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

Alicia Forner · Ismael Aranda · André Granier · Fernando Valladares

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

Keywords Extreme drought · *Pinus nigra* · *Quercus faginea* · Climate change · Mediterranean forests

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A. Forner (✉) · F. Valladares
Laboratorio Internacional de Cambio Global (LINC-Global), Departamento de Biogeografía y Cambio Global, Museo Nacional de Ciencias Naturales (MNCN), CSIC, Serrano 115 dpdo, 28006 Madrid, Spain
e-mail: Alicia.forner@mncn.csic.es

I. Aranda
Department of Forest Ecology and Genetics, Forest Research Centre, INIA, Avda. A Coruña km 7.5, 28040 Madrid, Spain

A. Granier
UMR 1137 Ecologie et Ecophysiologie Forestières, INRA, 54280 Champenoux, France

F. Valladares
Departamento de Biología y Geología, Escuela Superior de Ciencias Experimentales y Tecnológicas, Universidad Rey Juan Carlos, c/Tulipán s/n, 28933 Móstoles, Spain

Introduction

Water scarcity is one of the most important limiting factors for tree species in Mediterranean ecosystems and is expected to become even more relevant due to the increased temperature and aridity projected for Mediterranean regions (IPCC 2013a). Mediterranean tree species are well adapted to dry periods and have developed different strategies to cope with multiple limiting factors. This explains the complex coexistence observed in Mediterranean ecosystems and promotes high biodiversity levels (Blondel and Aronson 1995). Different traits, such as alternative root systems, water use efficiencies, growth rates, phenologies or stomatal regulation of water use, are associated with different functional strategies to cope with drought (Kneitel and Chase 2004), allowing species coexistence at small spatial scales (Chesson and Huntly 1997). One important strategy for trees to keep relatively high water status during summer drought is developing a deep root system that allows the use of deep water resources that are not available for most plants (David et al. 2007).

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

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

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

Sap flow measurements allow researchers to make inferences about ecological strategies according to species-specific behaviors (Martínez-Vilalta and Piñol 2003; Chirino et al. 2011; Zapater et al. 2012), microclimatic impacts in the functional responses of trees (David et al. 2007) and influences in forest water use of structure and age of trees (Lagergren and Lindroth 2004; Forrester et al. 2010; Gyenge et al. 2011; Drake et al. 2012). Sap flow is also related with tree growth, as the latter results from net carbon balance, which is always in compromise with water consumption. Moreover, carbon uptake is functionally coupled with the control of water loss performed by stomatal regulation of transpiration, establishing a species-specific trade-off between water use and growth that is modulated at different time scales. Therefore, water use and growth are considered to be highly integrated in the overall functional response of plants under water-limiting conditions. Both response variables (water use and growth) have been treated thoroughly in previous studies, but few studies have focused on the interaction of both factors as an important way to understand tree response to climate change, with the exception of those inferring water use efficiency from the carbon isotopic signal of plant tissues (e.g., Maysek et al. 2011; Granda et al. 2014; Voltas et al. 2013). Despite the recognition of the importance of the microhabitat for plant performance, little attention has been paid to the role of microclimate on the regulation of tree response to drought (Zweifel et al. 2007) and how it could condition water use and growth depending on the species (Zweifel et al. 2009). All this supports the need for ecophysiological studies of extreme drought events, integrating both water use and growth and exploring how the responses are modulated by local microclimatic conditions.

We carried out a field study of two coexisting tree species, one evergreen (*P. nigra*) and one deciduous (*Q. faginea*), with two contrasting plant water strategies (isohydric and anisohydric, respectively) experiencing the most intense water stress event over the last half century. We determined accumulated basal area increment and sap flow over the period, spring growth rate and beginning and duration of sap flow and growth as key and interrelated response variables at the whole plant level that depict main trade-offs determining plant fitness in dry ecosystems. The main objective of this study was to quantify the effects of such extreme drought in growth, phenology and water use of both species. We also tested the importance of local microclimatic conditions for modulating the impacts of extreme drought events by comparing two slightly different sites. Specifically, we hypothesized that: (1) unusually dry periods have a strong impact on both species becoming disproportionally adverse at the dry microsite; (2) extreme droughts have a different effect on the functional properties of the study species in relation to the contrasting water strategies of each species, resulting in distinct impacts on growth and water use, and eventual whole plant vulnerabilities to increased frequencies of extreme droughts. We further discuss the implications of these two hypotheses for the coexistence of *P. nigra* and *Q. faginea*, which is maintained in part by differential interplays between water use and growth.

Materials and methods

Study sites

The study was carried out in an area located in Alto Tajo Natural Park, Guadalajara (central Spain). The climate is continental Mediterranean with hot and dry summers and cold winters. Mean annual precipitation and temperature is 490.8 mm and 10.2 °C, respectively, according to climatic data of the closest meteorological station Molina de Aragón (1951–2012, data provided by the Spanish Meteorological Agency, AEMET). Soils are calcisols (World Soil Classification, FAO) from Cretaceous and

Jurassic limestone that rendered shallow and poorly developed soil (Ferrero et al. 2006).

Two sites separated approximately by 8 km were chosen. The Armallones site (AR) (40°46′37″N, 2°19′42″W, 1,079 m a.s.l.) has a west orientation with a 48 % slope and a basal area of 13.7 m^2 ha^{-1}, where *Quercus faginea* (38.7 %), *Pinus nigra* (35.1 %), *Quercus ilex* (25.8 %) and *Juniperus oxycedrus* (0.2 %) coexist as the main woody species. The Huertapelayo site (HP) (40°47′33″N, 2°17′14″W, 907 m a.s.l.) has a north orientation, 68 % slope and a basal area of 11.4 m^2 ha^{-1}. The main woody species are *P. nigra* (62.4 %), *Q. faginea* (35.1 %), *Juniperus phoenicea* (1.6 %) and *Juniperus oxycedrus* (0.9 %).

We randomly selected healthy and fully sun-exposed representative trees with similar DBH (diameter at breast height 1.3 m of height) of black pine, *P. nigra* subsp. *salzmanii* ($n = 8$; 4 in each site) and Portuguese oak, *Q. faginea* [$n = 5$ (AR) and 4 (HP)]. *P. nigra* mean diameters were in the range of 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. faginea*.

Meteorological data and drought intensity

Climatic data were obtained from the closest weather station (at ca. 36 km from the study area), Molina de Aragón (40°50′40″N, 1°53′07″W, 1,063 m a.s.l.) from AEMET (Spanish Meteorological Agency). Seasonal means of rainfall and temperature were calculated for two time series during 1951–2012 and 1970–2012, as a faster rate of change has been observed since the 70s in Spain (Bladé and Castro Díez 2010) and at global scale (Alexander et al. 2006; Bladé and Castro Díez 2010).

Microclimatic conditions were also measured continuously during the study period at the study sites (2009–2012). At each site, we installed a soil moisture sensor (CR10X-ECH$_2$O; Decagon Devices, Inc., Pullman WA, USA) at 70 cm depth to measure relative soil volumetric water content (Θ). Readings of each sensor were recorded every 2 h. Air temperature was recorded every hour using a temperature sensor with an accuracy of ±0.3 °C installed in a dendrometer increment sensor (DRL 26, Environmental Measuring Systems, Brno, Czech Republic) at both sites [$n = 3$ (AR) and 4 (HP)]. Also, we installed a HOBO® (Onset Computer Co., Bourne, MA, USA) weather station at the Armallones site with a rain gauge (RGA-MoXX), temperature and relative air humidity (12-Bit Temperature/RH Smart Sensor), solar radiation (S-Lib-MOO3) and wind speed (Wind Speed Smart Sensor, S-WA-MOO3) sensors. Readings of each sensor were recorded every 30 min with a data logger (HOBO® H21-001; Onset Computer Co.). Air vapor pressure deficit (VPD) and potential evapotranspiration (PET) were calculated following Campbell (Campbell and Norman 1998) and the Penman equation (Penman 1948), respectively.

Drought intensity for the study period was characterized by estimating the daily relative extractable water in the soil (REW). REW values were only calculated for the Armallones site because the required meteorological data for its calculations were not available for the Huertapelayo site. REW was calculated daily as the ratio of available soil water to maximum extractable water. It ranges from 1.0 (field capacity) to 0.0 (permanent wilting point). Water stress is assumed to occur when REW drops below the threshold 0.4 (REW_c), under which soil water becomes limiting for transpiration, and stomatal closure happens for most temperate forest tree species. Radial growth has been observed to cease in forest trees at REWc (Granier et al. 1999). Daily REW was simulated by running the BILJOU© water balance model (Granier et al. 1999) with measurements of daily rainfall, air temperature and relative humidity, global radiation and wind speed from the Armallones meteorological station. BILJOU© also uses stand characteristics: leaf area index (LAI), dates of bud burst and leaf fall for deciduous species and soil properties. LAI was estimated with a LAI 2000 Plant Canopy Analyzer (PCA, LI-COR, Lincoln, NE, USA) in 2012 (data provided by Pollastrini, M). LAI was kept constant over the period of 1961–2012 to check if there was a climatic drift independently of the LAI effect on drought intensity variation. Meteorological data for autumn and winter of 2011 were not available because of storage memory failure. Data gap filling for that period was performed using the Agri4cast database (Institute for Environment and Sustainability, IES, European Commission; http://mars.jrc.ec.europa.eu/mars/About-us/AGRI4CAST). As missing data occurring during the winter, when evapotranspiration is low and soil is at its field capacity, errors in REW calculation were considered negligible. Maximum extractable water in calcisol soils is low due to a high stone content, so we fixed it at 80 mm (according to Gaultier et al. 2000).

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

Growth and sap flow measurements

Plant growth was monitored from September 2009 to October 2012 measuring stem diameter changes at the breast height of the selected trees using automatic dendrometer bands (DRL26, EMS Brno, Czech Republic). A rotary position sensor with a stainless steel tape, which encircles the tree trunk, measured length variations every hour (accuracy 1 μm). The sensor was fixed to the trunk by the strength of the tape without using invasive fixing parts. Dead bark was brushed off before the dendrometers were installed. Data were stored in the same data logger as sap flow measurements. All data were thoroughly revised looking for possible abrupt or unusual jumps due to freezing events or resin, which can impede tape movement. Those data were corrected erasing the unusual jump (>0.1 mm between two records). Basal area increment (BAI) was calculated to obtain the stem increment and calculate growth rates according to: $\mathrm{BAI} = \pi(r_t^2 - r_{t-1}^2)$; where r is the tree radius, and t is the hour of the day (Jump et al. 2006). Accumulated basal area increment per month (BAI$_c$) was calculated by summing the BAI of that month and all previous monthly BAI since the beginning of the study period (September 2009). BAI evolution over study period allows observing differences of growth not only between seasons but also between years, species and sites, giving detailed information of growth patterns. The beginning and duration of the growth period during spring were determined for each tree considering changes in the slope of the BAI evolution over time for both study sites and for the three study years (2010–2012). We considered the end of the spring growth period to be over when the slope of the BAI evolution over time was lower than 5 %. As spring is the main growth season for most of Mediterranean species (Durante et al. 2009) and studies showed that growth of both study species is favored by spring rainfall (Granda et al. 2013), daily spring growth rates (SGR, cm^2 day^{-1}) were calculated. SGR was obtained by dividing BAI for the whole growth period by its duration in days.

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

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

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

Statistical analysis

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

A nonparametric Mann–Whitney U test was used to check significant differences in seasonal T and Θ values between the two study sites. Differences in phenological variables and annual basal area increment (BAI) between years for each species and site were analyzed using a nonparametric Kruskal–Wallis test. These analyses were performed using Statistica 8.0 (StatSoft Inc., Tulsa, OK, USA). A linear regression model was used to assess the temporal evolution of the water stress index over time. Percentiles (5 and 95 %) for water stress index from 1961 to 2012 were calculated to identify unusual water stress over the last 50 years. Differences in accumulated basal area increment between species at each site were analyzed by a linear model. Linear mixed-effects models (LMMs) were used to assess the effect of year (fixed factor) in growth rate (Zuur et al. 2007). Individual trees were considered as random effects. The model was fitted based on a restricted maximum likelihood method using the nlme package (Pinheiro et al. 2007). To test differences in sap flow per unit of basal area between periods (2009–2012), linear models were made for each species and site. Further, we assessed the relationship between REW and spring growth rate and relative sap flow per tree using Spearman's rank correlation coefficients. These analyses were carried out using the R statistical software (version R3.0.1: R Development Core Team 2013, Vienna).

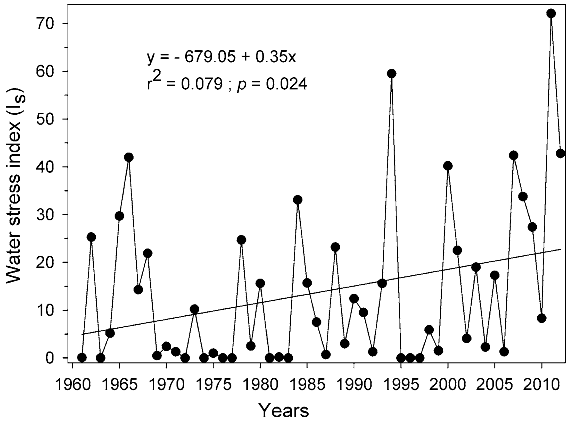

Fig. 1 Evolution of annual water stress index (I_s) for the period 1961–2012. Higher values of the index indicate higher water stress. *Line* represents the fitted linear model

Results

Climate trends and extreme events

Extreme drought events have increased their frequency over the last decade. Extremely high values of water stress (I_s) were found in three years (1994, 2011 and 2012) during the decade 1992–2012 while no extreme values were found between 1961 and 1992. Additionally, there was a significant increase in water stress (I_s) since 1961 ($p = 0.024$). Four of the eight most stressful years for vegetation (water stress index, I_s) over the last 50 years took place over the last 6 years (2007–2012) (Fig. 1). The year 2011 exerted the highest water stress on vegetation over the half century historical record as indicated by the I_s series calculated for 1961–2012 period.

In agreement with increases in water stress during last decade, mean annual decreased by 46.1 mm and temperature increased by 0.6 °C in the last decade (2002–2012), compared with the long-term data series (1951–2012). Summer and spring temperatures of 2009 were unusually high compared with the long-term data (1970–2012) (Online Resource 2). The spring of 2011 was extremely hot, and both summer and winter seasons were unusually dry, which allows

Table 1 Seasonal mean ± SE temperature (*T*) and soil volumetric water content (Θ) of the meteorological sensors installed at both study sites (Sp: spring, Su: summer, Au: autumn and Wi: winter)

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

Total rainfall (*P*) and vapor pressure deficit (VPD) were obtained from the meteorological station located at Armallones site. Potential evapotranspiration (PET) was calculated following the Penman equation. Values between parentheses represent means of total annual rainfall and mean annual temperature for the year indicated 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

+, – means for only 2 months of the season and data not available, respectively

Significant differences in temperature and water soil content between both study sites are indicated with asterisk (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$)

considering 2011 as an extremely dry year. These results were corroborated by comparing the long-term data series 1951–2012. Summer rainfall during 2012 was also slightly lower than expected from the series 1951–2012 (Online Resource 2). The year 2010 can be considered a normal year compared with 2009, 2011 and 2012, since total annual rainfall and mean annual temperatures were the closest to long-term averages. Furthermore, 2010 showed lower water stress index (I_s) compared with 2011 and 2012 (Fig. 1).

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

Due to low PET and therefore low transpiration, relative extractable water of the soil (REW) was close to 1; soil water was near field capacity from late autumn to early spring for all study years (Fig. 2). REW decreased sharply during the late spring and summer of all study years due to the low water holding capacity. Water stress occurred during each summer of the 4 year periods, but its intensity and duration varied among years. The lowest REW level was reached in the summer of 2011, which confirmed that 2011 was the driest year compared with the other study years. Days under water stress (NDWS) were more than two times higher in the dry year (2011) than in the normal year (2010), being 110 and 32 days, respectively (Table 1). The beginning of the water stress period (BEGWS) was advanced over the years due to higher temperatures being reached earlier, being up to 19 days earlier in 2012 than 2010, the normal year. Water stress duration was 2 and a half month longer in 2011 than 2010, which confirmed a more lasting drought during the extreme dry year.

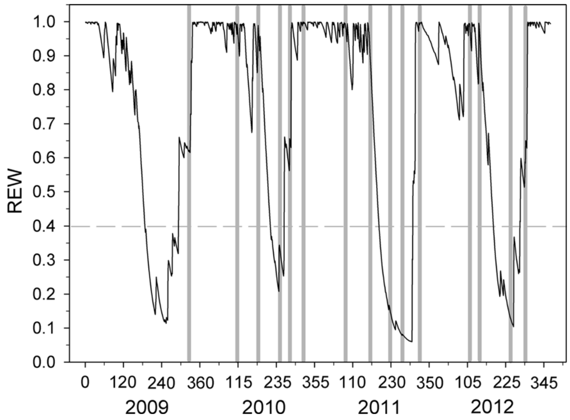

Fig. 2 Daily values of modeled relative extractable water (REW) from the soil of Armallones site since 2009 to 2012 (Julian days). *Dashed line* indicates the critical REW value ($REW_c = 0.4$) at which tree transpiration begins to decrease. *Bars* in *gray* represent periods of sap flow measurements

Spring growth patterns

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

During the spring, the main growth season for the study species, both species showed similar patterns in

Table 2 Day of year (Julian day, mean ± SE) for the beginning of spring growth and its duration (days ± SE). Mean ± SE of annual basal area increment (BAI, cm^2 $year^{-1}$)

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

Data are shown for both study species (*P. nigra* and *Q. faginea*), sites (*AR* Armallones, *HP* Huertapelayo) and years (2010–2012). Significant *p* values are shown in bold

growth rates (SGR) at each site (Fig. 4), although higher rates were found for *P. nigra* during all years. After the exceptionally extreme year (2011), both species decreased their SGR at both sites, decreasing more at the dry site. At this site, reduction in growth was significantly higher for *Q. faginea* (−59.8 %) than for *P. nigra* (−35.9 %), while at the mesic site, higher reduction was found for *P. nigra* [−24.2 %; −16 to 7 % (*Q. faginea*)].

The beginning of spring growth was earlier in the mesic site than in the dry site for both species and in all study years, but only significant results were found for 2012 (Table 2). Moreover, spring growth was advanced significantly in *Q. faginea* starting between 17 (mesic site) and 20 (dry site) days before, during the exceptionally extreme year 2011 compared with 2010. In addition, growth during 2011 lasted between 9 and 28 days more in both species at both study sites. Growth duration was significantly different between years for *P. nigra* at the dry site but not at the mesic site, while *Q. faginea* had significantly different growth duration between years at the mesic site.

Sap flow patterns

Higher seasonality in water use, measured as sap flow, was found at the dry site (AR), especially in *P. nigra*. Moreover, differences between species were accentuated during the exceptionally extreme 2011 year (Fig. 5). *Q. faginea* had highest sap flow rates during the late spring, summer and early autumn at the dry site, while at the mesic site, similar sap flow rates were found for both species. In all study summers (period p3), the lowest sap flow rates were recorded for *P. nigra* at the dry site, reaching values close to zero in 2011 since limited water resources were available due to the extreme drought. Both species showed higher reductions in water use due to the summer drought (period 2 compared with period 3) at the dry site and particularly after the exceptionally extreme year (*P. nigra*: −25.3 %; *Q. faginea*: −22.7 %) (Fig. 5). During 2011 and 2012, *P.* nigra was not able to recover water use after the summer drought (period 3 and 4), indicating that autumn rainfall was not abundant enough to reestablish its sap flow. Looking at the seasonal evolution of the relative sap flow rates, *Q. faginea* showed similar patterns at both sites, while *P. nigra* appeared to be more sensitive to water shortage conditions at the dry site (Fig. 6). During the summer

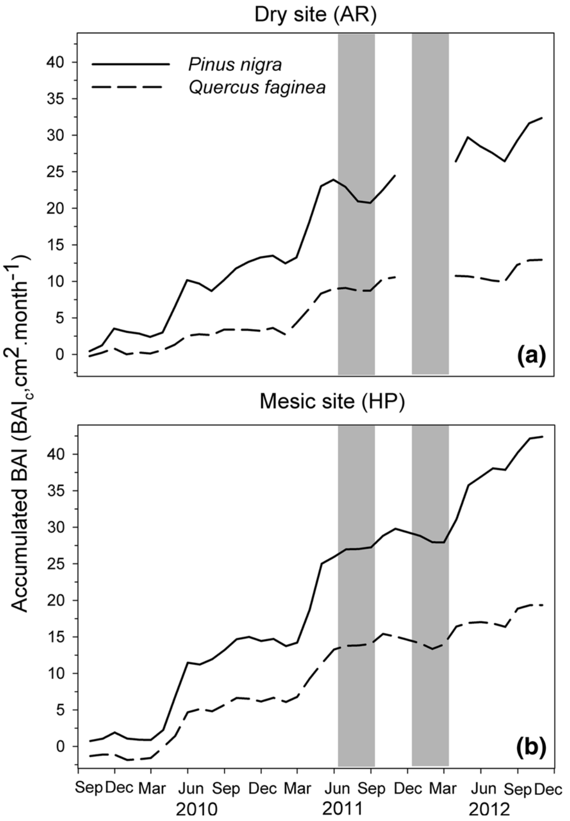

Fig. 3 Mean monthly accumulated basal area increment (BAI$_c$) for the study period 2009–2012 for each species and site [Armallones (**a**) and Huertapelayo (**b**)]. *Bars* in *gray* represent the two unusually dry seasons over the exceptionally dry year 2011, summer and winter, respectively. No available data since December 2011 to March 2012 at the dry site (AR)

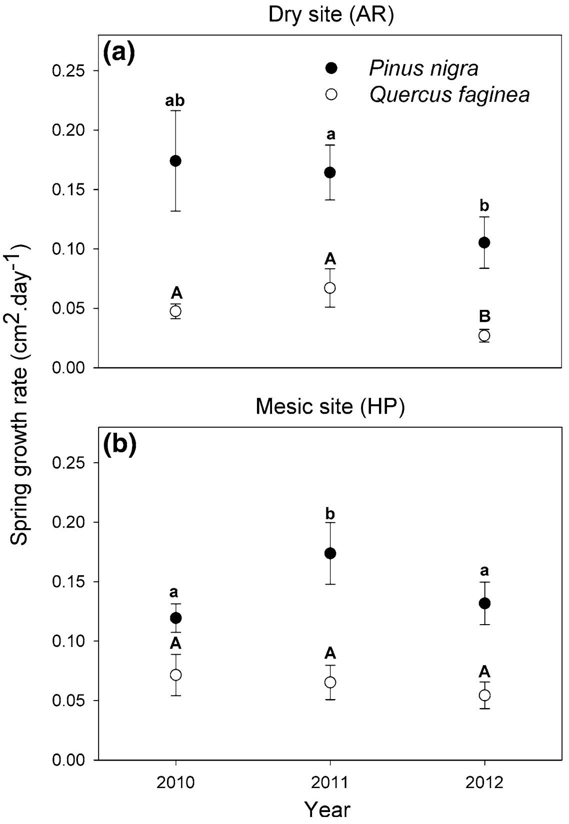

Fig. 4 Mean of daily spring growth rate (cm^2 day^{-1}) for each species, site [Armallones (**a**) and Huertapelayo (**b**)] and study year for the period (2010–2012). *Bars* are standard mean errors unless eclipsed by *symbols*. For each species and site, *different letters* indicate significant differences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

drought, both species decreased water use overall both sites, but the species were more affected at the dry site, decreasing their sap flow by 25–45 % (years range) in *Q. faginea* and 69–90 % in *P. nigra*. Higher reductions in water use were found in the dry year for *P. nigra* but not for *Q. faginea*. At the mesic site, *Q. faginea* was not able to recover its sap flow (period p4) during the exceptionally extreme year but it did over the following year, while the opposite patters were true for *P. nigra*. Relative sap flow (Q_r) was marginally correlated with REW for *P. nigra* at the dry site ($r = 0.829$, $p = 0.058$) but not for *Q. faginea* ($r = 0.257$, $p = 0.658$).

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

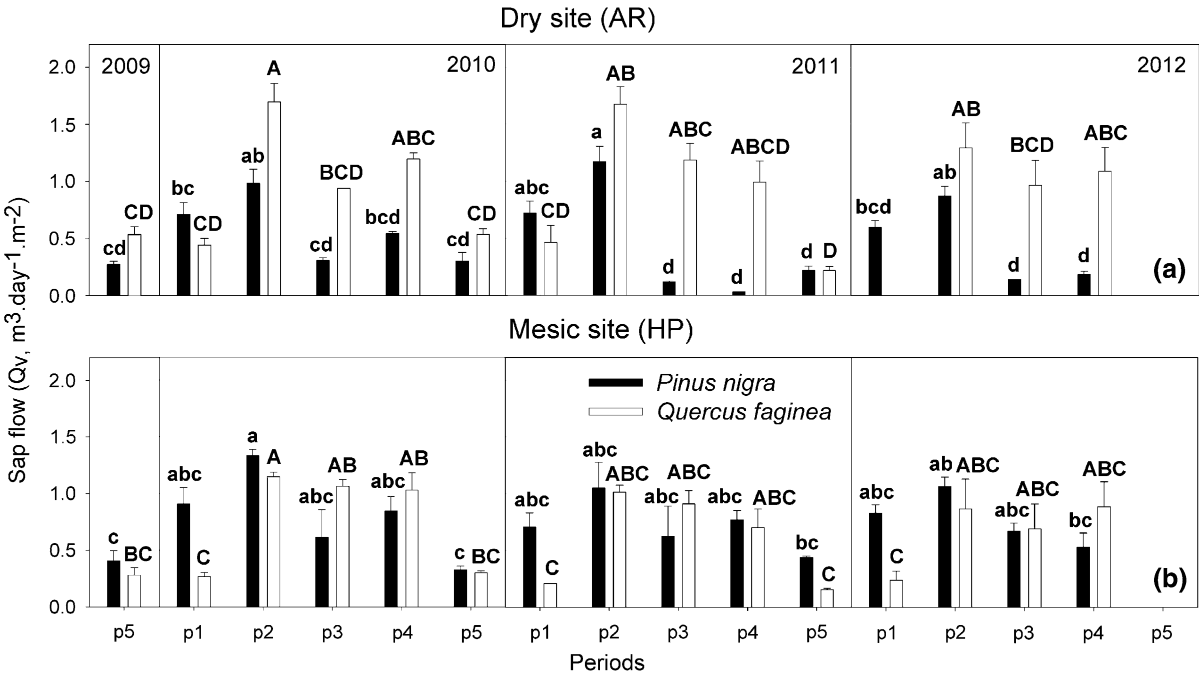

Fig. 5 Mean ± SE of daily mean sap flow per basal area (Q_v, $m^3\ day^{-1}\ m^{-2}$) for each species, site [Armallones (**a**) and Huertapelayo (**b**)] and measurement period (*p1*: beginning of spring water use; *p2*: maximum evapotranspiration during late spring; *p3*: minimum values during the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

Discussion

Our study site experienced an increased aridity due to a 0.6 °C increase in mean annual temperature and a 46.1 mm decrease in annual rainfall over the last decade. This is in agreement with warming trends observed in Mediterranean ecosystems since the 70s, both in the Iberian Peninsula (Bladé and Castro Díez 2010) and at the global scale (IPCC 2013b). Higher occurrence of extreme drought events over the Mediterranean region (Della-Marta et al. 2007) is particularly relevant for forest ecosystems, which are already showing symptoms of decline by water stress worldwide (Allen and Breshears 1998; Allen et al. 2010; Linares and Camarero 2012). The year 2011 was an extremely dry and warm year at our study site, with a severe and long-lasting drought resulting in very low relative extractable water from late spring to early autumn that resulted in the most stressful year over the last half century. This extreme event occurred in 2011 was preceded by another extreme summer drought with unusual high temperatures during summer just 2 years before, in 2009, supporting an increased frequency of extreme droughts in the area.

Reductions in the growth of Mediterranean trees have been associated with decreases in annual rainfall since the 70s (Sarris et al. 2007). This pattern was confirmed for *P. nigra* and *Q. faginea* at our study site, not only by our detailed 3-year study but also by dendrochronological studies (Granda et al. 2013). The evergreen species *P. nigra* showed not only a higher basal area increment per year but also higher spring growth rates than the deciduous *Q. faginea*, which is in agreement with a previous dendrochronological study at the site (Granda et al. 2013). This is in agreement with the higher intrinsic water use efficiency of *P. nigra* (Granda et al. 2014). The effects in growth due to the unusual drought were noticeable the year after the exceptionally dry year. This one-year delay in growth response to drought is based on the reported dependence of growth on previous climatic conditions (Sarris et al. 2007; Morán-López et al. 2014).

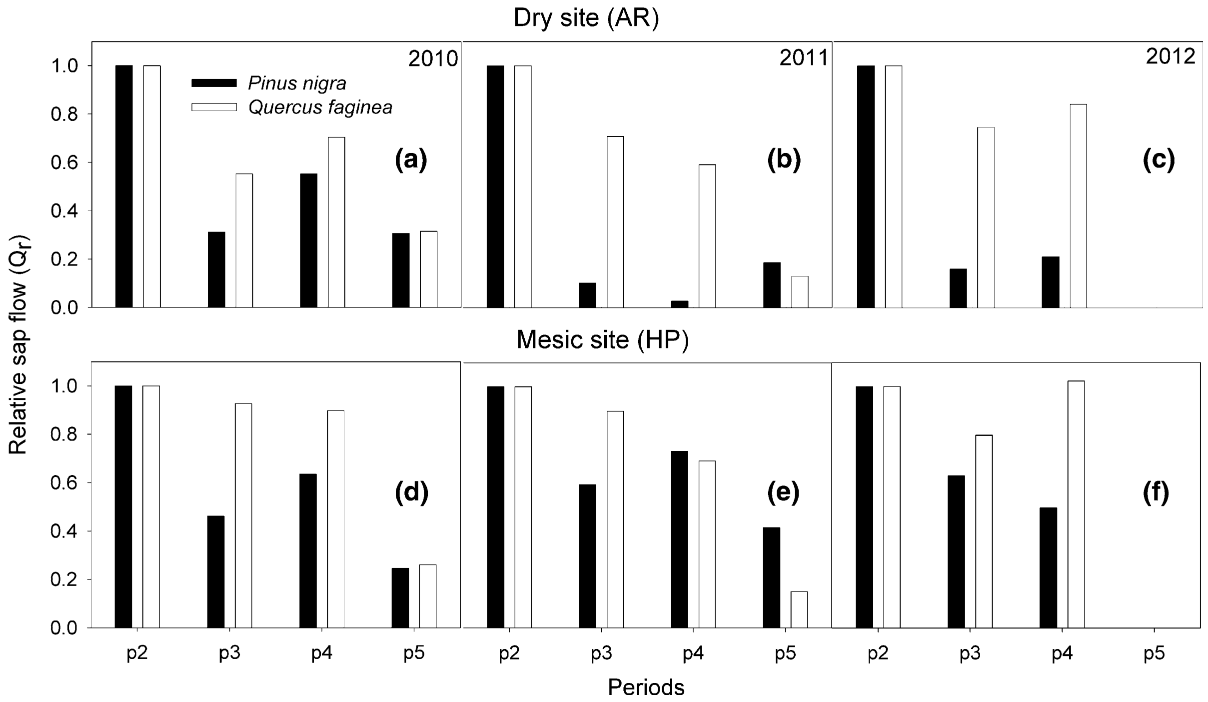

Fig. 6 Relative sap flow (Q_r) obtained from dividing mean daily sap flow per basal area by the mean maximum sap flow measured that year (period 2, *p2*) and calculated for each species, year and site [Armallones (**a**–**c**) and Huertapelayo (**d**–**f**)]. Periods are considered as following: *p2*: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

Reductions in annual growth the year after the extreme drought in relative terms were higher for *Q. faginea* than for *P. nigra*. Opposite results were found by Granda et al. (2013), where *P. nigra* experienced the sharpest growth decline due to the extreme drought events compared with the coexisting *Q. faginea*. These different results may be explained by the different approaches followed in each study to determine tree growth; while our study focused on processes and mechanisms involved in the responses to one unique extreme event, Granda et al. (2013) followed a dendrochronological approach over a time series with many dry and mesic years. However, and in agreement with Granda et al. (2013), *P. nigra* was able to recover after the extreme event while *Q. faginea* was not, suggesting a higher resilience of the former.

As expected, the impact of the extreme drought on growth was more adverse at the dry site for both species, observing a 60 % reduction in spring growth rate for *Q. faginea* and 36 % for *P. nigra* at the dry site, while decreases at the mesic site were 17 and 24 %, respectively. Daily stem fluctuations are a combination of both water storage changes and growth processes (Steppe et al. 2005; Zweifel et al. 2005). In the Mediterranean region, water storage during spring increases significantly due to the abundant rainfall, resulting in increases in stem size due to processes. However, growth processes are still relevant at the daily scale during spring (Drew and Downes 2009) since growth is greater when water is not limiting, which usually occurs during spring for Mediterranean trees (Durante et al. 2009). Some studies have observed high dependency between growth and water availability (e.g., Ibáñez et al. 1998; Ogaya and Peñuelas 2007; Zapater et al. 2012), which is correlated with water use by plants. Water use was assessed through sap flow measurements since it is considered an overall estimator of the water transpired by trees (Köstner et al. 1996; Burgess 2006; Poyatos et al. 2007), and therefore, as an indicator of tree performance in terms of transpiration control. The study species followed the typical

Table 3 Day of year (Julian day, mean ± SE) for the beginning and maximum of spring sap flow and its duration (days ± SE)

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

Data are shown for both study species (*P. nigra* and *Q. faginea*), sites (*AR* Armallones, *HP* Huertapelayo) and years (2010–2012). Significant *p* values are shown in bold

Mediterranean transpiration patterns, which peak in late spring and strongly decrease during the summer drought (Tognetti et al. 1998). *P. nigra* was able to better use soil moisture in late winter and early spring, while *Q. faginea* was leafless and with no sap movement for most of this time. As expected from its deep root system and its anisohydric strategy, *Q. faginea* showed higher and more sustained sap flow rates than *P. nigra*. Our ongoing field research on both species is showing different predawn and mid-day water potentials (unpublished data) that support the higher water availability for *Q. faginea*, particularly during the summer.

Despite the fact that both species were sensitive to water stress and decreased their water use during dry periods, stronger reductions in transpiration were found in *P. nigra*, an isohydric species that closes stomata during drought. By contrast, *Q. faginea*, a water spender in comparison with *P. nigra*, was able to sustain an active sap flow rate longer over the summer even at the dry site. The pattern observed in *Q. faginea* has been considered characteristic of higher drought tolerance (McDowell 2011). As expected and in agreement with growth results, the impact of the extreme drought on transpiration was higher at the dry site and in *P. nigra* when compared with *Q. faginea* (90 vs. 45 %). These results were noticeable due to the rather minor differences in annual temperature and soil volumetric water content at the end of the summer between the two sites (from 0.3 to 0.9 °C and from 0.05 to 0.06 $m^3\ m^{-3}$, respectively). Our results, thus, highlight the important role of microclimatic conditions of species responses to drought.

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

Considering all our results, we suggest that under more frequent and extreme drought events, *Q. faginea* could experience hydraulic failure, combined with eventual reductions in autumn rainfall; this could compromise species recovery and significantly reduce its growth. Although *P. nigra* is also prone to starvation during intense drought events, we suggest that its higher water use efficiency (Granda et al. 2014) may confer competitive advantages over *Q. faginea*. Intrinsic water use efficiency increased during unfavorable years in both species while growth decreased (Granda et al. 2014). Therefore, despite the fact that growth and intrinsic water use efficiency were higher for *P. nigra*, growth reductions during the extremely dry year were higher for *Q. faginea* (Granda et al. 2013; 2014). Thus, we suggest that *P. nigra* may perform better than *Q. faginea* at our study site under a scenario with more frequent and intense extreme droughts. However, due to the complexity of species responses to drought events and as many factors are involved in the overall impact of extreme climatic events over the life cycle of a tree, more studies should address how species-specific responses could lead to future shifts in community composition. Nonetheless, the different responses observed between *P. nigra* and *Q. faginea* may lead to changes in dominance and in community composition, and dynamics presumably favor *P. nigra*. Mild autumn and winter seasons are likely to increase transpiration at the community level if evergreen species, such as *P. nigra*, dominate canopy composition in detriment of deciduous species, such as *Q. faginea*. This is supported by Brantley et al. (2013), who found that an increase in deciduous species decreased evapotranspiration during winter time. As a consequence of this eventual replacement of the deciduous by the evergreen species, more water resources will be used by the community over the year, which in combination with increases in aridity and evaporative demand under increasing temperatures (Nadal-Sala et al. 2013) could have important and negative consequences at the basin level (Otero et al. 2011), therefore affecting the water cycle at large spatial and temporal scales (Brantley et al. 2013).

Decreases in species growth and changes in forest stand composition due to climate change can deeply affect carbon cycle, decreasing carbon uptake and affecting the role of forests as CO_2 sinks (Grace 2004). In fact, models have simulated a decrease in net primary production in Iberian Peninsula forests after the mid-twenty-first century due to increases in aridity in combination with higher respiration rates and evaporative demand (Nadal-Sala et al. 2013). As a result, forests could even change from their actual role as carbon sinks to carbon sources (Nadal-Sala et al. 2013).

In conclusion, despite the fact that the species experienced the most stressful drought over the last half century and that species performance was significantly affected by this extreme event, in terms of growth and water use, the trees studied did not exceed their tolerance thresholds at our study site as suggested by the lack of mortality after the extreme event. Therefore, the high resilience observed for these Mediterranean species could be counteracting the impact derived from an extreme drought event. Studies considering different time scales, involving mechanistic understanding of species responses to extreme events and monitoring other variables such as decline or mortality, are needed to make sound predictions of species shifts and dynamics, and its implications for future ecosystem functioning.

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