

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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26 **Keywords:** Holm oak, experimental drought, stable isotopes, water uptake,
27 Mediterranean forest, climate change, extreme drought, water-use strategies, *Arbutus*
28 *unedo*, *Quercus ilex*, *Phillyrea latifolia*.

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30 Type of paper: Primary Research Article.

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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 δ 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⁻¹) dominated by *Q. ilex* (3850 stems ha⁻¹ and 50 Mg ha⁻¹), *P. latifolia* (12 683 stems
190 ha⁻¹ and 29 Mg ha⁻¹) and *A. unedo* (667 stems ha⁻¹ and 9 Mg ha⁻¹), 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-m² 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_{sample} and R_{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±1.56 vs 14.75±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±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 (Ψ_{md}) than the plants in the control plots (-3.1±0.29 vs -2.8±0.28 MPa,
359 $F=5.43$, $n=6$, $p < 0.05$). Ψ_{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 Ψ_{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 Ψ_{md} was significantly lower in *P. latifolia* than in *Q. ilex* and *A. unedo* (-3.71±0.46, -
365 2.48±0.17 and -2.74±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 ± 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 ± 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 ± 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 ± 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 ± 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 Ψ_{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 Ψ_{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 Ψ_{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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608 **Acknowledgments**

609 This research was supported by the Spanish Government projects CGL2010-17172 and
610 Consolider Ingenio Montes (CSD2008-00040), by the Catalan Government project SGR
611 2009-458 and the European Research Council Synergy grant ERC-2013-SyG-610028
612 IMBALANCE-P. A.B. acknowledges an FPI predoctoral fellowship from the Spanish
613 Ministry of Economy and Competitiveness that supported his visit to UC Berkeley. The
614 authors would like to thank Pilar Sopeña (University of Lleida) and Paul Brooks,
615 Stefania Mambelli and Allison Kidder (UC Berkeley) for lab assistance and the three
616 anonymous reviewers who helped to improve the manuscript with insightful comments.
617 The authors declare no conflicts of interest. This study is dedicated to the memory of
618 our beloved friend and colleague Monica Mejía-Chang.

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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.

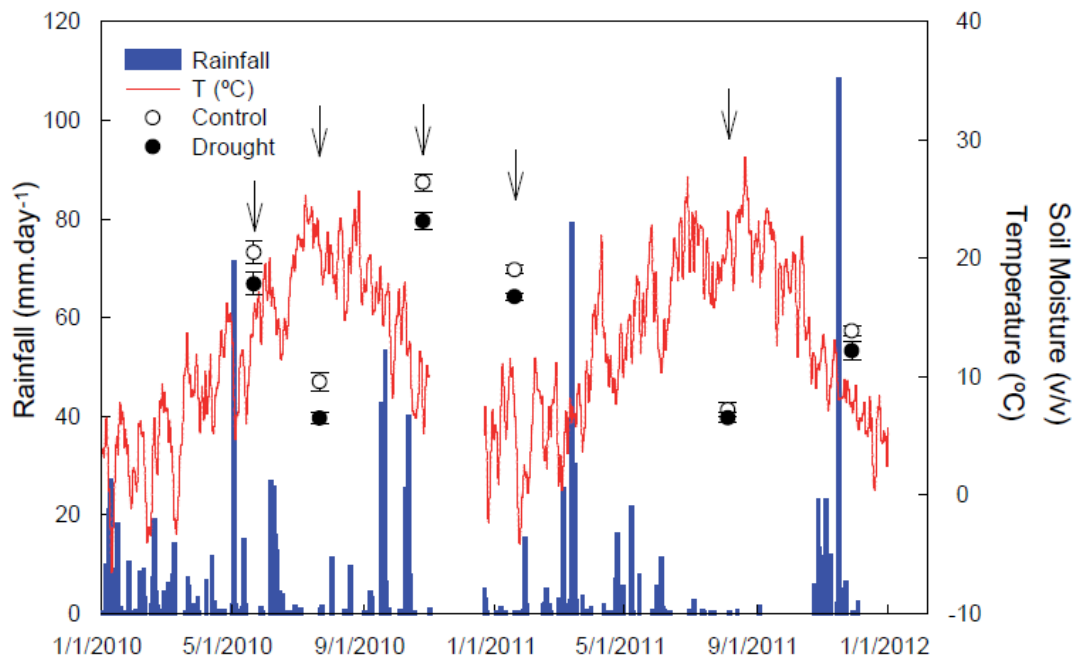
880 **Fig. 7** Stem mortality rates for *Quercus ilex* and *Phillyrea latifolia* (2010 and 2011)
881 calculated for the plots where the isotope samples were collected. Different letters
882 indicate significantly different stem mortality rates, which were assessed by ANOVAs
883 ($p<0.05$).

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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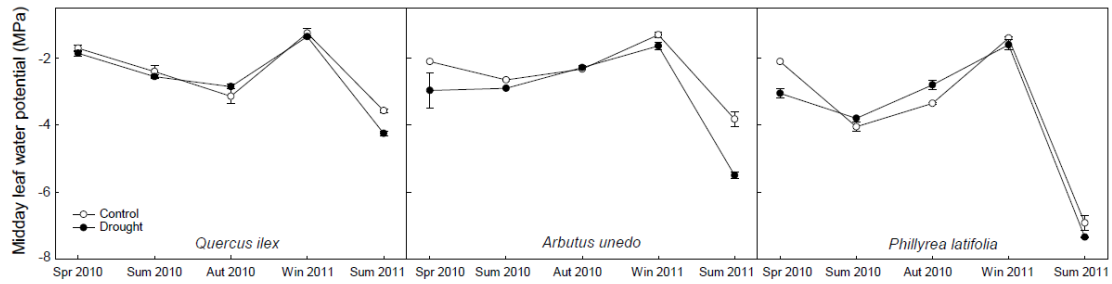
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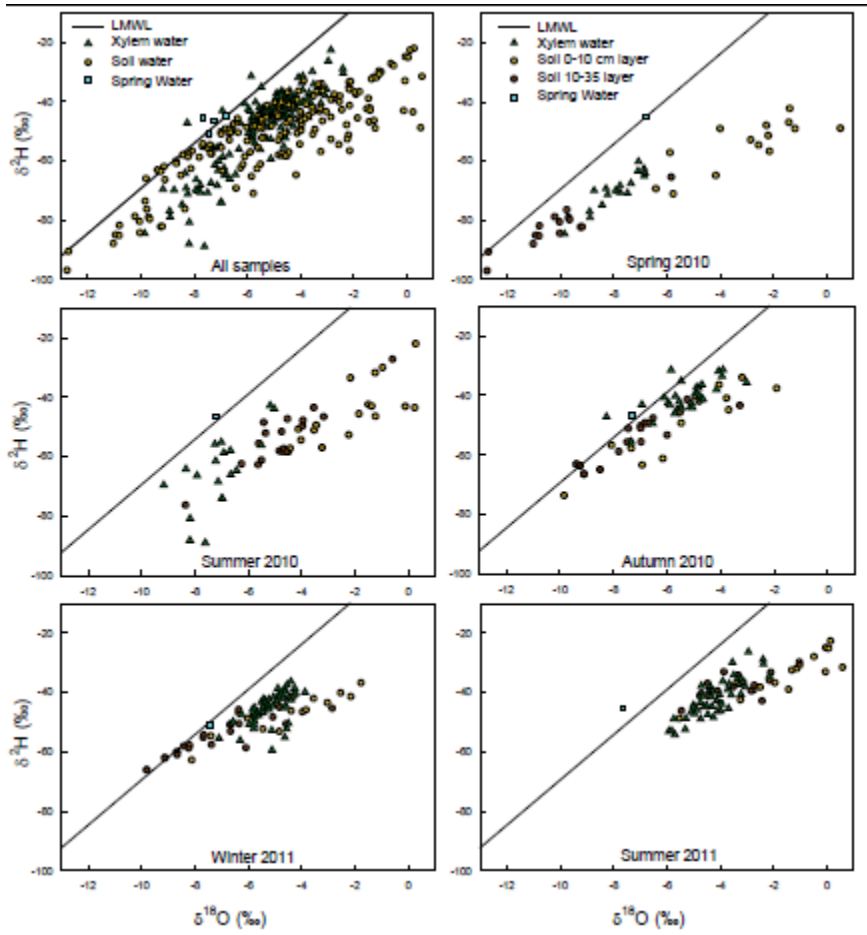
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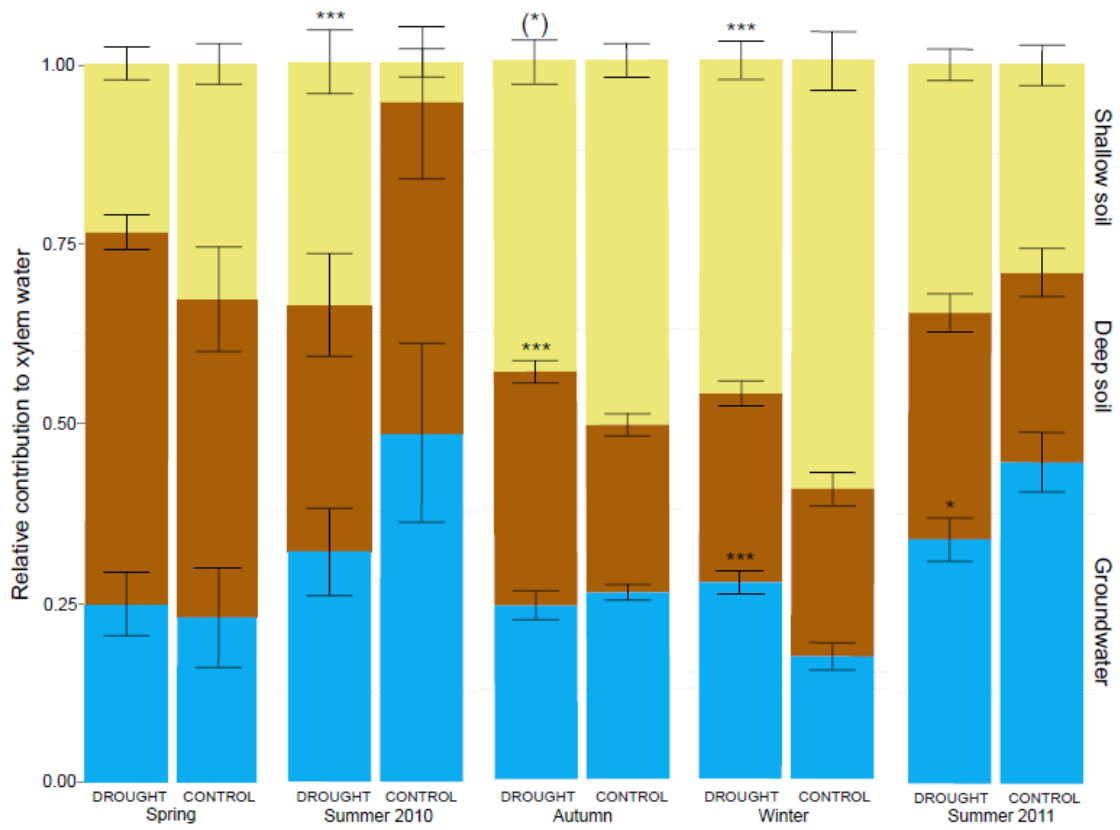
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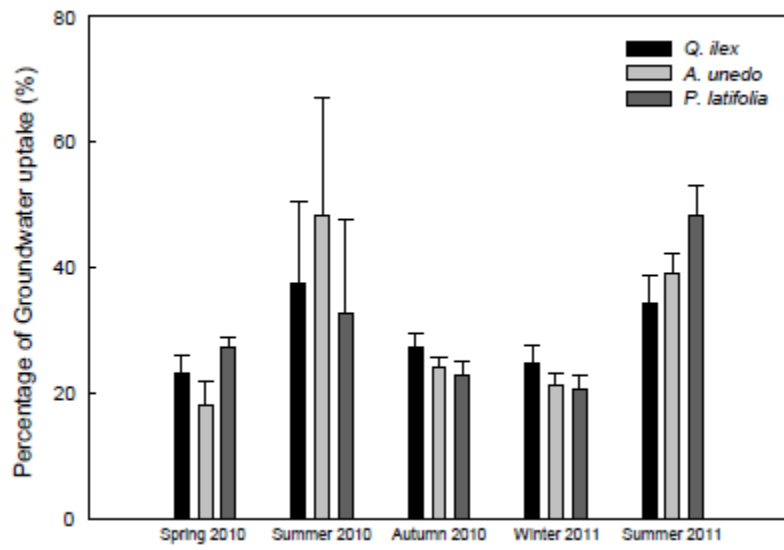
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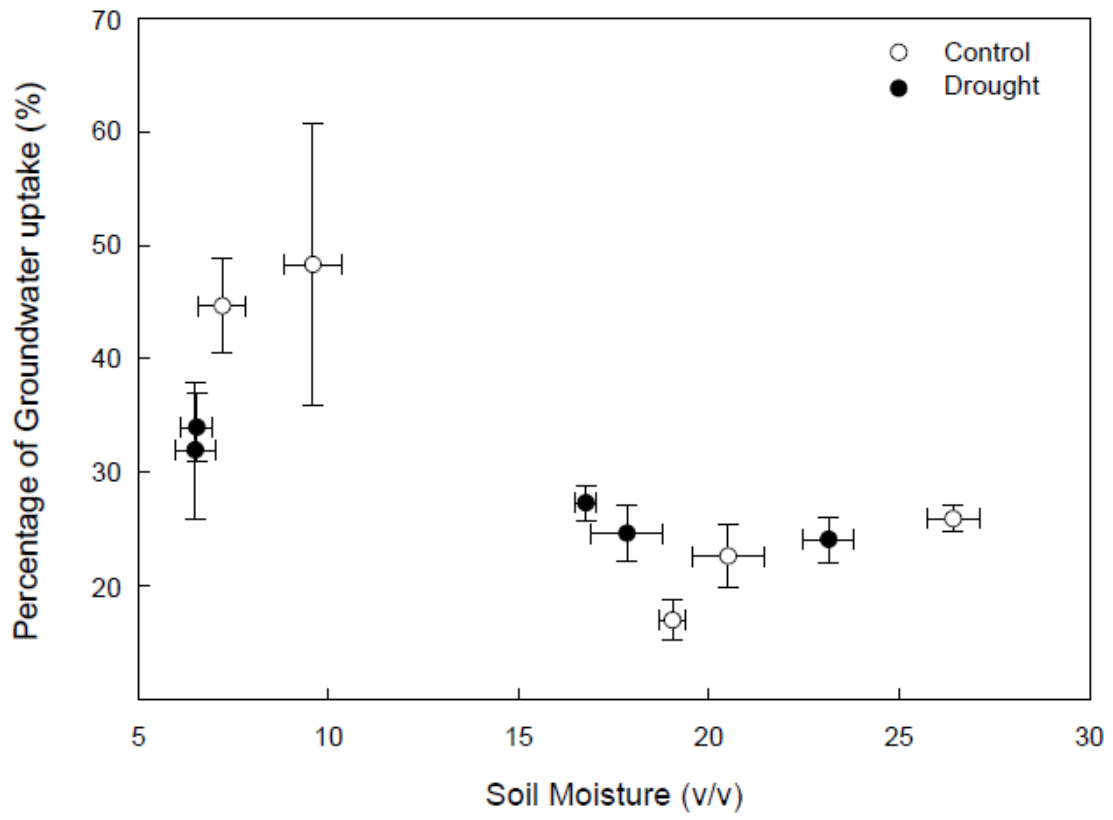
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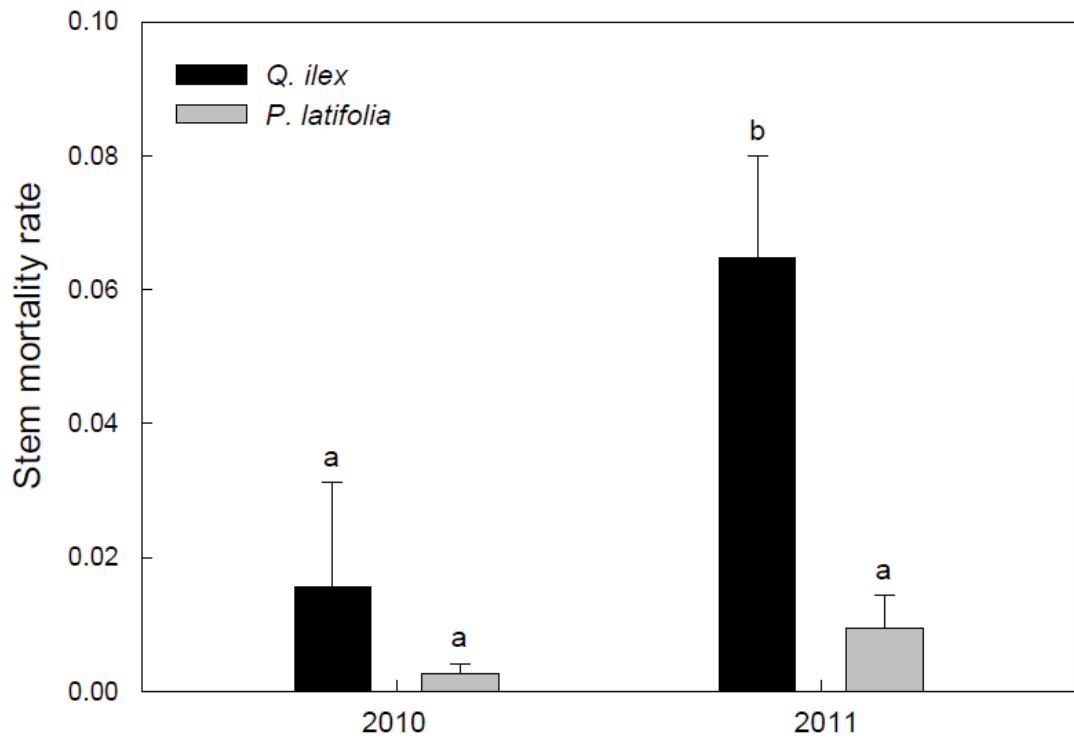
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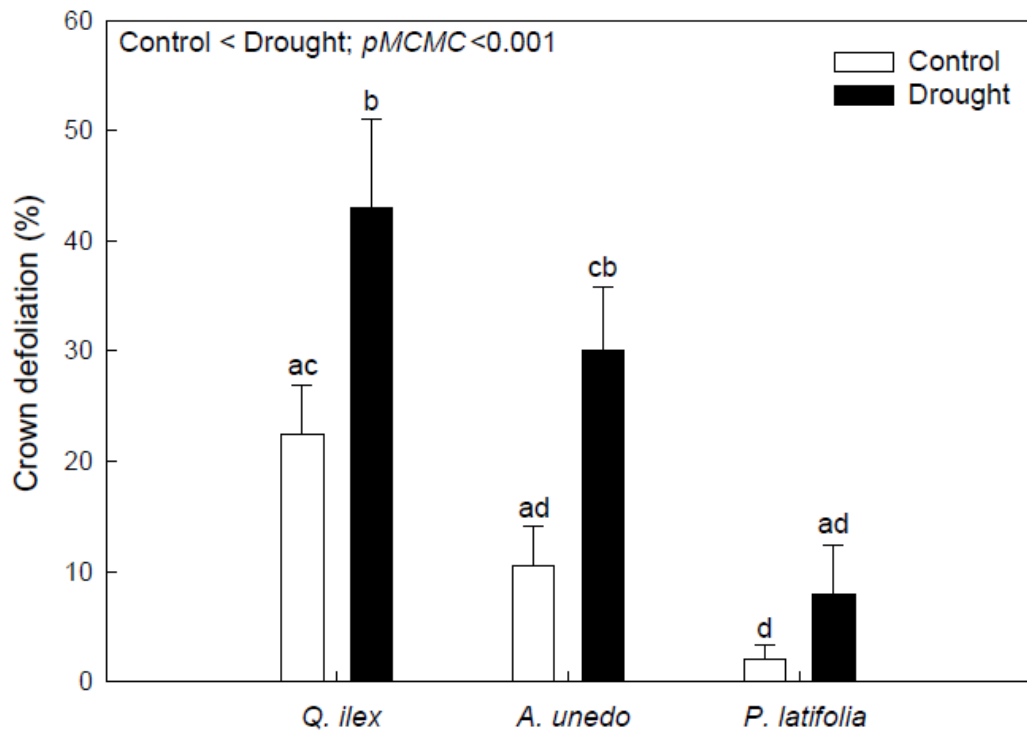
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1027 **Supplementary Materials**

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 (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, (*) $p < 0.1$).

Shallow soil (0-10 cm)	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	***
Deep soil (10-35 cm)				
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	***
Groundwater				
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 (***) $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, (*) $p < 0.1$).

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

Groundwater

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

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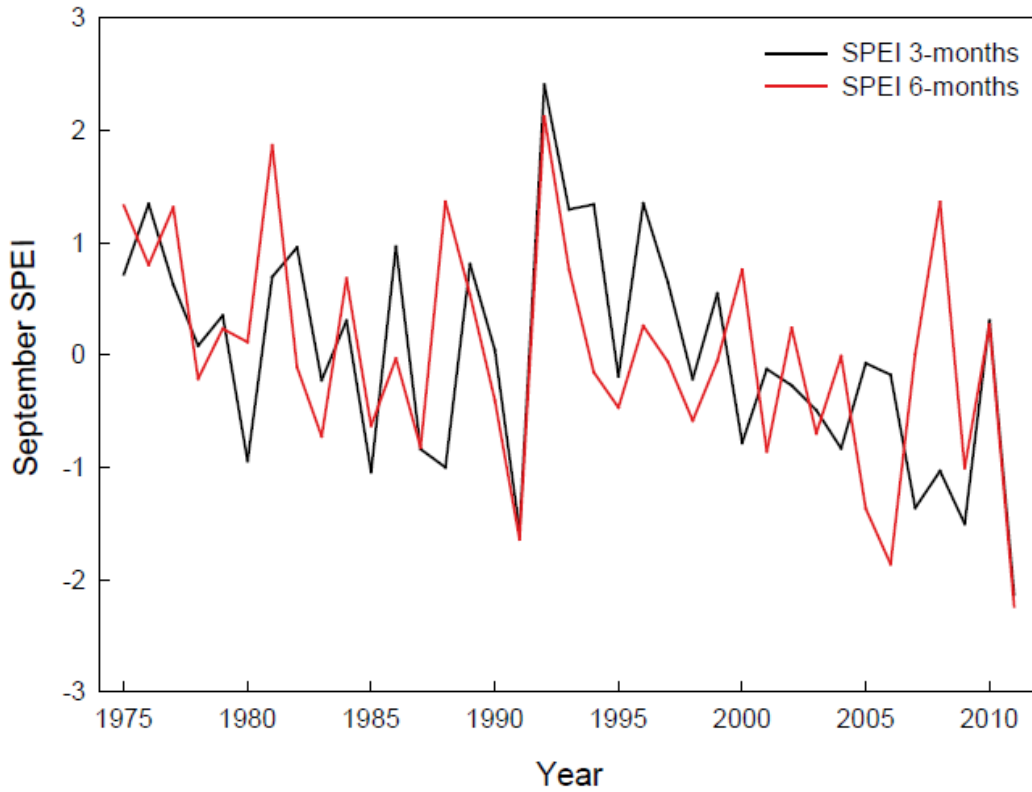
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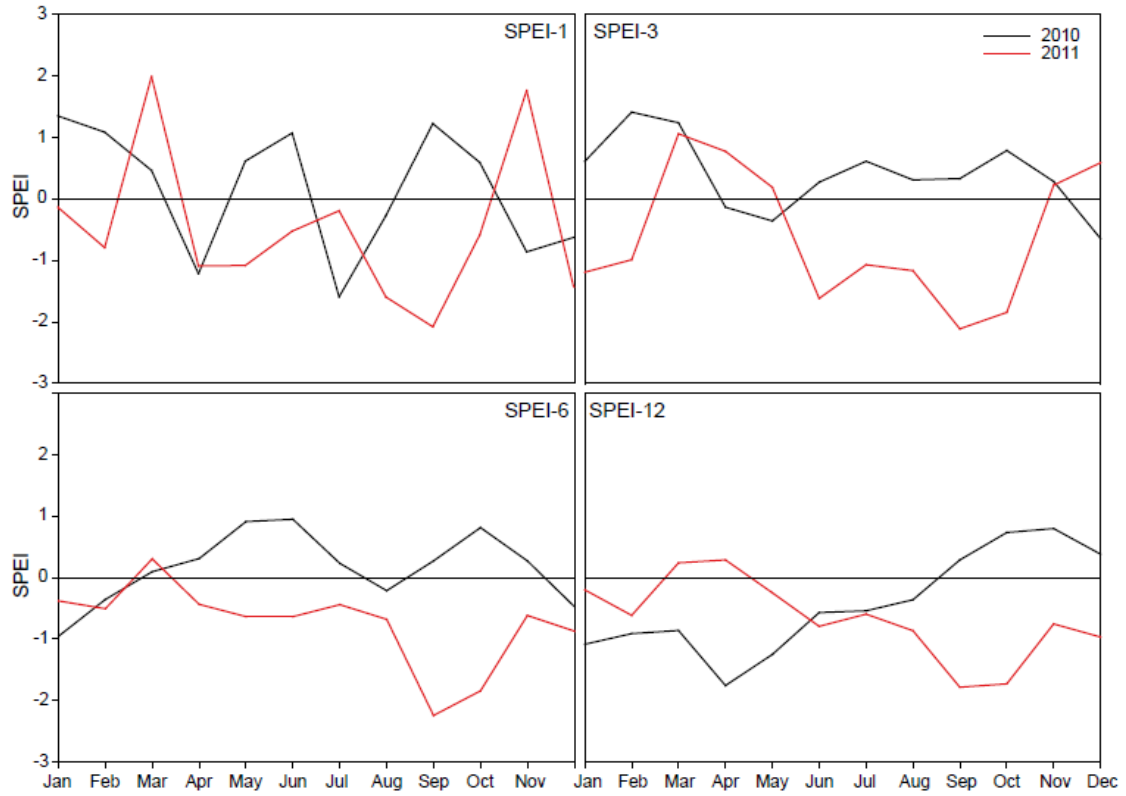
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1053 **Fig. S1** Temporal series (1975-2011) of the Standardized Precipitation and
1054 Evapotranspiration Index (SPEI) for September calculated for two timescales: 3 months
1055 (black line), which integrates the water balances of July, August and 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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