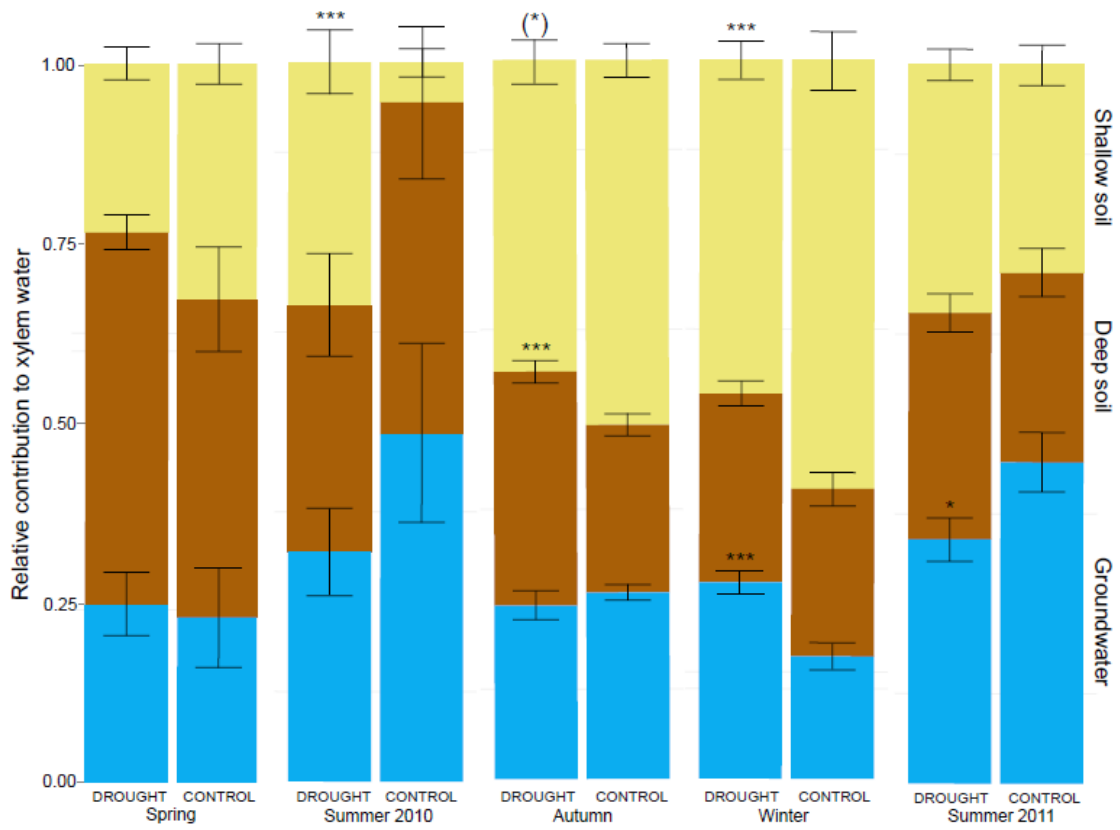
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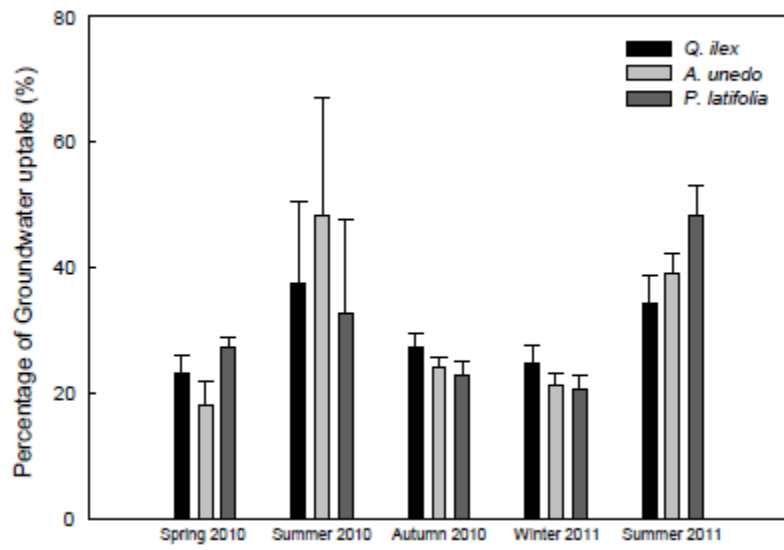
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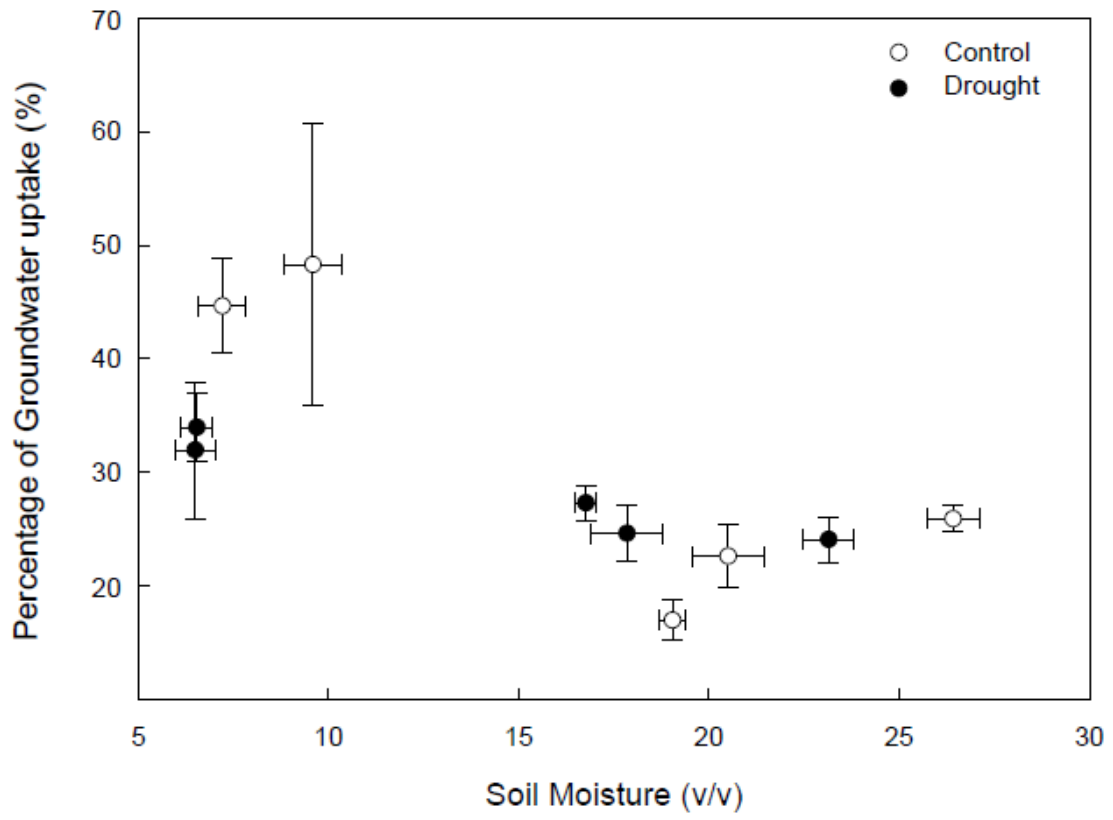
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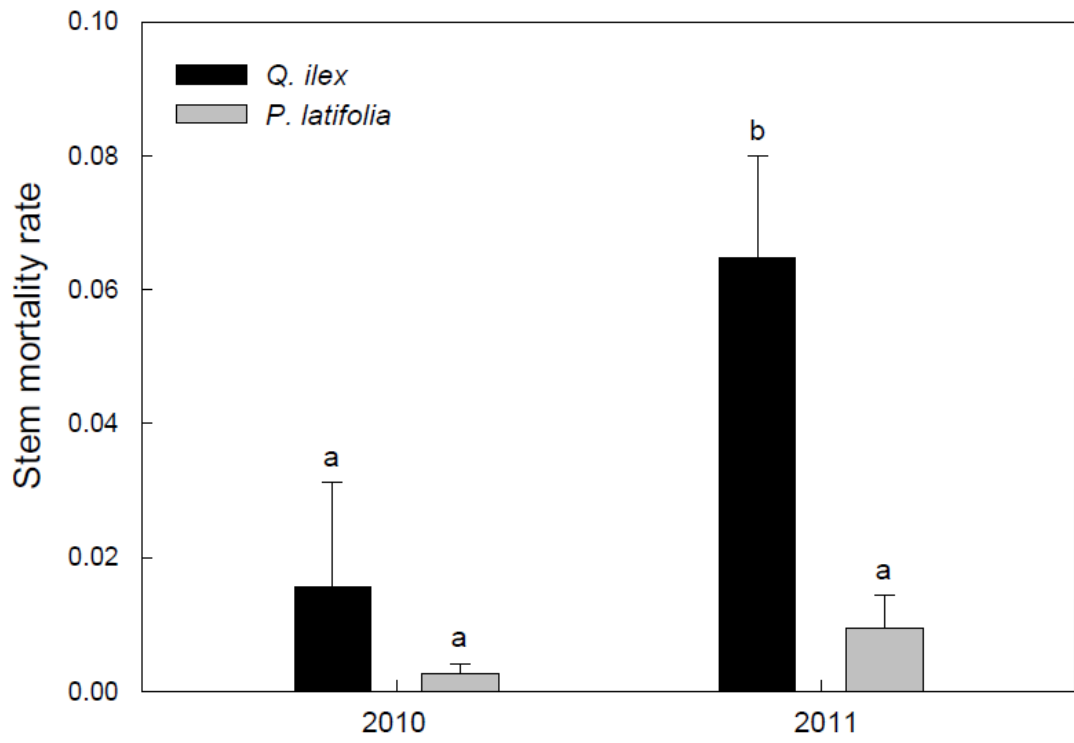
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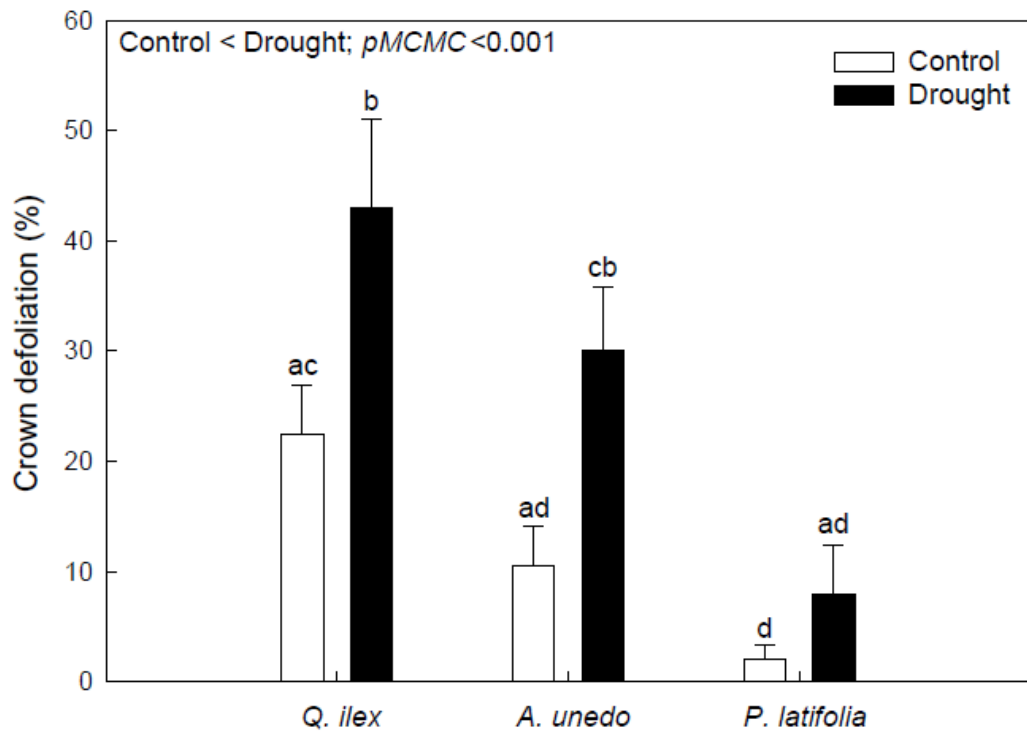
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1027 **Supplementary Materials**

1028 Table S1. Pairwise comparison between the relative seasonal contributions of water  
 1029 sources using Tukey's HSD post-hoc tests. The mean difference is between pairs of  
 1030 seasons, and the range is the 95% confidence interval. The asterisks denote significance  
 1031 levels (\*\*\*  $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$ , (\*)  $p < 0.1$ ).

<b>Shallow soil (0-10 cm)</b>	Mean difference	Range	$p$	
Winter 2011 - Summer 2011	0.21	0.08	<0.001	***
Summer 2010 - Summer 2011	-0.17	0.11	<0.001	***
Spring 2010 - Summer 2011	-0.05	0.12	0.767	
Autumn 2010 - Summer 2011	0.15	0.10	<0.001	***
Summer 2010 - Winter 2011	-0.37	0.11	<0.001	***
Spring 2010 - Winter 2011	-0.26	0.11	<0.001	***
Autumn 2010 - Winter 2011	-0.06	0.09	0.414	
Spring 2010 - Summer 2010	0.12	0.14	0.124	
Autumn 2010 - Summer 2010	0.32	0.12	<0.001	***
Autumn 2010 - Spring 2010	0.20	0.12	<0.001	***
<b>Deep soil (10-35 cm)</b>				
Winter 2011 - Summer 2011	-0.04	0.09	0.804	
Summer 2010 - Summer 2011	0.13	0.13	0.041	*
Spring 2010 - Summer 2011	0.20	0.13	<0.001	***
Autumn 2010 - Summer 2011	0.00	0.11	1.000	
Summer 2010 - Winter 2011	0.17	0.13	0.003	**
Spring 2010 - Winter 2011	0.24	0.13	<0.001	***
Autumn 2010 - Winter 2011	0.03	0.11	0.896	
Spring 2010 - Summer 2010	0.07	0.16	0.724	
Autumn 2010 - Summer 2010	-0.14	0.14	0.056	(*)
Autumn 2010 - Spring 2010	-0.21	0.14	<0.001	***
<b>Groundwater</b>				
Winter 2011 - Summer 2011	-0.17	0.09	<0.001	***
Summer 2010 - Summer 2011	0.03	0.13	0.947	
Spring 2010 - Summer 2011	-0.16	0.13	<0.05	*
Autumn 2010 - Summer 2011	-0.15	0.11	0.003	**
Summer 2010 - Winter 2011	0.20	0.13	<0.001	***
Spring 2010 - Winter 2011	0.01	0.13	0.998	
Autumn 2010 - Winter 2011	0.02	0.11	0.972	
Spring 2010 - Summer 2010	-0.19	0.16	0.009	**
Autumn 2010 - Summer 2010	-0.18	0.14	0.004	**
Autumn 2010 - Spring 2010	0.01	0.14	1.000	

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1035 Table S2. Evaluation of the effect of the drought treatment and the species factor plus  
 1036 their interaction on the relative seasonal contribution of water sources by ANOVAs. The  
 1037 asterisks denote significance levels (\*\*\*)  $p < 0.001$ , \*\*  $p < 0.01$ , \*  $p < 0.05$ , (\*)  $p < 0.1$ ).

<b>Shallow soil (0-10 cm)</b>	<b>Df</b>	<b>SS</b>	<b>Mean Sq</b>	<b>F</b>	<b>p</b>	
<b>Drought</b>	1	0.034	0.034	1.967	0.188	
<b>Species</b>	2	0.000	0.000	0.01	0.990	
<b>Drought x Species</b>	2	0.024	0.012	0.695	0.520	
Residuals	11	0.192	0.017			
<b>Drought</b>	1	0.319	0.319	81.876	<0.001	***
<b>Species</b>	2	0.003	0.001	0.32	0.732	
<b>Drought x Species</b>	2	0.061	0.030	7.795	0.007	
Residuals	12	0.047	0.004			
<b>Drought</b>	1	0.041	0.041	3.123	0.090	(*)
<b>Species</b>	2	0.028	0.014	1.064	0.361	
<b>Drought x Species</b>	2	0.002	0.001	0.076	0.927	
Residuals	24	0.312	0.013			
<b>Drought</b>	1	0.279	0.279	10.942	0.002	**
<b>Species</b>	2	0.126	0.063	2.461	0.097	
<b>Drought x Species</b>	2	0.079	0.040	1.551	0.223	
Residuals	45	1.147	0.026			
<b>Drought</b>	1	0.035	0.035	2.476	0.124	
<b>Species</b>	2	0.022	0.011	0.763	0.473	
<b>Drought x Species</b>	2	0.055	0.028	1.965	0.154	
Residuals	39	0.550	0.014			
<b>Deep soil (10-35 cm)</b>						
<b>Drought</b>	1	0.021	0.021	0.765	0.400	
<b>Species</b>	2	0.013	0.007	0.237	0.793	
<b>Drought x Species</b>	2	0.051	0.026	0.929	0.424	
Residuals	11	0.304	0.028			
<b>Drought</b>	1	0.057	0.057	0.308	0.589	
<b>Species</b>	2	0.024	0.012	0.064	0.939	
<b>Drought x Species</b>	2	0.105	0.052	0.283	0.758	
Residuals	12	2.219	0.185			
<b>Drought</b>	1	0.063	0.063	15.987	<0.001	***
<b>Species</b>	2	0.005	0.002	0.579	0.568	
<b>Drought x Species</b>	2	0.001	0.000	0.083	0.920	
Residuals	24	0.094	0.004			
<b>Drought</b>	1	0.016	0.016	1.597	0.213	
<b>Species</b>	2	0.037	0.019	1.883	0.164	
<b>Drought x Species</b>	2	0.041	0.021	2.085	0.136	
Residuals	45	0.447	0.010			
<b>Drought</b>	1	0.029	0.029	1.387	0.246	
<b>Species</b>	2	0.053	0.026	1.238	0.301	
<b>Drought x Species</b>	2	0.011	0.005	0.256	0.775	
Residuals	39	0.827	0.021			

**Groundwater**

<b>Drought</b>	1	0.002	0.002	0.33	0.577	
<b>Species</b>	2	0.014	0.007	1.507	0.264	
<b>Drought x Species</b>	2	0.021	0.010	2.166	0.161	
Residuals	11	0.053	0.005			
<b>Drought</b>	1	0.107	0.107	0.627	0.444	
<b>Species</b>	2	0.033	0.017	0.098	0.907	
<b>Drought x Species</b>	2	0.074	0.037	0.218	0.808	
Residuals	12	2.038	0.170			
<b>Drought</b>	1	0.002	0.002	0.5	0.486	
<b>Species</b>	2	0.010	0.005	1.025	0.374	
<b>Drought x Species</b>	2	0.002	0.001	0.206	0.815	
Residuals	24	0.117	0.005			
<b>Drought</b>	1	0.162	0.162	26.477	<0.001	***
<b>Species</b>	2	0.026	0.013	2.142	0.129	
<b>Drought x Species</b>	2	0.006	0.003	0.508	0.605	
Residuals	45	0.275	0.006			
<b>Drought</b>	1	0.128	0.128	4.485	0.041	*
<b>Species</b>	2	0.135	0.067	2.351	0.109	
<b>Drought x Species</b>	2	0.025	0.013	0.441	0.647	
Residuals	39	1.117	0.029			

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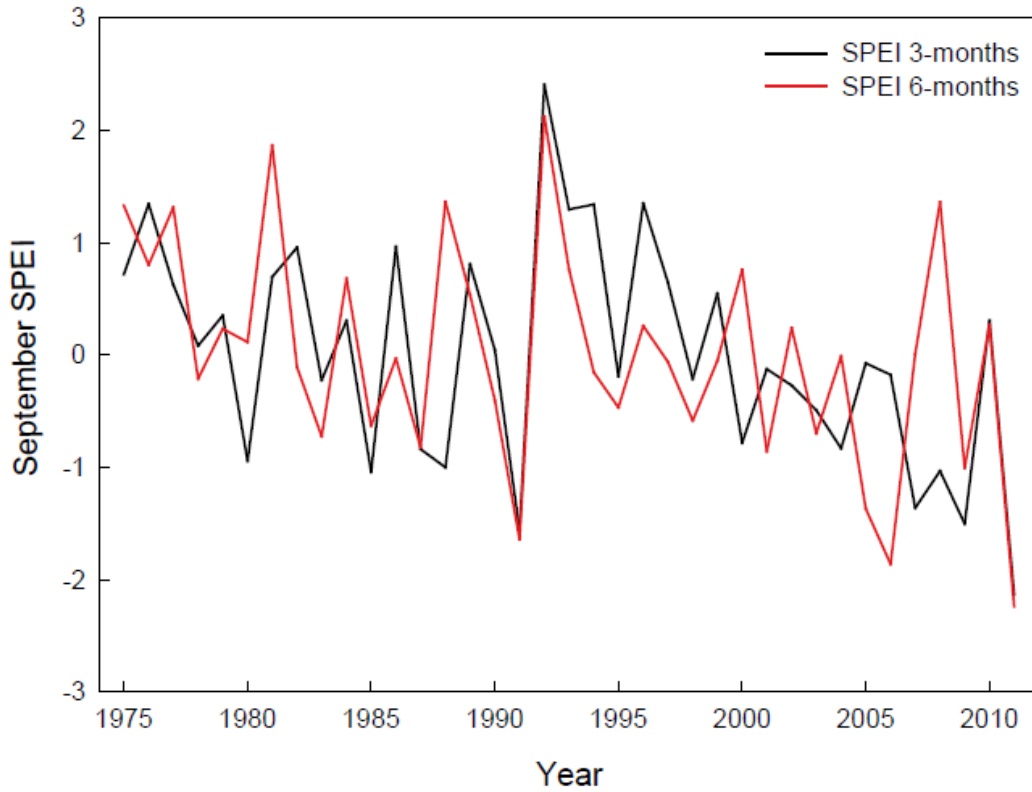
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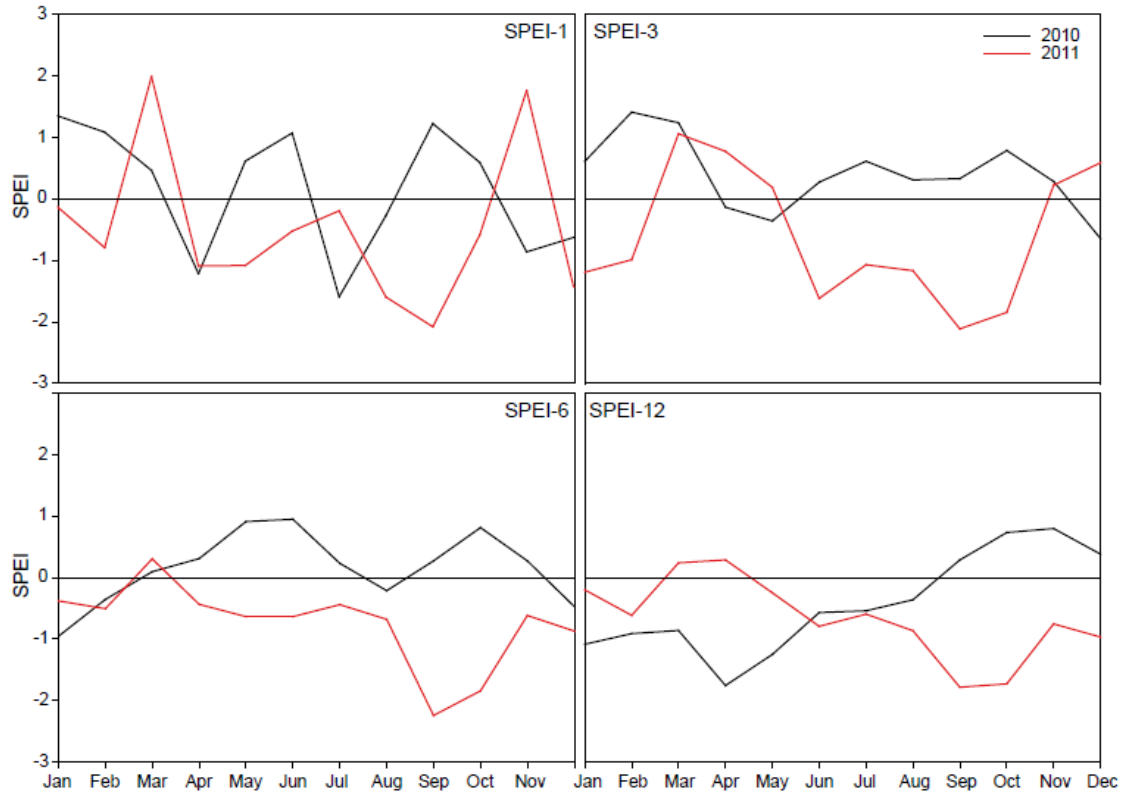


1053 **Fig. S1** Temporal series (1975-2011) of the Standardized Precipitation and  
1054 Evapotranspiration Index (SPEI) for September calculated for two timescales: 3 months  
1055 (black line), which integrates the water balances of July, August and September, and 6  
1056 months (red line), which integrates the water balances of April, May, June, July, August  
1057 and September. Note that both indices reached the period's minimum in 2011.



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1070 **Fig. S2** Monthly values of the Standardized Precipitation and Evapotranspiration Index  
 1071 (SPEI) during the study period (2010, black line; 2011, red line). Each panel  
 1072 corresponds to the timescale at which the index was calculated (1 month, 3 months, 6  
 1073 months and 12 months).



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