

1 **Differential impact of the most extreme drought event over the last half century on growth**  
2 **and sap flow in two coexisting Mediterranean trees**

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14

15 **Abstract**

16 Extreme climatic events such as intense droughts are becoming more frequent in Mediterranean regions,  
17 but our understanding of their impact on tree performance is still fragmentary. We analyzed growth and  
18 sap flow responses for a 3-year period including the most stressful drought over the last half century in  
19 the evergreen *Pinus nigra* and the deciduous *Quercus faginea*, two dominant tree species in the  
20 continental plateau of the Iberian Peninsula. Our aim was to quantify the differential impacts of this event  
21 on the performance of both species and their modulation by local microclimate. Growth was registered  
22 with digital dendrometers and water use was assessed by continuously recording sap flow in 8-9  
23 coexisting adult individuals of each species in two sites. *Q. faginea* spring growth rate decreased by 60%  
24 during the dry year at the dry site, while the decrease in *P. nigra* was around 36%. *P. nigra* exhibited  
25 larger sap flow reductions during the dry season and also larger decreases during the extreme year, but in  
26 contrast to *Q. faginea*, it was able to recover growth and sap flow values after the extreme drought. Minor  
27 microclimatic differences between sites had significant effects on growth and water use, with slightly  
28 more mesic conditions significantly attenuating the impact of drought on both species. Findings suggest  
29 that the study species were near to their tolerance thresholds so that even moderate increases in the  
30 intensity and frequency of unusual droughts have important consequences for individual tree  
31 performance, and eventually species coexistence and ecosystem processes.

32

33 **Key words:** extreme drought, *Pinus nigra*, *Quercus faginea*, climate change, Mediterranean forests

34

35 **Introduction**

36 Water scarcity is one of the most important limiting factors for tree species in Mediterranean ecosystems  
37 and is expected to become even more relevant due to the increased temperature and aridity projected for  
38 Mediterranean regions (IPCC 2007). Mediterranean tree species are well adapted to dry periods and have  
39 developed different strategies to cope with multiple limiting factors. This explains the complex  
40 coexistence observed in Mediterranean ecosystems and promotes high biodiversity levels (Blondel and  
41 Aronson 1995). Different traits, such as alternative root systems, water use efficiencies, growth rates,  
42 phenologies or stomatal regulation of water use are associated with different functional strategies to cope  
43 with drought (Kneitel and Chase 2004), allowing species coexistence at small spatial scales (Chesson and  
44 Huntly 1997). One important strategy for trees to keep relatively high water status during summer  
45 drought is developing a deep root system that allows the use of deep water resources that are not available  
46 for most plants (David et al. 2007).

47 Complementary water use strategies also play an important role for coexistence of species  
48 coping with drought. Isohydic and anisohydric performances are two strategies that represent extremes in  
49 the range of water use by plants (McDowell et al. 2013). Both strategies have been observed in  
50 Mediterranean tree species (Chirino et al. 2011; Quero et al. 2011). For example, *P. sylvestris* (considered  
51 an isohydric species) quickly closes stomata when a water potential threshold is exceeded to avoid  
52 hydraulic failure by cavitation, while *Q. pubescens* (considered an anisohydric species) keeps relatively  
53 high transpiration rates during extended dry periods with low hydraulic failure (Poyatos et al. 2008). In  
54 general, pine species are characteristic of harsh environments and maintain an isohydric performance  
55 under water stress conditions (Himmelsbach et al. 2012; Klein et al. 2013; Brito et al. 2014). This  
56 contrasts with the functional strategy of many oaks (*Quercus* spp.), which are more anisohydric species as  
57 observed, for example in temperate beech-oak forests (Aranda et al. 2005) and in typical Mediterranean  
58 stands (Chirino et al. 2011; Himmelsbach et al. 2012). Although it is difficult to forecast which strategy  
59 could be more successful under severe droughts, several studies have shown that isohydric species were  
60 more affected by extreme drought events (Allen and Breshears 1998; Leuzinger et al. 2005; Poyatos et al.  
61 2008; Linares et al. 2010; Morán-López et al. 2014). These differences can break tree species coexistence  
62 and cause shifts in species distribution, as observed with the replacement of *Fagus sylvatica* and *Calluna*  
63 *vulgaris* by *Quercus ilex* by Peñuelas and Boada (2003). In turn, extreme droughts may result in  
64 modifications of carbon sequestration rates and net carbon balance (Lindner et al. 2010) due to the

65 increment of defoliation events (Carnicer et al. 2011), and decreases of Mediterranean forest net  
66 production as simulated by Ciais et al. (2005) and Nadal-Sala et al. (2013) under climate change scenarios  
67 and extreme drought events, respectively.

68         It is unlikely, however, that any of these traits can fully offset the impact of the increased  
69 frequency of extremely dry periods forecast for Mediterranean ecosystems (Della-Marta et al. 2007; IPCC  
70 2012). Lack of individual recovery after the incidence of an extreme drought could lead to unstable  
71 coexistence on long time scales (Chesson 2000). In fact, a significant increment of defoliation in  
72 Mediterranean forests due to extreme drought events has been observed by Carnicer et al. (2011) over the  
73 last two decades, with defoliation trends being consistent with significant increments in tree mortality  
74 rates. Despite all these reports of severe impacts of extreme droughts and heat events on forests (revised  
75 for instance in Allen et al. 2010), plant communities are very resilient and several mechanisms have been  
76 discussed to explain the lack of vegetation changes despite the occurrence of extreme climatic events  
77 (Lloret et al. 2012a). This apparent lack of impact on vegetation could be more frequent than typically  
78 assumed due to publication bias towards positive results, in this case towards significant vegetation  
79 dieback following extreme events (Lloret et al. 2012a).

80 Several studies have addressed the impact of extreme droughts in Mediterranean species (e.g. Peñuelas et  
81 al. 2000; Peñuelas et al. 2001; Poyatos et al. 2008; Camarero et al. 2012; del Cacho and Lloret 2012)  
82 although long-term studies including periods before, during, and after an extreme drought event are still  
83 scarce (Lloret 2012b; Morán-López et al. 2014). Monitoring the response of species to summer drought  
84 over several years allows for a better understanding of not only how plants cope with extreme events, but  
85 also how these events could amplify water stress effects on species (Peñuelas et al. 2001; Bréda et al.  
86 2006). Studies with high temporal resolution focused on the actual water use and the alternative  
87 functional strategies are paramount for understanding tree species coexistence across ranges of water  
88 availability and how it can be affected by a changing climate. At the tree level, measurement of sap flow  
89 is widely used to evaluate water consumption spanning over different time intervals from daily to annual  
90 scales (Granier et al. 2000; Aranda et al. 2005). In addition, this methodology has been used at different  
91 biological scales ranging from individuals (Kunert et al. 2010; Zapater et al. 2012), to the entire forest  
92 canopy (Granier and Breda 1996; Granier et al. 2000; Aranda et al. 2012).

93         Sap flow measurements allow researchers to make inferences about ecological strategies  
94 according to species-specific behaviors (Martínez-Vilalta and Piñol 2003; Chirino et al. 2011; Zapater et

95 al. 2012), microclimatic impacts in the functional responses of trees (David et al. 2007), and influences in  
96 forest water use of structure and age of trees (Lagergren and Lindroth 2004; Forrester et al. 2010; Gyenge  
97 et al. 2011; Drake et al. 2012). Sap flow is also related with tree growth, as the latter results from net  
98 carbon balance which is always in compromise with water consumption. Moreover, carbon uptake is  
99 functionally coupled with the control of water loss performed by stomatal regulation of transpiration,  
100 establishing a species-specific trade-off between water use and growth that is modulated at different time  
101 scales. Therefore, water use and growth are considered to be highly integrated in the overall functional  
102 response of plants under water limiting conditions. Both response variables (water use and growth) have  
103 been treated thoroughly in previous studies, but few studies have focused on the interaction of both  
104 factors as an important way to understand tree response to climate change, with the exception of those  
105 inferring water use efficiency from the carbon isotopic signal of plant tissues (e.g. Maseyk et al. 2011;  
106 Granda et al. 2014; Voltas et al. 2013). Despite the recognition of the importance of the microhabitat for  
107 plant performance, little attention has been paid to the role of microclimate on the regulation of tree  
108 response to drought (Zweifel et al. 2007) and how it could condition water use and growth depending on  
109 the species (Zweifel et al. 2009). All this supports the need for ecophysiological studies of extreme  
110 drought events, integrating both water use and growth and exploring how the responses are modulated by  
111 local microclimatic conditions.

112

113 We carried out a field study of two coexisting tree species, one evergreen (*P. nigra*) and one deciduous  
114 (*Q. faginea*), with two contrasting plant water strategies (isohydric and anisohydric respectively)  
115 experiencing the most intense water stress event over the last half century. We determined accumulated  
116 basal area increment and sap flow over the period, spring growth rate, and beginning and duration of sap  
117 flow and growth as key and interrelated response variables at the whole plant level that depict main  
118 tradeoffs determining plant fitness in dry ecosystems. The main objective of this study was to quantify the  
119 effects of such extreme drought in growth, phenology and water use of both species. We also tested the  
120 importance of local microclimatic conditions for modulating the impacts of extreme drought events by  
121 comparing two slightly different sites. Specifically, we hypothesized that: (i) unusually dry periods have a  
122 strong impact on both species becoming disproportionately adverse at the dry microsite, (ii) extreme  
123 droughts have a different effect on the functional properties of the study species in relation to the  
124 contrasting water strategies of each species, resulting in distinct impacts on growth and water use, and

125 eventual whole plant vulnerabilities to increased frequencies of extreme droughts. We further discuss the  
126 implications of these two hypotheses for the coexistence of *P. nigra* and *Q. faginea*, which is maintained  
127 in part by differential inter-plays between water use and growth.

128

## 129 **Materials and methods**

### 130 *Study sites*

131 The study was carried out in an area located in Alto Tajo Natural Park, Guadalajara (Central Spain). The  
132 climate is continental Mediterranean with hot and dry summers and cold winters. Mean annual  
133 precipitation and temperature is 490.8 mm and 10.2 °C, respectively, according to climatic data of the  
134 closest meteorological station Molina de Aragón (1951-2012, data provided by the Spanish  
135 Meteorological Agency, AEMET). Soils are calcisols (World Soil Classification, FAO) from Cretaceous  
136 and Jurassic limestone that rendered shallow and poorly developed soil (Ferrero et al. 2006).

137 Two sites separated approximately by 8 km were chosen. The Armallones site (AR)  
138 (40°46'37"N, 2°19'42"W, 1079 m a. s. l.) has a west orientation with a 48% slope and a basal area of 13.7  
139 m<sup>2</sup>.ha<sup>-1</sup>, where *Quercus faginea* (38.7%), *Pinus nigra* (35.1%), *Quercus ilex* (25.8%) and *Juniperus*  
140 *oxycedrus* (0.2%) coexist as the main woody species. The Huertapelayo site (HP) (40°47'33"N,  
141 2°17'14"W, 907 m a. s. l.) has a north orientation, 68% slope and a basal area of 11.4 m<sup>2</sup>.ha<sup>-1</sup>. The main  
142 woody species are *Pinus nigra* (62.4%), *Quercus faginea* (35.1%), *Juniperus phoenicea* (1.6%) and  
143 *Juniperus oxycedrus* (0.9%).

144 We randomly selected healthy and fully sun-exposed representative trees with similar DBH (diameter at  
145 breast height 1.3 m of height) of black pine, *Pinus nigra* subsp. *salzmanii* [n = 8; 4 in each site] and  
146 Portuguese oak, *Quercus faginea* (n = 5 [AR] and 4 [HP]). *P. nigra* mean diameters were in the range of  
147 73.7 ± 7.9 cm and 80.0 ± 9.3 cm for AR and HP, respectively, and 56.0 ± 4.4 cm and 68.0 ± 7.2 cm for *Q.*  
148 *faginea*.

149

### 150 *Meteorological data and drought intensity*

151 Climatic data were obtained from the closest weather station (at ca. 36 km from the study area), Molina  
152 de Aragón (40°50'40"N, 1°53'07"W, 1.063 m a.s.l.) from AEMET (Spanish Meteorological Agency).  
153 Seasonal means of rainfall and temperature were calculated for two time series during 1951-2012 and

154 1970-2012, as a faster rate of change has been observed since the 70's in Spain (Bladé and Castro Diez  
155 2010) and at global scale (Alexander et al. 2006; Bladé and Castro Diez 2010).

156 Microclimatic conditions were also measured continuously during the study period at the study  
157 sites (2009-2012). At each site, we installed a soil moisture sensor (CR10X-ECH<sub>2</sub>O; Decagon Devices,  
158 Inc., Pullman WA, USA) at 70 cm depth to measure relative soil volumetric water content ( $\Theta$ ). Readings  
159 of each sensor were recorded every 2 hours. Air temperature was recorded every hour using a temperature  
160 sensor with an accuracy of  $\pm 0.3$  °C installed in a dendrometer increment sensor (DRL 26, Environmental  
161 Measuring Systems, Brno, Czech Republic) at both sites (n = 3 [AR] and 4 [HP]). Also, we installed a  
162 HOBO® (Onset Computer Co., Bourne, MA, USA) weather station at the Armallones site with a rain  
163 gauge (RGA-MoXX), temperature and relative air humidity (12-Bit Temperature/RH Smart Sensor), solar  
164 radiation (S-Lib-MOO3) and wind speed (Wind Speed Smart Sensor, S-WA-MOO3) sensors. Readings  
165 of each sensor were recorded every 30 minutes with a data logger (HOBO® H21-001; Onset Computer  
166 Co.). Air vapor pressure deficit (VPD) and potential evapotranspiration (PET) were calculated following  
167 Campbell (Campbell and Norman 1998) and the Penman equation (Penman 1948), respectively.

168 Drought intensity for the study period was characterized by estimating the daily relative  
169 extractable water in the soil (REW). REW values were only calculated for the Armallones site because  
170 the required meteorological data for its calculations were not available for the Huertapelayo site. REW  
171 was calculated daily as the ratio of available soil water to maximum extractable water. It ranges from 1.0  
172 (field capacity) to 0.0 (permanent wilting point). Water stress is assumed to occur when REW drops  
173 below the threshold 0.4 ( $REW_c$ ), under which soil water becomes limiting for transpiration, and stomatal  
174 closure happens for most temperate forest tree species. Radial growth has been observed to cease in forest  
175 trees at  $REW_c$  (Granier et al. 1999). Daily REW was simulated by running the BILJOU© water balance  
176 model (Granier et al. 1999) with measurements of daily rainfall, air temperature and relative humidity,  
177 global radiation and wind speed from the Armallones meteorological station. BILJOU© also uses stand  
178 characteristics: leaf area index (LAI), dates of bud burst and leaf fall for deciduous species and soil  
179 properties. LAI was estimated with a LAI 2000 Plant Canopy Analyzer (PCA, LI-COR, Lincoln, NE,  
180 USA) in 2012 (data provided by Pollastrini, M). LAI was kept constant over the period of 1961-2012 to  
181 check if there was a climatic drift independently of the LAI effect on drought intensity variation.  
182 Meteorological data for autumn and winter of 2011 was not available because of storage memory failure.  
183 Data gap filling for that period was performed using the Agri4cast database (Institute for Environment

184 and Sustainability, IES, European Commission; <http://mars.jrc.ec.europa.eu/mars/About->  
185 [us/AGRI4CAST](http://mars.jrc.ec.europa.eu/mars/About-)). As missing data occurring during the winter, when evapotranspiration is low and soil is  
186 at its field capacity, errors in REW calculation were considered negligible. Maximum extractable water in  
187 calcisol soils is low due to a high stone content, so we fixed it at 80 mm (according to Gaultier et al.  
188 2000).

189 The beginning date (BEGWS) and duration (NDWS) of water stress ( $REW < 0.4$ ), as well as a  
190 water stress index ( $I_s$ ), was calculated to compare drought intensity between years.  $I_s$  for a given period is  
191 the sum of the difference between REW and  $REW_c$  when  $REW < REW_c$  and divided by  $REW_c$ . Higher  
192 values of  $I_s$  correspond to higher drought stress.  $I_s$  was calculated for the period 1961-2012 to analyze the  
193 temporal evolution of water stress over the last half century.

194

#### 195 *Growth and sap flow measurements*

196 Plant growth was monitored from September 2009 to October 2012 measuring stem diameter changes at  
197 the breast height of the selected trees using automatic dendrometer bands (DRL26, EMS Brno, Czech  
198 Republic). A rotary position sensor with a stainless steel tape, which encircles the tree trunk, measured  
199 length variations every hour (accuracy 1  $\mu\text{m}$ ). The sensor was fixed to the trunk by the strength of the  
200 tape without using invasive fixing parts. Dead bark was brushed off before the dendrometers were  
201 installed. Data were stored in the same data logger as sap flow measurements. All data were thoroughly  
202 revised looking for possible abrupt or unusual jumps due to freezing events or resin, which can impede  
203 tape movement. Those data were corrected erasing the unusual jump ( $> 0.1$  mm between two records).  
204 Basal area increment (BAI) was calculated to obtain the stem increment and calculate growth rates  
205 according to:  $BAI = \pi(r_t^2 - r_{t-1}^2)$ ; where  $r$  is the tree radius and  $t$  is the hour of the day (Jump et al. 2006).  
206 Accumulated basal area increment per month ( $BAI_c$ ) was calculated by summing the BAI of that month  
207 and all previous monthly BAI since the beginning of the study period (September 2009). BAI evolution  
208 over study period allows observing differences of growth not only between seasons but also between  
209 years, species and sites, giving detailed information of growth patterns. The beginning and duration of the  
210 growth period during spring was determined for each tree considering changes in the slope of the BAI  
211 evolution over time for both study sites and for the three study years (2010-2012). We considered the end  
212 of the spring growth period to be over when the slope of the BAI evolution over time was lower than 5%.  
213 As spring is the main growth season for most of Mediterranean species (Durante et al. 2009) and studies



214 showed that growth of both study species is favored by spring rainfall (Granda et al. 2013), daily spring  
215 growth rates (SGR,  $\text{cm}^2 \cdot \text{day}^{-1}$ ) were calculated. SGR was obtained by dividing BAI for the whole growth  
216 period by its duration in days.

217 Sap flow, as a surrogate of tree performance in terms of transpiration control, was continuously  
218 monitored at the same time as growth in selected trees at each site using the sap flow sensors EMS 51  
219 (Environmental Measuring Systems, Brno, Czech Republic) installed at breast height on the north side of  
220 each trunk. These sensors are based on the stem heat balance (THB) method applied to a stem section  
221 with internal heating of tissues (Čermák et al. 2004). Sensors were covered with reflective insulation to  
222 avoid the influence of natural temperature gradients in the trunk and the effect of climatic conditions, e.g.  
223 radiation. Sap flow was measured every minute; 10-minute averages were recorded by an EMS data  
224 logger (Environmental Measuring Systems, Brno, Czech Republic). Heat losses from the sensors were  
225 subtracted calculating a baseline taking into account meteorological conditions and using Mini 32  
226 software. After revising the data, unusual values due to freezing events or energy supply problems were  
227 removed from the study.

228 Sap flow per tree ( $\text{L} \cdot \text{h}^{-1}$ ) was calculated by multiplying the measurements in the trunk sector by  
229 the tree perimeter (Čermák et al. 2004). We calculated sap flow per unit of basal area ( $Q_v$ ,  $\text{m}^3 \cdot \text{day}^{-1} \cdot \text{m}^{-2}$ )  
230 considering the individual tree basal area and the integration of the sap flow throughout the day. Five  
231 representative periods of tree transpiration along the year were selected independently of the study years  
232 (2009-2012). The first period (p1) corresponds to the beginning of a significant water use by both species  
233 during early spring ( $\text{REW} \sim 1$ ), when deciduous trees as *Quercus faginea* are developing their leaves. The  
234 second period (p2) shows the maximum tree transpiration which was recorded during the late spring. The  
235 third period (p3) considers tree performance at the peak of summer stress when minimum values of sap  
236 flow were recorded ( $\text{REW} < \text{REW}_c$ ). The fourth period (p4) depicts sap flow recovery during early  
237 autumn rainfall ( $\text{REW}_c < \text{REW} < 1$ ). Finally, the fifth period (p5) considers the minimum values recorded  
238 during late autumn and early winter. We selected seven representative days with similar meteorological  
239 conditions during each study period (Online Resource 1). The relative sap flow was calculated ( $Q_r$ ) to  
240 observe the decrease in water consumption by trees along the summer drought and later recovery due to  
241 autumn rainfall.  $Q_r$  was obtained as the ratio between sap flow ( $Q_v$ ) and the maximum sap flow ( $Q_{\text{max}, \text{p2}}$ ),  
242 both per unit of basal area, measured for the considered species, in both sites and every year.

243 Growth phenology was assessed from growth resumption in spring until maximum seasonal  
244 growth was recorded. The beginning and duration of growth give information of the possible positive  
245 effects of increasing temperatures, i.e. advance and extension of growth period due to high temperatures  
246 if water resource is not limited. The beginning, maximum and duration of water use was calculated to  
247 determine the changes of water use during dry years.

248

#### 249 *Statistical analysis*

250 Percentiles (5%, 50% and 95%) for temperature (T) and rainfall (P) from both time series (1951-2012 and  
251 1970-2012) were obtained to identify unusually seasonal values along the study period (2009-2012).

252 A non-parametric Mann-Whitney U test was used to check significant differences in seasonal T and  $\Theta$   
253 values between the two study sites. Differences in phenological variables and annual basal area increment  
254 (BAI) between years for each species and site were analyzed using a non-parametric Kruskal-Wallis test.

255 These analyses were performed using Statistica 8.0 (StatSoft Inc., Tulsa, OK, USA). A linear regression  
256 model was used to assess the temporal evolution of the water stress index over time. Percentiles (5% and  
257 95%) for water stress index from 1961 to 2012 were calculated to identify unusual water stress over the  
258 last 50 years. Differences in accumulated basal area increment between species at each site were analyzed  
259 by a linear model. Linear mixed-effects models (LMMs) were used to assess the effect of year (fixed  
260 factor) in growth rate (Zuur et al. 2007). Individual trees were considered as random effects. The model  
261 was fitted based on a restricted maximum likelihood method using the nlme package (Pinheiro et al.  
262 2007). To test differences in sap flow per unit of basal area between periods (2009-2012), linear models  
263 were made for each species and site. Further, we assessed the relationship between REW and spring  
264 growth rate and relative sap flow per tree using Spearman's rank correlation coefficients. These analyses  
265 were carried out using the R statistical software (version R3.0.1: R Development Core Team 2013,  
266 Vienna).

267

## 268 **Results**

### 269 *Climate trends and extreme events*

270 Extreme drought events have increased their frequency over the last decade. Extremely high values of  
271 water stress ( $I_s$ ) were found in three years (1994, 2011 and 2012) during the decade 1992-2012 while no  
272 extreme values were found between 1961 and 1992. Additionally, there was a significant increase in

273 water stress ( $I_s$ ) since 1961 ( $p = 0.024$ ). Four of the eight most stressful years for vegetation (water stress  
274 index,  $I_s$ ) over the last 50 years took place over the last six years (2007-2012)(Fig. 1). The year 2011  
275 exerted the highest water stress on vegetation over the half century historical record as indicated by the  $I_s$   
276 series calculated for 1961-2012 period.

277 In agreement with increases in water stress during last decade, mean annual decreased by 46.1  
278 mm and temperature increased by 0.6 °C in the last decade (2002-2012), compared to the long-term data  
279 series (1951-2012). Summer and spring temperatures of 2009 were unusually high compared to the long-  
280 term data (1970-2012) (Online Resource 2). The spring of 2011 was extremely hot and both summer and  
281 winter seasons were unusually dry, which allows considering 2011 as an extremely dry year. These  
282 results were corroborated by comparing the long-term data series 1951-2012. Summer rainfall during  
283 2012 was also slightly lower than expected from the series 1951-2012 (Online Resource 2). The year  
284 2010 can be considered a normal year compared with 2009, 2011 and 2012, since total annual rainfall and  
285 mean annual temperatures were the closest to long-term averages. Furthermore, 2010 showed lower water  
286 stress index ( $I_s$ ) compared with 2011 and 2012 (Fig. 1).

287 Microclimatic differences were found between both study sites. The Armallones (AR) site was  
288 hotter and drier than the Huertapelayo (HP) site for all study years, with significantly higher air  
289 temperatures during the summer of 2009 and 2011 and the winter of 2011 (Table 1). AR was significantly  
290 drier than HP comparing annual soil volumetric water content values for almost all seasons. As all those  
291 seasons correspond to extremely hot and dry periods (Online Resource 2), the trees at the AR site were  
292 expected to experience severe drought stress. Spring air temperatures were significantly different in 2010  
293 and 2011 only for the AR site ( $p = 0.033$ , between years). The AR site experienced significantly higher  
294 temperatures, between 1.3 and 3.6 °C, during all study summers ( $p < 0.001$ ) and also during the spring of  
295 2009 and the autumn of 2012 ( $p < 0.05$ ) compared to the long-term time series. Spring potential  
296 evapotranspiration (PET) increased around 5.7% per year since 2010. This increase was also found in the  
297 summer (6.7% in 2011 and 3.1% in 2012, increase from previous year). Because of this higher PET and  
298 rainfall reduction, water stress ( $I_s$ ) was 88.5% lower in 2010 than in 2011 (Table 1).

299 Due to low PET and therefore low transpiration, relative extractable water of the soil (REW) was  
300 close to 1, soil water was near field capacity from late autumn to early spring for all study years (Fig. 2).  
301 REW decreased sharply during the late spring and summer of all study years due to the low water holding  
302 capacity. Water stress occurred during each summer of the 4 year periods, but its intensity and duration

303 varied among years. The lowest REW level was reached in the summer of 2011, which confirmed that  
304 2011 was the driest year compared with the other study years. Days under water stress (NDWS) were  
305 more than two times higher in the dry year (2011) than in the normal year (2010), being 110 and 32 days,  
306 respectively (Table 1). The beginning of the water stress period (BEGWS) was advanced over the years  
307 due to higher temperatures being reached earlier, being up to 19 days earlier in 2012 than 2010, the  
308 normal year. Water stress duration was 2 and a half months longer in 2011 than 2010, which confirmed a  
309 more lasting drought during the extreme dry year.

310

### 311 *Spring growth patterns*

312 Annual growth, measured as annual basal area increment (BAI), was higher in *P. nigra* than in *Q. faginea*  
313 at both sites and in all study years. No significant differences in growth were found between sites and  
314 years, although higher annual BAI was observed at the mesic site (HP) for both species. (Table 2). The  
315 exceptionally extreme year (2011) had a higher effect on growth at the dry site in both species.  
316 Differences between sites in reductions of annual BAI, derived from the extreme dry year, were higher  
317 for *P. nigra* (AR: -38.0%; HP: -9.4%) than for *Q. faginea* (AR: -48.4%; HP: -43.7%). Growth evolution,  
318 as the accumulated basal area increment per month (BAI<sub>c</sub>), was higher in *P. nigra* than in *Q. faginea* over  
319 the study period (2009-2012) and at both sites (Fig.3). Both species showed higher growth in spring,  
320 being faster in *P. nigra* at the beginning of this season. No significant growth differences were found  
321 between species at each site ( $p > 0.05$ ).

322 During the spring, the main growth season for the study species, both species showed similar  
323 patterns in growth rates (SGR) at each site (Fig. 4), although higher rates were found for *P. nigra* during  
324 all years. After the exceptionally extreme year (2011), both species decreased their SGR at both sites,  
325 decreasing more at the dry site. At this site, reduction in growth was significantly higher for *Q. faginea* (-  
326 59.8%) than for *P. nigra* (-35.9%), while at the mesic site, higher reduction was found for *P. nigra* (-  
327 24.2%; -16.7% (*Q. faginea*)).

328 The beginning of spring growth was earlier in the mesic site than in the dry site for both species  
329 and in all study years, but only significant results were found for 2012 (Table 2). Moreover, spring  
330 growth was advanced significantly in *Q. faginea* starting between 17 (mesic site) and 20 (dry site) days  
331 before, during the exceptionally extreme year 2011 compared to 2010. In addition, growth during 2011  
332 lasted between 9 and 28 days more in both species at both study sites. Growth duration was significantly

333 different between years for *P. nigra* at the dry site but not at the mesic site, while *Q. faginea* had  
334 significantly different growth duration between years at the mesic site.

335

### 336 *Sap flow patterns*

337 Higher seasonality in water use, measured as sap flow, was found at the dry site (AR), especially in *P.*  
338 *nigra*. Moreover, differences between species were accentuated during the exceptionally extreme 2011  
339 year (Fig. 5). *Q. faginea* had highest sap flow rates during the late spring, summer and early autumn at the  
340 dry site, while at the mesic site similar sap flow rates were found for both species. In all study summers  
341 (period p3) the lowest sap flow rates were recorded for *P. nigra* at the dry site, reaching values close to  
342 zero in 2011 since limited water resources were available due to the extreme drought. Both species  
343 showed higher reductions in water use due to the summer drought (period 2 compared with period 3) at  
344 the dry site and particularly after the exceptionally extreme year (*P. nigra*: -25.3%; *Q. faginea*: -22.7%)  
345 (Fig. 5). During 2011 and 2012, *P. nigra* was not able to recover water use after the summer drought  
346 (period 3 and 4) indicating that autumn rainfall was not abundant enough to reestablish its sap flow.  
347 Looking at the seasonal evolution of the relative sap flow rates, *Q. faginea* showed similar patterns at  
348 both sites, while *P. nigra* appeared to be more sensitive to water shortage conditions at the dry site (Fig.  
349 6). During the summer drought, both species decreased water use overall both sites, but the species were  
350 more affected at the dry site, decreasing their sap flow by 25-45% (years range) in *Q. faginea* and 69-90%  
351 in *P. nigra*. Higher reductions in water use were found in the dry year for *P. nigra* but not for *Q. faginea*.  
352 At the mesic site, *Q. faginea* was not able to recover its sap flow (period p4) during the exceptionally  
353 extreme year but it did over the following year, while the opposite patterns were true for *P. nigra*. Relative  
354 sap flow ( $Q_r$ ) was marginally correlated with REW for *P. nigra* at the dry site ( $r = 0.829$ ,  $p = 0.058$ ) but  
355 not for *Q. faginea* ( $r = 0.257$ ,  $p = 0.658$ ).

356 As expected due to their dependence on water resources and temperatures, the beginning of sap  
357 flow followed the same pattern as spring growth, being earlier in the mesic site for both species during  
358 study years. Due to water scarcity, water use started later in 2011, the exceptionally extreme year, than in  
359 2010 for both species at the dry site (Table 3). Sap flow duration, indicating the spring water use period  
360 before summer drought, was opposite to the one observed for growth in pine species at the dry site, being  
361 longer for growth and shorter for sap flow in 2011 compared to 2010. However, sap flow as well as  
362 growth started later and did not last as long in 2012 as the previous year. Maximum sap flow occurred

363 later in the exceptionally extreme 2011 year for both species and at both sites, although differences were  
364 significant only for *P. nigra* at the dry site.

365

### 366 **Discussion**

367 Our study site experienced an increased aridity due to a 0.6°C increase in mean annual temperature and a  
368 46.1 mm decrease of annual rainfall over the last decade. This is in agreement with warming trends  
369 observed in Mediterranean ecosystems since the 70's, both in the Iberian Peninsula (Bladé and Castro  
370 Díez 2010) and at the global scale (IPCC 2013). Higher occurrence of extreme drought events over the  
371 Mediterranean region (Della-Marta et al. 2007) is particularly relevant for forest ecosystems, which are  
372 already showing symptoms of decline by water stress worldwide (Allen and Breshears 1998; Allen et al.  
373 2010; Linares and Camarero 2012). The year 2011 was an extremely dry and warm year at our study site,  
374 with a severe and long-lasting drought resulting in very low relative extractable water from late spring to  
375 early autumn that resulted in the most stressful year over the last half century. This extreme event  
376 occurred in 2011 was preceded by another extreme summer drought with unusual high temperatures  
377 during summer just two years before, in 2009, supporting an increased frequency of extreme droughts in  
378 the area.

379         Reductions in the growth of Mediterranean trees have been associated with decreases in annual  
380 rainfall since the 70's (Sarris et al. 2007). This pattern was confirmed for *P. nigra* and *Q. faginea* at our  
381 study site, not only by our detailed 3-year study but also by dendrochronological studies (Granda et al.  
382 2013). The evergreen species *P. nigra* showed not only a higher basal area increment per year but also  
383 higher spring growth rates than the deciduous *Q. faginea*, which is in agreement with a previous  
384 dendrochronological study at the site (Granda et al. 2013). This is in agreement with the higher intrinsic  
385 water use efficiency of *P. nigra* (Granda et al. 2014). The effects in growth due to the unusual drought  
386 were noticeable the year after the exceptionally dry year. This one-year delay in growth response to  
387 drought is based on the reported dependence of growth on previous climatic conditions (Sarris et al. 2007;  
388 Morán-López et al. 2014). Reductions in annual growth the year after the extreme drought in relative  
389 terms were higher for *Q. faginea* than for *P. nigra*. Opposite results were found by Granda et al. (2013),  
390 where *P. nigra* experienced the sharpest growth decline due to the extreme drought events compared with  
391 the coexisting *Q. faginea*. These different results may be explained by the different approaches followed  
392 in each study to determine tree growth; while our study focused on processes and mechanisms involved in

393 the responses to one unique extreme event, Granda et al. (2013) followed a dendrochronological approach  
394 over a time series with many dry and mesic years. However, and in agreement with Granda et al. (2013),  
395 *P. nigra* was able to recover after the extreme event while *Q. faginea* was not, suggesting a higher  
396 resilience of the former.

397 As expected, the impact of the extreme drought on growth was more adverse at the dry site for  
398 both species, observing a 60% reduction of spring growth rate for *Q. faginea* and 36% for *P. nigra* at the  
399 dry site, while decreases at the mesic site were 17% and 24% respectively. Daily stem fluctuations are a  
400 combination of both water storage changes and growth processes (Steppe et al. 2005; Zweifel et al. 2005).  
401 In the Mediterranean region, water storage during spring increases significantly due to the abundant  
402 rainfall, resulting in increases in stem size due to processes. However, growth processes are still relevant  
403 at the daily scale during spring (Drew and Downes 2009) since growth is greater when water is not  
404 limiting, which usually occurs during spring for Mediterranean trees (Durante et al. 2009). Some studies  
405 have observed high dependency between growth and water availability (e.g. Ibáñez et al. 1998; Ogaya  
406 and Peñuelas 2007; Zapater et al. 2012), which is correlated with water use by plants. Water use was  
407 assessed through sap flow measurements since it is considered an overall estimator of the water transpired  
408 by trees (Köstner et al. 1996; Burgess et al. 2006; Poyatos et al. 2007), and therefore, as an indicator of  
409 tree performance in terms of transpiration control. The study species followed the typical Mediterranean  
410 transpiration patterns, which peak in late spring and strongly decrease during the summer drought  
411 (Tognetti et al. 1998). *P. nigra* was able to better use soil moisture in late winter and early spring, while  
412 *Q. faginea* was leafless and with no sap movement for most of this time. As expected from its deep root  
413 system and its anisohydric strategy, *Q. faginea* showed higher and more sustained sap flow rates than *P.*  
414 *nigra*. Our ongoing field research on both species is showing different predawn and midday water  
415 potentials (unpublished data) that support the higher water availability for *Q. faginea*, particularly during  
416 the summer.

417 Despite the fact that both species were sensitive to water stress and decreased their water use  
418 during dry periods, stronger reductions in transpiration were found in *P. nigra*, an isohydric species that  
419 closes stomata during drought. By contrast, *Q. faginea*, a water spender in comparison with *P. nigra*, was  
420 able to sustain an active sap flow rate longer over the summer even at the dry site. The pattern observed in  
421 *Q. faginea* has been considered characteristic of higher drought tolerance (McDowell 2011). As expected  
422 and in agreement with growth results, the impact of the extreme drought on transpiration was higher at

423 the dry site and in *P. nigra* when compared to *Q. faginea* (90% versus 45%). These results were  
424 noticeable due to the rather minor differences in annual temperature and soil volumetric water content at  
425 the end of the summer between the two sites (from 0.3 to 0.9 °C and from 0.05 to 0.06 m<sup>3</sup>.m<sup>-3</sup>,  
426 respectively). Our results, thus, highlight the important role of microclimatic conditions of species  
427 responses to drought.

428         Differences found in growth and water use between the study species in response to the impact  
429 of the extreme drought can be explained by differential water strategies. Despite the fact that the  
430 distinction among water strategies remains unclear in some cases, with many intermediate behaviors  
431 (Franks et al. 2007), we still claim that *Q. faginea* could be ascribed to an anisohydric behavior while *P.*  
432 *nigra* follows an isohydric strategy (Tardieu and Simonneau 1998). *Q. faginea* maintained rather high  
433 transpiration rates during summer droughts, while *P. nigra*, as other *Pinus* species do in the  
434 Mediterranean region, closed stomata early on to maintain the water potential well above its hydraulic  
435 failure threshold but compromised carbon uptake (Martínez-Ferri et al. 2000; Martínez-Vilalta et al. 2002;  
436 Anderegg et al. 2014). Under an extreme and prolonged drought, the drought-avoidance strategy that  
437 followed *P. nigra* could result in carbon starvation (McDowell 2011; Sala et al. 2012). In contrast, *Q.*  
438 *faginea* may be in risk of hydraulic failure and death due to cavitation processes during these events. In  
439 fact, *Q. faginea* could have been close to hydraulic failure in 2011 since its transpiration rates did not  
440 recover during early autumn rainfall while the opposite was true during wetter years. This could originate  
441 differences in competitive ability of *Q. faginea* between mesic and dry years. In fact, Zweifel et al. (2007)  
442 found that the related species *Q. pubescens* was a less efficient competitor during extremely dry years,  
443 showing massive leaf loss and almost a cessation of physiological activity. Although we did not study  
444 die-back processes or find higher tree mortality for these two species at the study site, we did observe leaf  
445 death in both species during and after the extreme summer drought of 2011. This could be the prelude of  
446 a severe defoliation event observed in some species in Europe (Carnicer et al. 2011), where these events  
447 were related to tree mortalities. Moreover, mortality is expected to increase since the expected warmer  
448 temperatures can greatly accelerate tree decay and death (Adams et al. 2009) as already observed in many  
449 forest types around the world (Allen et al. 2010).

450         Considering all our results, we suggest that under more frequent and extreme drought events *Q.*  
451 *faginea* could experience hydraulic failure, combined with eventual reductions in autumn rainfall, this  
452 could compromise species recovery and significantly reduce its growth. Although, *P. nigra* is also prone



453 to starvation during intense drought events, we suggest that its higher water use efficiency (Granda et al.  
454 2014) may confer competitive advantages over *Q. faginea*. Intrinsic water use efficiency increased during  
455 unfavorable years in both species while growth decreased (Granda et al. 2014). Therefore, despite the fact  
456 that growth and intrinsic water use efficiency were higher for *P. nigra*, growth reductions during the  
457 extremely dry year were higher for *Q. faginea* (Granda et al. 2013; 2014). Thus, we suggest that *P. nigra*  
458 may perform better than *Q. faginea* at our study site under a scenario with more frequent and intense  
459 extreme droughts. However, due to the complexity of species responses to drought events and as many  
460 factors are involved in the overall impact of extreme climatic events over the life cycle of a tree, more  
461 studies should address how species-specific responses could lead to future shifts in community  
462 composition. Nonetheless, the different responses observed between *P. nigra* and *Q. faginea* may lead to  
463 changes in dominance and in community composition, and dynamics presumably favour *P. nigra*. Mild  
464 autumn and winter seasons are likely to increase transpiration at the community level if evergreen  
465 species, like *P. nigra*, dominate canopy composition in detriment of deciduous species, like *Q. faginea*.  
466 This is supported by Brantley et al. (2013), who found that an increase of deciduous species decreased  
467 evapotranspiration during winter time. As a consequence of this eventual replacement of the deciduous by  
468 the evergreen species, more water resources will be used by the community over the year, which in  
469 combination with increases in aridity and evaporative demand under increasing temperatures (Nadal-Sala  
470 et al. 2013) could have important and negative consequences at the basin level (Otero et al. 2010)  
471 therefore affecting the water cycle at large spatial and temporal scales (Brantley et al. 2013).

472         Decreases in species growth and changes in forest stand composition due to climate change can  
473 deeply affect carbon cycle, decreasing carbon uptake and affecting the role of forests as CO<sub>2</sub> sinks (Grace  
474 2004). In fact, models have simulated a decrease in net primary production in Iberian Peninsula forests  
475 after the mid 21<sup>st</sup> century due to increases in aridity in combination with higher respiration rates and  
476 evaporative demand (Nadal-Sala et al. 2013). As a result, forests could even change from their actual role  
477 as carbon sinks to carbon sources (Nadal-Sala et al. 2013).

478         In conclusion, despite the fact that the species experienced the most stressful drought over the  
479 last half century and that species performance was significantly affected by this extreme event, in terms of  
480 growth and water use, the trees studied did not exceed their tolerance thresholds at our study site as  
481 suggested by the lack of mortality after the extreme event. Therefore, the high resilience observed for  
482 these Mediterranean species could be counteracting the impact derived from an extreme drought event.

483 Studies considering different time scales, involving mechanistic understanding of species responses to  
484 extreme events and monitoring other variables like decline or mortality are needed to make sound  
485 predictions of species shifts and dynamics, and its implications for future ecosystem functioning.

486

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501

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717 **Table 1** Seasonal mean  $\pm$  SE temperature (T) and soil volumetric water content ( $\Theta$ ) of the meteorological sensors installed at both study sites (Sp: spring, Su: summer, Au:  
718 autumn, Wi: winter). Total rainfall (P) and vapor pressure deficit (VPD) were obtained from the meteorological station located at Armallones site. Potential evapotranspiration  
719 (PET) was calculated following the Penman equation. Values between parentheses represent means of total annual rainfall and mean annual temperature for the year indicated  
720 above at Armallones site. Water stress index ( $I_s$ ), beginning of water stress (BEGWS, Julian day) and number of days of water stress (NDWS) were calculated for each year.  
721 Significant differences in temperature and water soil content between both study sites are indicated with asterisk (\*:  $p < 0.05$ ; \*\*:  $p < 0.01$ ; \*\*\*:  $p < 0.001$ ). + and - indicates  
722 means for only two months of the season and data not available, respectively

Site	Armallones						Huertapelayo				
	P (mm)	T (°C)	VPD (kPa)	PET (mm)	$\Theta$ (m <sup>3</sup> /m <sup>3</sup> )	$I_s$	BEGWS	NDWS	T (°C)	$\Theta$ (m <sup>3</sup> /m <sup>3</sup> )	
2009 (630.1, 12.6)	Sp	134.6 $\pm$ 14.1	11.1 $\pm$ 2.7	0.53 $\pm$ 0.15	227.6 $\pm$ 20.7	-			10.7 $\pm$ 2.8	-	
	Su	32.9 $\pm$ 2.6	23.3 $\pm$ 1.3*	1.64 $\pm$ 0.19	421.4 $\pm$ 9.6	-			22.3 $\pm$ 1.0	-	
	Au	87.0 $\pm$ 6.4	13.3 $\pm$ 2.7	0.57 $\pm$ 0.14	135.9 $\pm$ 15.0	0.028 $\pm$ 0.003***	27.4	174	70	12.3 $\pm$ 2.8	0.050 $\pm$ 0.002
	Wi	375.6 $\pm$ 43.9	2.7 $\pm$ 0.3	0.11 $\pm$ 0.01	37.4 $\pm$ 2.4	0.071 $\pm$ 0.002***				3.0 $\pm$ 0.2	0.142 $\pm$ 0.018
2010 (688.8, 11.4)	Sp	247.9 $\pm$ 8.6	9.7 $\pm$ 2.1	0.36 $\pm$ 0.07	200.6 $\pm$ 16.1	0.083 $\pm$ 0.002***			9.8 $\pm$ 2.1	0.149 $\pm$ 0.003	
	Su	92.6 $\pm$ 24.4	21.4 $\pm$ 2.2	1.21 $\pm$ 0.27	385.8 $\pm$ 13.5	0.037 $\pm$ 0.018***			20.8 $\pm$ 1.8	0.094 $\pm$ 0.022	
	Au	172.4 $\pm$ 7.2	10.8 $\pm$ 3.7	0.42 $\pm$ 0.18	121.8 $\pm$ 17.4	0.049 $\pm$ 0.015	8.3	212	32	9.7 $\pm$ 3.5	0.054 $\pm$ 0.012
	Wi	175.9 $\pm$ 16.7	3.5 $\pm$ 0.7	0.14 $\pm$ 0.04	40.0 $\pm$ 3.6	0.053 $\pm$ 0.002***				2.5 $\pm$ 0.4	0.140 $\pm$ 0.002
2011 (-, 12.5)	Sp	214.4 $\pm$ 12.9	11.8 $\pm$ 2.8	0.39 $\pm$ 0.10	212.5 $\pm$ 18.7	0.092 $\pm$ 0.013***			11.5 $\pm$ 2.7	0.120 $\pm$ 0.016	
	Su	36.1 $\pm$ 10.9	21.7 $\pm$ 1.4*	0.95 $\pm$ 0.25	413.7 $\pm$ 4.6	0.038 $\pm$ 0.023***			21.0 $\pm$ 1.0	0.014 $\pm$ 0.013 <sup>+</sup>	
	Au	-	13.7 $\pm$ 3.6	-	145.7 $\pm$ 22.0	0.012 $\pm$ 0.001*** <sup>+</sup>	72.1	191	110	12.2 $\pm$ 3.1	-
	Wi	-	2.8 $\pm$ 0.6**	-	41.6 $\pm$ 6.0	0.084 $\pm$ 0.016 <sup>+</sup> ***				1.7 $\pm$ 0.4	0.035 $\pm$ 0.005 <sup>+</sup>
2012 (561.1, 12.4)	Sp	168.9 $\pm$ 31.9	11.0 $\pm$ 2.8	0.54 $\pm$ 0.17	225.6 $\pm$ 19.2	0.088 $\pm$ 0.013***			10.9 $\pm$ 2.7	0.030 $\pm$ 0.006	
	Su	23.1 $\pm$ 2.1	23.6 $\pm$ 0.9	1.75 $\pm$ 0.16	426.9 $\pm$ 6.3	0.019 $\pm$ 0.007***			23.0 $\pm$ 0.7	0.006 $\pm$ 0.003	
	Au	234.7 $\pm$ 14.0	12.1 $\pm$ 3.2	0.41 $\pm$ 0.23	119.2 $\pm$ 18.7	0.068 $\pm$ 0.019	42.8	193	79	11.8 $\pm$ 3.0	0.388 $\pm$ 0.233
	Wi	134.4 $\pm$ 13.1	3.0 $\pm$ 0.3	0.11 $\pm$ 0.02	-	0.074 $\pm$ 0.002***				2.6 $\pm$ 0.2	0.602 $\pm$ 0.226

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725 **Table 2** Day of year (Julian day, mean  $\pm$  SE) for the beginning of spring growth and its duration (days  $\pm$  SE). Mean  $\pm$  SE of annual basal area increment (BAI,  $\text{cm}^2\cdot\text{yr}^{-1}$ ). Data  
 726 are shown for both study species (*Pinus nigra* and *Quercus faginea*), sites (AR: Armallones; HP: Huertapelayo) and years (2010-2012). Significant *p*-values are shown in bold

Site	Sp.	Spring growth											
		Beginning				Duration				BAI			
		2010	2011	2012	<i>p</i> -value	2010	2011	2012	<i>p</i> -value	2010	2011	2012	<i>p</i> -value
AR	<i>P. nigra</i>	105 $\pm$ 5	99 $\pm$ 1	109 $\pm$ 3	0.082	51 $\pm$ 6	65 $\pm$ 6	46 $\pm$ 2	<b>0.047</b>	10.14 $\pm$ 1.18	11.22 $\pm$ 0.76	6.96 $\pm$ 1.16	0.077
	<i>Q. faginea</i>	107 $\pm$ 5	87 $\pm$ 7	105 $\pm$ 1	<b>0.029</b>	60 $\pm$ 1	88 $\pm$ 9	51 $\pm$ 8	0.075	3.55 $\pm$ 1.15	7.35 $\pm$ 2.45	3.79 $\pm$ 0.76	0.184
HP	<i>P. nigra</i>	101 $\pm$ 0	97 $\pm$ 1	98 $\pm$ 5	0.167	79 $\pm$ 2	70 $\pm$ 9	74 $\pm$ 9	0.387	12.49 $\pm$ 2.37	15.34 $\pm$ 3.14	13.90 $\pm$ 3.47	0.735
	<i>Q. faginea</i>	90 $\pm$ 6	73 $\pm$ 2	81 $\pm$ 2	<b>0.027</b>	92 $\pm$ 7	108 $\pm$ 10	71 $\pm$ 3	<b>0.034</b>	7.27 $\pm$ 2.37	9.07 $\pm$ 1.61	5.11 $\pm$ 0.97	0.292

727 **Table 3** Day of year (Julian day, mean  $\pm$  SE) for the beginning and maximum of spring sap flow and its duration (days  $\pm$  SE). Data are shown for both study species (*Pinus*  
728 *nigra* and *Quercus faginea*), sites (AR: Armallones; HP: Huertapelayo) and years (2010-2012). Significant *p*-values are shown in bold

Site	Sp.	Sap flow											
		Beginning				Maximum				Duration			
		2010	2011	2012	<i>p</i> -value	2010	2011	2012	<i>p</i> -value	2010	2011	2012	<i>p</i> -value
AR	<i>P. nigra</i>	62 $\pm$ 11	84 $\pm$ 6	101 $\pm$ 3	<b>0.092</b>	159 $\pm$ 8	161 $\pm$ 0	133 $\pm$ 1	<b>0.023</b>	126 $\pm$ 12	96 $\pm$ 6	49 $\pm$ 2	<b>0.007</b>
	<i>Q. faginea</i>	134 $\pm$ 4	149 $\pm$ 6	133 $\pm$ 1	<b>0.041</b>	157 $\pm$ 6	161 $\pm$ 14	156 $\pm$ 10	0.838	55 $\pm$ 4	126 $\pm$ 77	54 $\pm$ 10	0.864
HP	<i>P. nigra</i>	86 $\pm$ 16	83 $\pm$ 7	95 $\pm$ 11	0.616	126 $\pm$ 8	125 $\pm$ 13	128 $\pm$ 5	0.938	93 $\pm$ 24	109 $\pm$ 10	60 $\pm$ 10	0.167
	<i>Q. faginea</i>	115 $\pm$ 1	118 $\pm$ 29	117 $\pm$ 8	0.645	146 $\pm$ 3	155 $\pm$ 12	136 $\pm$ 3	0.154	73 $\pm$ 4	76 $\pm$ 26	64 $\pm$ 32	0.692

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738 **Captions**

739 **Fig.1** Evolution of annual water stress index ( $I_s$ ) for the period 1961-2012. Higher values of the index  
740 indicate higher water stress. Line represents the fitted linear model

741 **Fig.2** Daily values of modeled relative extractable water (REW) from the soil of Armallones site since  
742 2009 to 2012 (Julian days). Dashed line indicates the critical REW value ( $REW_c = 0.4$ ) at which tree  
743 transpiration begins to decrease. Bars in grey represent periods of sap flow measurements

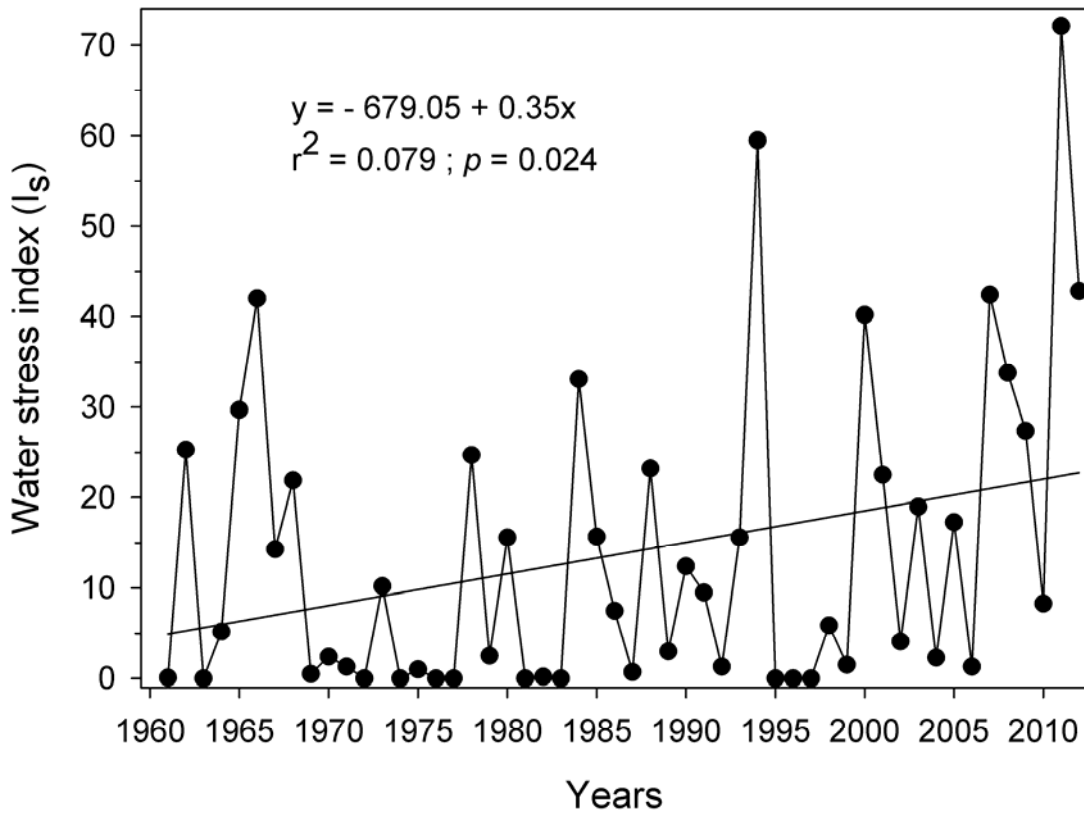
744 **Fig.3** Mean monthly accumulated basal area increment ( $BAI_c$ ) for the study period 2009-2012 for each  
745 species and site. Bars in grey represent the two unusually dry seasons over the exceptionally dry year  
746 2011, summer and winter, respectively. No available data since December 2011 to March 2012 at the dry  
747 site (AR)

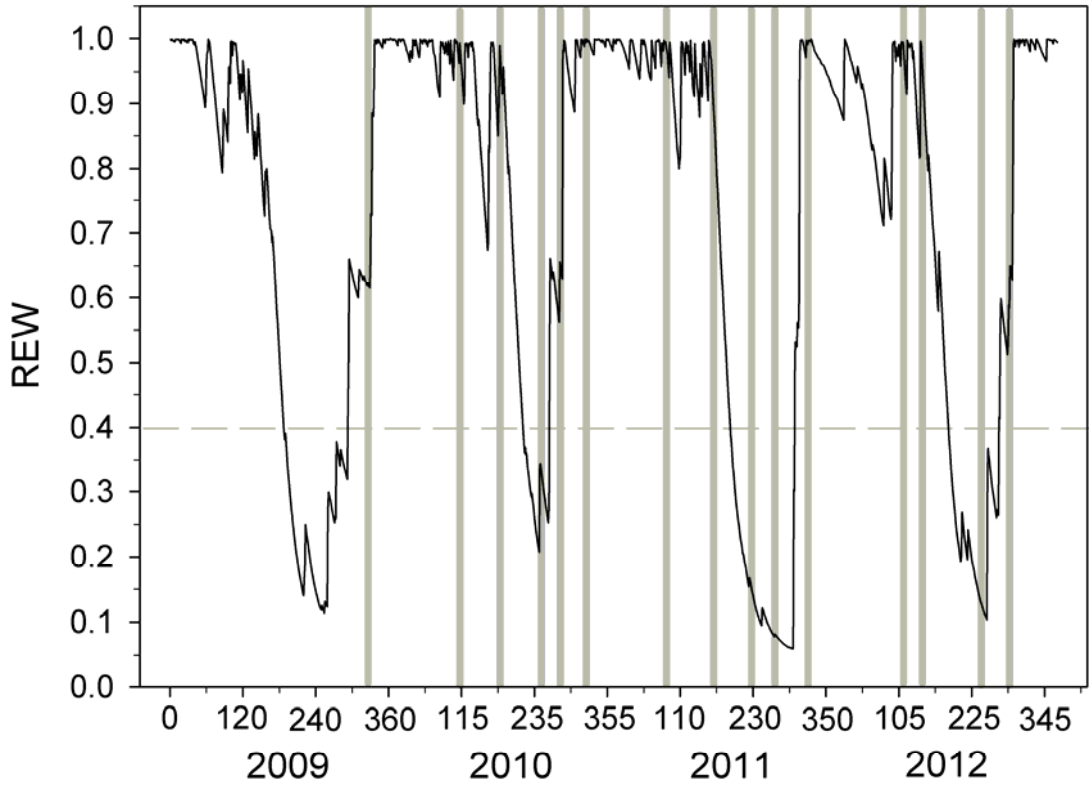
748 **Fig.4** Mean of daily spring growth rate ( $cm^2 \cdot day^{-1}$ ) for each species, site (Armallones (a) and  
749 Huertapelayo (b)) and study year for the period (2010-2012). Bars are standard mean errors unless  
750 eclipsed by symbols. For each species and site, different letters indicate significant differences between  
751 years at  $p = 0.05$  (Small letters for *Pinus nigra* and capital ones for *Quercus faginea*)

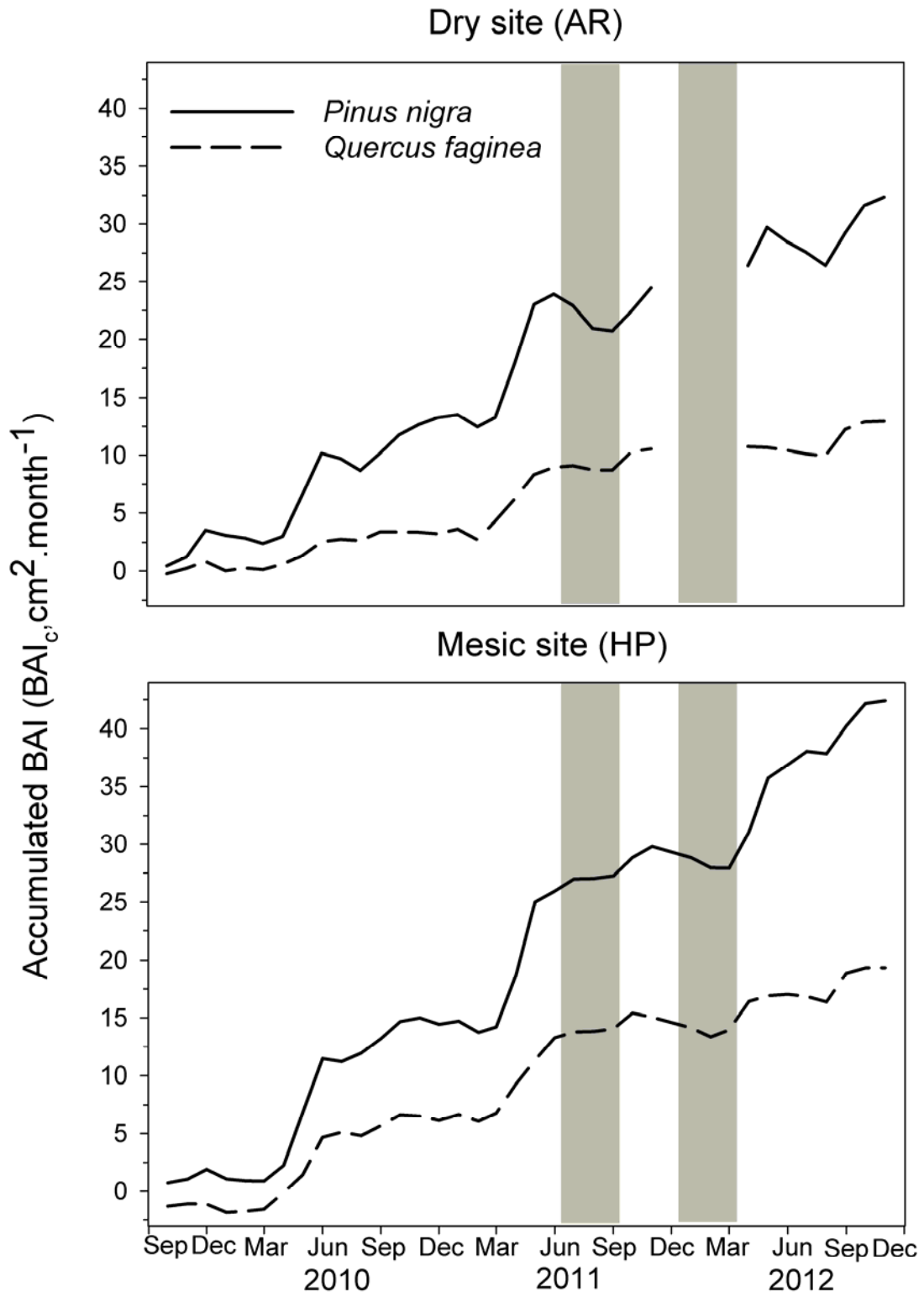
752 **Fig.5** Mean  $\pm$  SE of daily mean sap flow per basal area ( $Q_v$ ,  $m^3 \cdot day^{-1} \cdot m^{-2}$ ) for each species, site  
753 (Armallones (a) and Huertapelayo (b)) and measurement period (p1: beginning of spring water use; p2:  
754 maximum evapotranspiration during late spring; p3: minimum values during the peak of summer stress;  
755 p4: sap flow recovery during early autumn rainfall; p5: late autumn and early winter minimum values)  
756 since 2009 to 2012. For each species and site, different letters indicate significant differences between  
757 periods at  $p = 0.05$  (Small letters for *Pinus nigra* and capital ones for *Quercus faginea*). No available data  
758 for p5 in 2012 at both sites

759 **Fig.6** Relative sap flow ( $Q_r$ ) obtained from dividing mean daily sap flow per basal area by the mean  
760 maximum sap flow measured that year (period 2, p2) and calculated for each species, year and site  
761 (Armallones (a, b and c) and Huertapelayo (d, e and f)). Periods are considered as following: p2:  
762 maximum evapotranspiration during late spring; p3: minimum values during the peak of summer stress;  
763 p4: sap flow recovery during early autumn rainfall; p5: late autumn and early winter minimum values

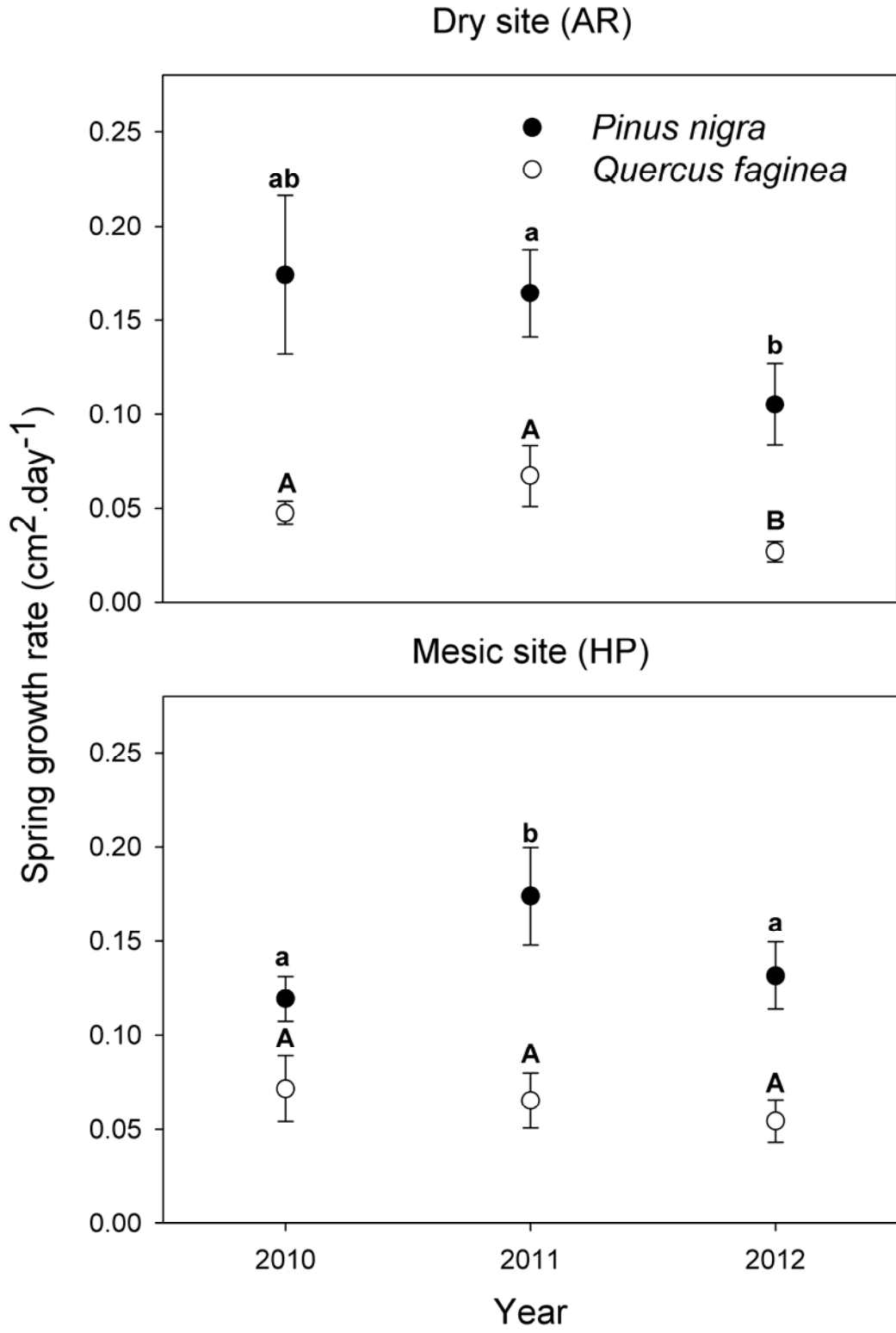
764

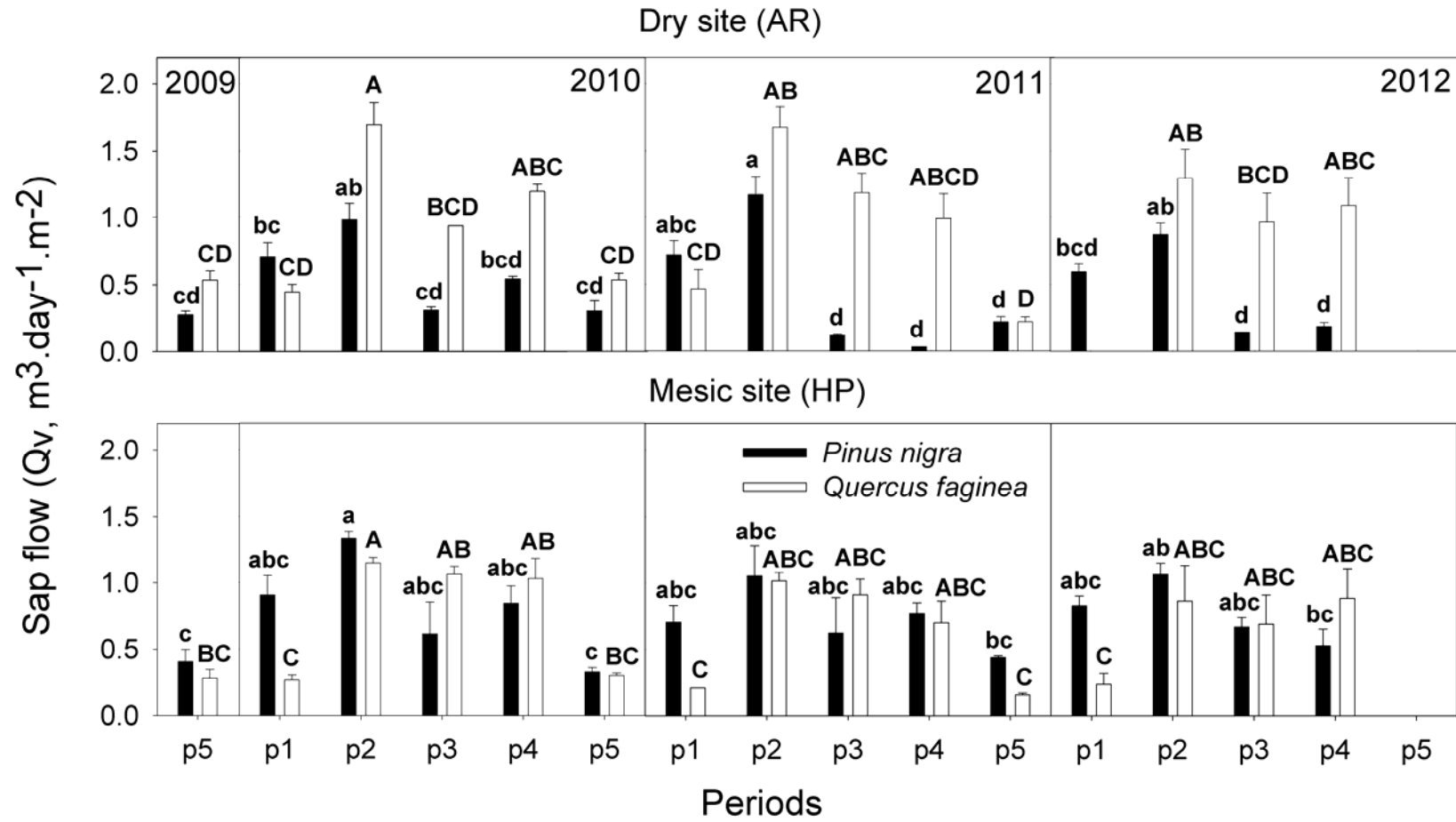












775 Fig.6

