

Rainfall exclusion and thinning can alter the relationships between forest functioning and drought

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Summary

- Increasing drought caused by the ongoing climate change, and forest management by thinning that aims at mitigating its impact, may modify the current relationships between forest functions and drought intensity and preclude our ability to forecast future ecosystem responses.
- We used 15 yr of data from an experimental rainfall exclusion (−27% of rainfall) combined with thinning (−30% stand basal area) to investigate differences in the drought–function relationships for each component of above-ground net primary productivity (ANPP) and stand transpiration in a Mediterranean *Quercus ilex* stand.
- Rainfall exclusion reduced stand ANPP by 10%, mainly because of lowered leaf and acorn production, whereas wood production remained unaffected. These responses were consistent with the temporal sensitivity to drought among tree organs but revealed an increased allocation to wood. Thinning increased wood and acorn production and reduced the sensitivity of standing wood biomass change to drought. Rainfall exclusion and thinning lowered the intercept of the transpiration–drought relationship as a result of the structural constraints exerted by lower leaf and sapwood area.
- The results suggest that historical drought–function relationships can be used to infer future drought impacts on stand ANPP but not on water fluxes. Thinning can mitigate drought effects and reduce forest sensitivity to drought.

Introduction

Forest ecosystems largely contribute to climate-change mitigation as they represent *c.* 50% of the terrestrial carbon (C) sink and store more than twice the amount of C present in the atmosphere (Bonan, 2008; Pan *et al.*, 2011; Anderegg *et al.*, 2013a), and forest transpiration influences the global water cycle substantially (Schlesinger & Jasechko, 2014). However, drought and heat-driven forest mortality (Allen *et al.*, 2010; McDowell *et al.*, 2016), dieback (Carnicer *et al.*, 2011) and productivity decline (Ciais *et al.*, 2005; Zhao & Running, 2010) have been evidenced in the last decades and are expected to become more frequent under current climate change (McDowell *et al.*, 2016). Such declines in forest functioning may reduce the strength of forest C sink and have large impacts on the water cycle, triggering positive feedbacks to climate warming and altering the provision of wood and ecosystem services by forests (Bonan, 2008; Anderegg *et al.*, 2013a; Nabuurs *et al.*, 2013).

Forecasts of future ecosystem responses to increasing drought are generally based on past relationships between indices of drought stress and ecosystem functioning. Such relationships arise either from spatial comparisons of sites across climatic drought gradients or from within-site temporal variations of ecosystem functions (Estiarte *et al.*, 2016; Knapp

et al., 2017). Spatial comparisons reflect the long-term influence of climate on ecosystem structure and functions, while temporal comparisons give insights into the ecosystem sensitivity to shorter-term variations in climate. Because spatial comparisons encompass differences in soil, vegetation type and functional traits, they generate much steeper relations between ecosystem functioning and drought than do the temporal relationships (Huxman *et al.*, 2004; Sala *et al.*, 2012; Biederman *et al.*, 2016; Estiarte *et al.*, 2016). By contrast, temporal relationships capture the ecosystem plastic responses to drought, such as reduced gas exchange, reduced growth and increased water-use efficiency (WUE), which are mostly reversible and recover when water availability increases (Linares & Camarero, 2012; Belmecheri *et al.*, 2014; Lempereur *et al.*, 2015; Skelton *et al.*, 2017). However, as rapid and unprecedented climate change may locally increase drought intensity and duration beyond the bounds of past variations, we still do not know whether ecosystem responses will continue to follow the past temporal relationships with drought or if they will develop towards new trajectories. Experiments using rainfall exclusion devices are particularly important to investigate these questions, as they provide insights into mid-term responses of ecosystems to aggravated drought (Wu *et al.*, 2011; Beier *et al.*, 2012; Grossiord *et al.*,

2018). New trajectories of response to drought may arise from drought legacy effects that have long-lasting consequences for ecosystem functioning after the release of water stress (Sala *et al.*, 2012; Anderegg *et al.*, 2015). These effects can be caused by the loss of plant hydraulic conductivity, the loss of plant parts (leaf shedding and branch dieback) or the mortality of some individuals (Anderegg *et al.*, 2013b; Reichmann *et al.*, 2013; Skelton *et al.*, 2017). Conversely, trees may develop physiological, anatomical or morphological acclimations enabling them to maintain better functioning during drought (Maseda & Fernández, 2006), for instance through osmotic adjustments to maintain leaf turgor (Bartlett *et al.*, 2012), increased C allocation to roots (Martin-StPaul *et al.*, 2013) or reduction of the transpiring leaf area (Limousin *et al.*, 2009). These acclimations, however, often come at the cost of reduced functioning under well-watered conditions, resulting in a lower sensitivity to drought (Limousin *et al.*, 2013; Plaut *et al.*, 2013; Zhou *et al.*, 2016). Many of these responses to chronic drought imply changes in C allocation among organs, such as vegetative vs reproductive, above-ground vs below-ground, or leaf vs wood (Maseda & Fernández, 2006; Poorter *et al.*, 2012; Pulido *et al.*, 2014). Studying the interannual relationships between drought and ecosystem functions within rainfall exclusion experiments can therefore help to reveal new trajectories arising from drought legacies or acclimations (Estiarte *et al.*, 2016). If experimental drought impacts on ecosystem functions are merely plastic and reversible, then we would expect the temporal relationships with drought to be similar in control and rainfall exclusion treatments. By contrast, drought legacies or acclimations to drought should be manifested by a change in intercept or slope of the drought–function relationship.

In many developed countries, forest ecosystems have experienced a strong densification as a result of land abandonment, reduced forest management, forest protection and fire-fighting policies (Nabuurs *et al.*, 2003; Linares *et al.*, 2009; Dolanc *et al.*, 2013). Increased competition is a major constraint for forest dynamics and productivity (Gómez-Aparicio *et al.*, 2011; Zhang *et al.*, 2015) and often exacerbates drought impacts (Linares *et al.*, 2009; Vayreda *et al.*, 2012; Young *et al.*, 2017). Reducing stand density by thinning usually decreases drought stress by a reduction of rainfall interception and competition for water among trees (Bréda *et al.*, 1995; Giuggiola *et al.*, 2015). Thinning is therefore increasingly advocated to reduce forest vulnerability to drought (Allen *et al.*, 2010; Kerhoulas *et al.*, 2013; McDowell & Allen, 2015; Sohn *et al.*, 2016; Vilà-Cabrera *et al.*, 2018). Conversely, trees in thinned stands may be more sensitive to increasing drought stress, because alleviation of water stress by thinning may drive opposite changes to those expected in response to drought, such as increased transpiration demand by the crown, increased leaf area per sapwood area or decreased WUE (McDowell *et al.*, 2003, McDowell *et al.*, 2006; Giuggiola *et al.*, 2013; Mausolf *et al.*, 2018). On the one hand, changes in hydraulic architecture that follow thinning may increase the drought vulnerability of thinned stands (D'Amato *et al.*, 2013; Sohn *et al.*, 2013; Bennett *et al.*, 2015) and result in trees with a

faster growth but also a higher sensitivity to drought stress (McDowell *et al.*, 2006). On the other hand, a lower vulnerability to extreme, punctual drought events has been seen in thinned stands across a variety of forests and species (Bottero *et al.*, 2016; Sohn *et al.*, 2016). Dendrochronological studies on changes in tree-level sensitivity to drought stress after thinning have brought contrasting results, with trees growing in thinned stands showing either higher (McDowell *et al.*, 2006; Gea-Izquierdo *et al.*, 2009; Mausolf *et al.*, 2018) or lower (Misson *et al.*, 2003, 2011; Martín-Benito *et al.*, 2010; Guillemot *et al.*, 2015) sensitivity to interannual drought. Most studies on drought and thinning interactions focused on tree growth and mortality, but much less attention has been paid to stand-level growth (but see Bottero *et al.*, 2016; Gleason *et al.*, 2017) or transpiration (but see del Campo *et al.*, 2019), and to our knowledge no study has addressed the combined effect of drought and thinning on total above-ground primary productivity. At the stand level, the consequences of thinning for ecosystem C and water cycles and their responses to drought thus remain poorly understood (Dore *et al.*, 2012; Ameztegui *et al.*, 2017; Lechuga *et al.*, 2017).

In this study, we use 15 yr of data from a combined rainfall exclusion and thinning experiment in a *Quercus ilex* L. stand to quantify the changes in above-ground primary productivity, water use and sensitivity to interannual water stress fluctuations. We hypothesized that rainfall reduction would decrease stand productivity and increase stand-level WUE, whereas thinning would have the opposite effects. Besides, we hypothesized that rainfall reduction would decrease the sensitivity of these functions to interannual drought stress fluctuations, whereas thinning would increase it.

Materials and Methods

Experimental site

The experiment was conducted in southern France (35 km northwest of Montpellier), on a flat area in the Puéchabon State Forest (43°44'29"N; 3°35'46"E, 270 m asl). This forest has been coppiced for centuries with clear cuts every *c.* 25 yr, until the last clear cut in 1942. The evergreen *Q. ilex* L. forms a dense canopy with a height of *c.* 5.5 m, a mean basal area of 30 m² ha⁻¹ and a density of *c.* 6000 stems ha⁻¹. The evergreen species *Buxus sempervirens*, *Phyllirea latifolia*, *Pistacia terebinthus* and *Juniperus oxycedrus* compose a sparse understorey shrubby layer with *c.* 25% cover. The bedrock is a hard Jurassic limestone and the soil is extremely rocky with *c.* 75% of stones and rocks in the top 0–50 cm and 90% below. The stone-free fraction of the soil within the 0–50 cm layer is a homogeneous silty clay loam (38.8% clay, 35.2% silt and 26% sand). The area has a Mediterranean-type climate with a mean annual temperature of 13.2°C (on-site meteorological station, 1984–2017), the coldest month being January (5.5°C) and the hottest July (22.9°C). The mean annual precipitation is 910 mm with a range of 550–1549 mm (1984–2017). Rainfall mainly occurs during autumn and winter with *c.* 80% between September and April.

Experimental design: rainfall exclusion and thinning experiments

In March 2003, a factorial combination of throughfall exclusion and thinning treatments was set up on three 20 × 20 m replicated blocks located 200 m apart one from the other. Each block comprises four treatments applied on a 10 × 10 m plot: control, throughfall exclusion (hereafter 'dry'), thinned, and thinned with throughfall exclusion (hereafter 'thinned dry'). In these plots, stems with a diameter at breast height (DBH) > 2 cm were individually tagged and their DBH was measured before and after treatment application in 2003. For the throughfall exclusion treatment, half of the block was equipped with parallel 14 m long and 0.19 m wide PVC gutters hung below the canopy with a slope, between 1 m and 2 m height, so as to cover 33% of the ground area under the tree canopy. Taking into account interception and stem flow, the net input of precipitation was reduced by 27% compared with the control plots (Limousin *et al.*, 2008). On the other half of the blocks, identical gutters were installed upside down to homogenize albedo and understorey microclimate without reducing precipitation inputs. Thinning was applied from below on half the plots by removing 30% of the initial plot basal area (27% of *Q. ilex* basal area; Table 1). Dead, diseased and suppressed stems were felled and the understorey cleared. One to four stems were cut on multistemmed clumps, in order to leave the larger stems. Other species than *Q. ilex* represented, on average, 3% of the basal area so they were neglected in the following analyses. After thinning, thinned plots had a 44% lower stand density and a 24% higher mean DBH compared with unthinned plots (Table 1), whereas these parameters did not differ between throughfall exclusion and control plots. Measures of predawn water potential performed on a subsample of trees confirmed that the rainfall exclusion treatment increased tree water stress, whereas thinning decreased it (Rodríguez-Calcerrada *et al.*, 2011).

Estimation of stand above-ground net primary productivity (ANPP), mortality and standing wood biomass change

Stem DBH was inventoried every year in winter for all the stems with a DBH > 2 cm. Stem DBH was converted into wood

Table 1 Characteristics of the holm oak stand in the different treatments before and after thinning (early 2003).

	<i>n</i> (stems ha ⁻¹)	Basal area (m ² ha ⁻¹)	Mean DBH (cm)
Before thinning			
Control	5933 ± 874	24.9 ± 0.9	6.9 ± 0.6
Dry	6433 ± 546	29.8 ± 1.7	7.2 ± 0.2
Thinned	6233 ± 1071	30.6 ± 4.9	7.3 ± 0.4
Thinned dry	7330 ± 689	30.9 ± 3.6	6.8 ± 0.5
After thinning			
Thinned	3300 ± 400	22.8 ± 3.4	9.0 ± 0.2
Thinned dry	3600 ± 155	22.5 ± 2.2	8.6 ± 0.4

Mean ± SE; *n* = 3 plots per treatment. DBH, diameter at breast height.

biomass (stem and living branches) using an allometric equation calibrated on the study site (Rambal *et al.*, 2004): Biomass (g C) = 92 × DBH^{2.171}. Wood production was calculated by summing annual biomass increment of the trees. From the stem inventories, we also computed annual stand mortality rates and the standing wood biomass change, which is the difference in living wood biomass between two consecutive years and integrates both tree mortality (loss of standing wood biomass) and growth.

Litterfall was collected monthly in 121 traps per plot placed regularly on a grid over the gutters at a height of 2 m. Litter traps represented a total area of 1.1 m² per plot. Litterfall was separated into leaves, wood, flowers and acorns, oven-dried at 60°C for 3 d and weighted. Annual litterfall was calculated for the years 2004–2017 as the sum of monthly litterfall and expressed as g C m⁻² using a conversion factor between dry mass and C of 0.48.

Above-ground net primary production was calculated as the sum of wood production, leaf production, and the litterfall of woody debris, flowers and acorns, neglecting volatile organic compound emissions and losses to consumers (Clark *et al.*, 2001). We estimated the leaf ANPP of a given year by considering that 20% of the leaves produced during this year fall before 1 yr (between September and March) and 80% during the following year. These proportions were derived from demographic analyses conducted on the experimental site (Limousin *et al.*, 2012).

Stand transpiration and WUE

Stem sap flow was continuously monitored on six trees per treatment within one of the blocks from 2004 to 2012. Sampled trees ranged from 7 to 16 cm in diameter (DBH), corresponding to a sapwood depth of 17–45 mm, and tree size distribution and mean diameter were similar in all treatments. Sap flow was monitored with 20-mm-long constant heat thermal dissipation probes constructed according to Granier (1987). All sensors were installed on the north side of trees to avoid direct solar heating, and shielded from rain and radiation with aluminum reflectors. Probe pairs were inserted radially into the stem of each tree at breast height after removing the bark to expose the outer surface of sapwood. The vertical separation between probes was 10 cm. The upper probe was heated by a constant current, whereas the lower probe was unheated and remained at trunk temperature. Half-hourly means of temperature difference between the probes were recorded by data loggers (Campbell Scientific Ltd, Shepshed, UK). Because the species studied is diffuse-porous, sap flux density was assumed to be uniform over the entire sapwood depth (Martínez-Vilalta *et al.*, 2003; David *et al.*, 2007). However, as calculation procedures were similar in all treatments, any error linked to this assumption would tend to be systematic and should not affect our comparative analysis in time and between treatments. Sap flux density was calculated using the empirical equation of Granier (1987), and taking the absolute maximum temperature difference over the preceding night (Rabbel *et al.*, 2016). Missing data for a given tree were gap-filled using a correlation with the mean of the other sensors of the treatment during the overlapping period (Pearson correlation coefficient ranged

from 0.78 to 0.96). Tree transpiration was scaled to the stand level by multiplying the sap flux density by the conducting sapwood area per unit ground area. Sapwood area was estimated by an allometric relationship calibrated on the study site (Limousin *et al.*, 2009): sapwood area (cm^2) = $0.363 \times \text{DBH}^{2.149}$. Sapwood area per unit ground area was calculated annually using the mean of the three blocks per treatment. Annual transpiration (E) was calculated as the sum of daily stem flow and expressed per unit ground area (mm yr^{-1}).

Stand-level WUE (g C mm^{-1}) was defined as the ratio between stand ANPP and transpiration. In order to take into account the uncertainty in both stand ANPP and transpiration estimates, we calculated the mean WUE and SE by a bootstrapping procedure. For each treatment and year, we created a random sample of transpiration estimates with replacement (E^*), a random sample of ANPP estimates (A^* , with the same length) and calculated the WUE by dividing A^* by E^* . This procedure was repeated 1000 times for each treatment and year combination and used to assess the mean and SD of WUE.

Meteorological data and drought quantification

Meteorological data were collected on the study site in a clearing < 200 m away from the experimental plots. Precipitation was measured with a tipping bucket rain gauge calibrated to 0.2 mm per tip and placed 1 m above the ground surface; air temperature and net radiation were recorded half-hourly at 2 m above the ground surface. To characterize annual and seasonal drought we used the difference between precipitation and potential evapotranspiration calculated with the Priestley–Taylor formula (hereafter $P - \text{PET}$, in mm). Precipitations and $P - \text{PET}$ were summed annually, for spring (April–June), summer (July–September) and autumn (October–December). For the dry treatments, we applied a 27% reduction of incoming precipitations (Limousin *et al.*, 2008).

Statistical analyses

We first tested rainfall exclusion and thinning treatment effects on stand average functions: wood, acorn and leaf production, ANPP, mortality, wood biomass change, transpiration and WUE. For all variables related to productivity, we used a linear mixed model with year and block as random effects and a correlation structure to account for repeated measures. For stand transpiration, year and tree sampled for sap flow measurement were included as random effects. For WUE, at each iteration of the bootstrapping procedure, we computed a t -statistic (t^*) for each pair of treatments. The probability of rejecting the null hypothesis of equality of means was computed as the proportion of t^* exceeding the threshold taken from a Student law (1.6254 at level 0.05).

The relationships between drought indexes (annual, spring, summer and previous year $P - \text{PET}$) and mean stand functions were then analyzed by linear models including drought indexes separately, rainfall exclusion and thinning treatments as covariates and all interactions. Model assumptions of normality and

homoscedasticity were checked through diagnostic plots, and annual mortality rates and acorn production were log-transformed. The model with the best empirical support was selected by minimizing the corrected Akaike information criterion for small sample size using the R package MUMIN (Bartoń, 2018). The percentage of variance explained by each predictor was assessed with the R package RELAIMPO (Grömping, 2006). Finally, we tested for temporal trends in treatment effects for the functions for which we had data for 15 yr consecutively. Treatment effects were calculated each year as the difference between the treatment mean and the control mean. Temporal trends in treatment effects were tested through linear models with years since the beginning of the experiment as explanatory variable. Treatment effects on drought–function relationships and temporal trends were also tested with mixed models including block as a random factor, except for water-related variables that were not assessed in each plot. These analyses yielded similar estimates and are provided as Supporting Information (Tables S1, S2; Fig. S1). All analyses were performed using the R software v.3.4.3 (R Core Team, 2017).

Results

Environmental conditions and experimental drought

Annual precipitation during the study period was 936 mm on average (range 614–1276 mm), not differing from the long-term site average (910 mm). The rainfall exclusion treatment excluded, on average, 253 mm yr^{-1} (166–345 mm). Precipitations were generally lower than PET on an annual basis, except in 2003, 2008 and 2014, and always lower than PET in spring (Fig. S2). Spring drought was particularly marked in 2006 and 2011 whereas summer drought was stronger in 2009, 2010 and 2017. Mean annual temperature was 13.7°C on average and varied between 12.9 and 14.4°C. The temperature of the warmest month was 23.6°C on average, and was particularly high in 2006 (26.4°C).

Stand ANPP

Stand ANPP was lowest in 2006 for all treatments and peaked in 2007 (unthinned) or 2008 (thinned), ranging from 125 g C m^{-2} in the dry treatment in 2006 to 322 g C m^{-2} in the thinned treatments in 2008 (Fig. S3). Stand ANPP was highly correlated with wood production ($r=0.7$). Rainfall exclusion reduced stand ANPP by 11% ($P<0.001$) and thinning increased it by 7% ($P=0.02$) with no interaction between these factors ($P=0.8$; Fig. 1a; Table S3). Stand ANPP was correlated with spring $P - \text{PET}$ (explained variance of 44%), with a higher intercept in the thinned treatments (explained variance of 3.5%; Figs 2a, 3; Table S4). Moreover, the dry treatment effect on ANPP exhibited an increasing trend over time (Fig. 4) which was not detected in thinned stands or for the different ANPP components (Fig. S4).

Wood production ranged from a minimum of 14 g C m^{-2} across all treatments in 2014 to a maximum of 132 g C m^{-2} for

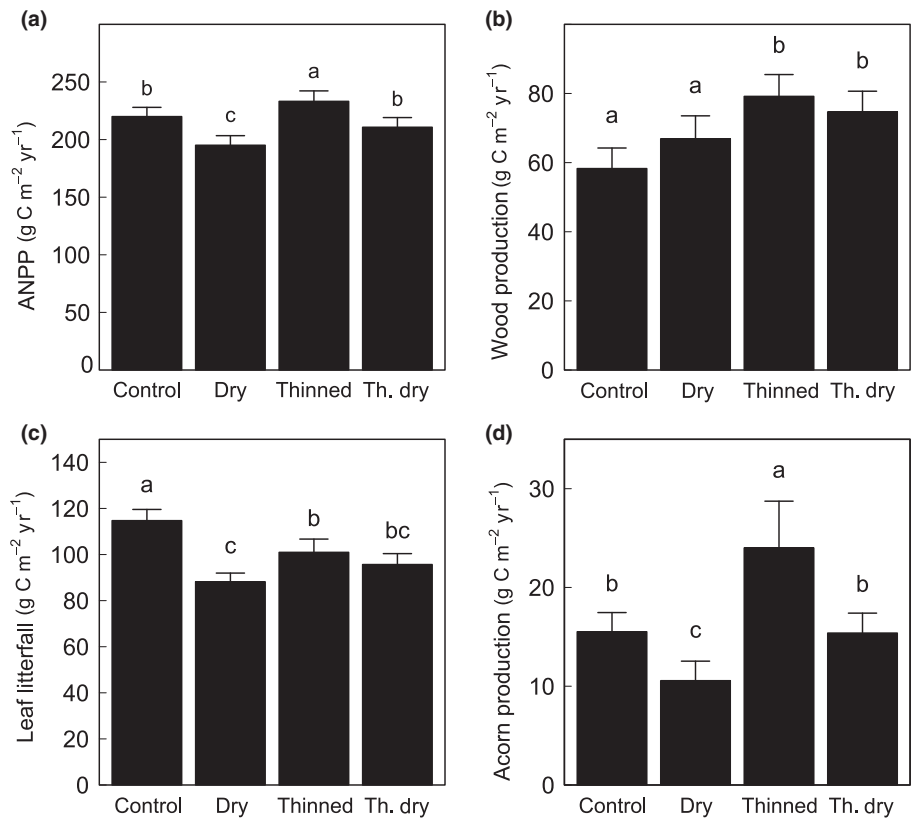


Fig. 1 Above-ground net primary productivity (ANPP) (a), wood production (b), leaf litterfall (c) and acorn production (d) of a *Quercus ilex* stand according to rainfall exclusion and thinning treatments. Total ANPP is calculated as the sum of annual stem, leaf, acorn, flower and branch production. Data are means \pm SE over 14 yr; different letters denote significant differences between treatments (Supporting Information Table S3). Th. dry, thinned dry treatment.

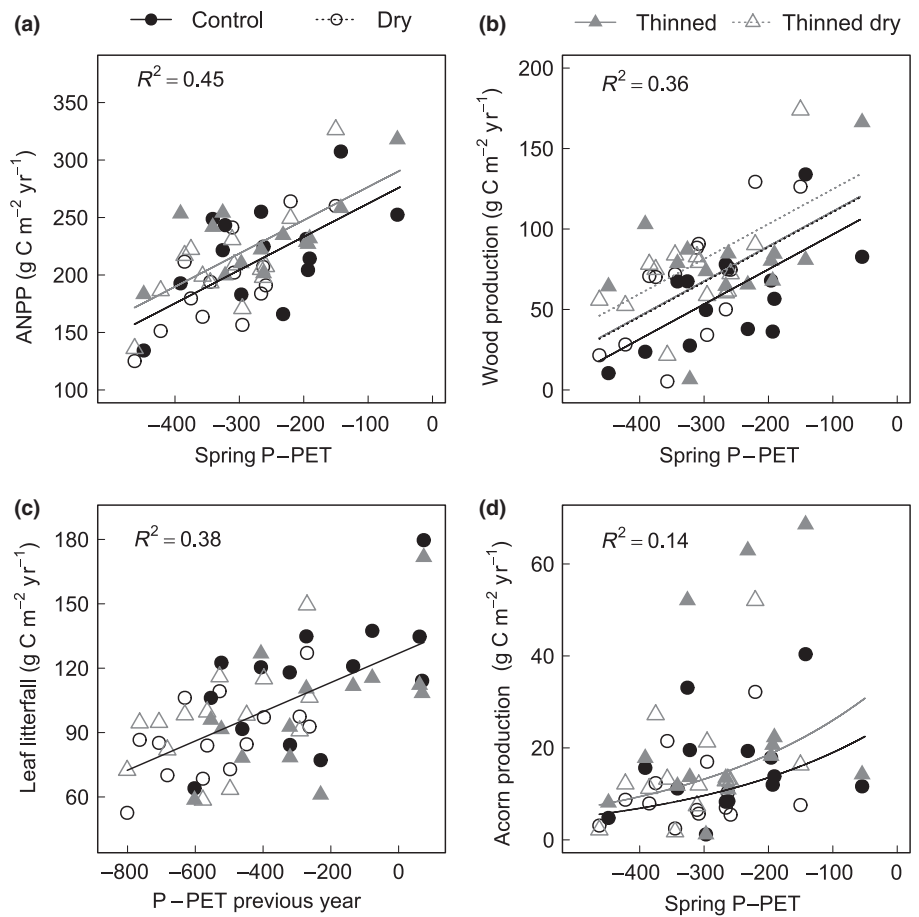


Fig. 2 Above-ground net primary productivity (ANPP) (a), wood production (b), leaf litterfall (c) and acorn production (d) of a *Quercus ilex* stand according to annual drought index, rainfall exclusion and thinning treatments. The adjusted R^2 of the full model is shown (see Fig. 3 for variance decomposition and Supporting Information Table S4 for model equations). P – PET, difference between precipitation and potential evapotranspiration calculated with the Priestley–Taylor formula.

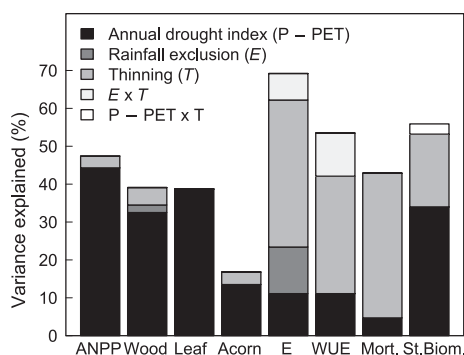


Fig. 3 Variance partitioning of the linear models of *Quercus ilex* stand mean above-ground net primary productivity (ANPP), wood production, leaf litterfall, acorn production, transpiration (E), water-use-efficiency (WUE), mortality (Mort.) and standing wood biomass change (St.Biom.) determined using the R package RELAIMPO. Models are presented in Supporting Information Table S4. $P - PET$, difference between precipitation and potential evapotranspiration calculated with the Priestley–Taylor formula.

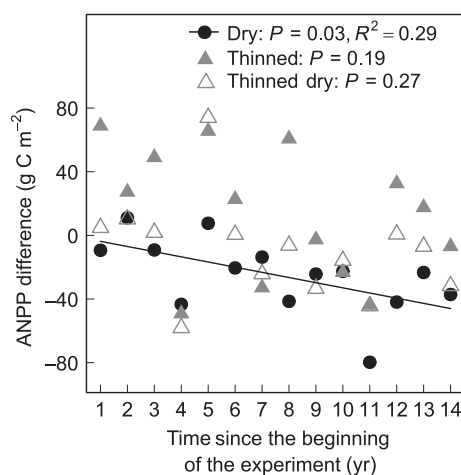


Fig. 4 Temporal trends in mean treatment effects on *Quercus ilex* stand above-ground net primary productivity (ANPP), expressed as ANPP treatment – ANPP control. P -value of the linear regressions between treatment effects and time are given, and the regression line is drawn when significant.

the unthinned treatments in 2007 and 170 g C m^{-2} for the thinned treatments in 2008 (Fig. S3). Wood production was increased by 36% by thinning ($P < 0.001$), but was not altered by rainfall exclusion or by treatment interaction (Table S3; Fig. 1b). Wood production was positively correlated with spring $P - PET$ (explained variance of 32%) with a higher intercept in response to thinning (explained variance = 4.6%) and rainfall exclusion (explained variance of 2%; Figs 2b, 3). Branch litterfall in the control treatment represented $34.8 \pm 2.1 \text{ g C m}^{-2} \text{ yr}^{-1}$ and was significantly reduced (by 13%) by both rainfall exclusion and thinning ($P < 0.001$) with no interaction between these factors ($P = 0.4$; Table S3; Fig. S5).

Leaf litterfall ranged from 52 g C m^{-2} in 2016 in the dry treatment to 180 g C m^{-2} in 2015 in the control treatment, with a strong synchronicity among treatments (Fig. S3). Leaf litterfall was influenced by the interaction between rainfall exclusion and

thinning treatments ($P < 0.001$; Table S3). Compared with the control, leaf litterfall was reduced by 23% in the dry treatment, by 13% in the thinned treatment and by 16% in the thinned dry treatment (Fig. 1c). Leaf litterfall was positively correlated with $P - PET$ of the previous year, which explained 38% of the variance and this relation was similar among treatments (Table S4; Fig. 2c).

Acorn production was highly variable among years, ranging from $1\text{--}2 \text{ g C m}^{-2}$ across treatments in 2005 to 69 g C m^{-2} in the thinned treatment in 2007, with the years 2004, 2007 and 2015 being particularly productive for all treatments (Fig. S3). Acorn production was reduced by 34% in rainfall exclusion plots and increased by 50% in thinned plots, with no interaction between these factors (Table S3; Fig. 1d), so that acorn production was comparable to the control in the thinned dry treatment. Annual acorn production was correlated with spring $P - PET$ (explained variance of 13.5%) with a higher intercept for the thinned plots (explained variance of 3.3%; Figs 2d, 3). Male flower production represented a part of the C budget similar to the production of acorns ($13 \pm 1 \text{ g C m}^{-2} \text{ yr}^{-1}$) and only a slight difference between the dry (11.7 ± 1.3) and the thinned dry (14.1 ± 1.4) treatments was detected (Table S3; Fig. S5).

Stand transpiration and WUE

Stand-level transpiration ranged between 208 mm in the thinned treatment in 2011 and 400 mm in the control treatment in 2012, being particularly low in 2006 and 2010 (Fig. S6). Stand transpiration was influenced by rainfall exclusion ($P < 0.001$), thinning ($P < 0.001$) and their interaction ($P = 0.005$), which resulted in a similar reduction by 23–27% compared with the control (Table S3; Fig. 5a). Stand transpiration correlated with spring $P - PET$ with different intercepts following the order, control > dry > thinned = thinned dry (Fig. 5c). Thinning explained the highest proportion of variance (39%) followed by rainfall exclusion (12%), spring $P - PET$ (11%) and the interaction between rainfall exclusion and thinning (7%; Fig. 3).

Water-use efficiency increased by 24% in the dry treatment compared with the control but this difference was not significant ($P = 0.08$; Fig. 5d). Compared with the control, WUE was higher by 68% in the thinned treatment and by 42% in the thinned dry treatments ($P < 0.001$). Annual WUE was slightly correlated with spring $P - PET$ (explained variance of 7.5%) but most of the variance was explained by thinning (32%) and its interaction with rainfall exclusion (11%; Figs 3, 5d).

Stand mortality and standing wood biomass change

Mortality was six times higher in unthinned than in thinned plots ($P < 0.001$), reaching a cumulated mortality of 29.0% in unthinned plots and 4.7% in thinned plots over the 15 yr period from 2003 to 2017 (Figs 6a, S7). Rainfall exclusion slightly increased the mortality rate, although not significantly ($P = 0.5$). Annual mortality rates were mostly influenced by thinning (explained variance = 38%), and negatively related to spring $P - PET$ (explained variance of 4.7%; Figs 3, 6c).

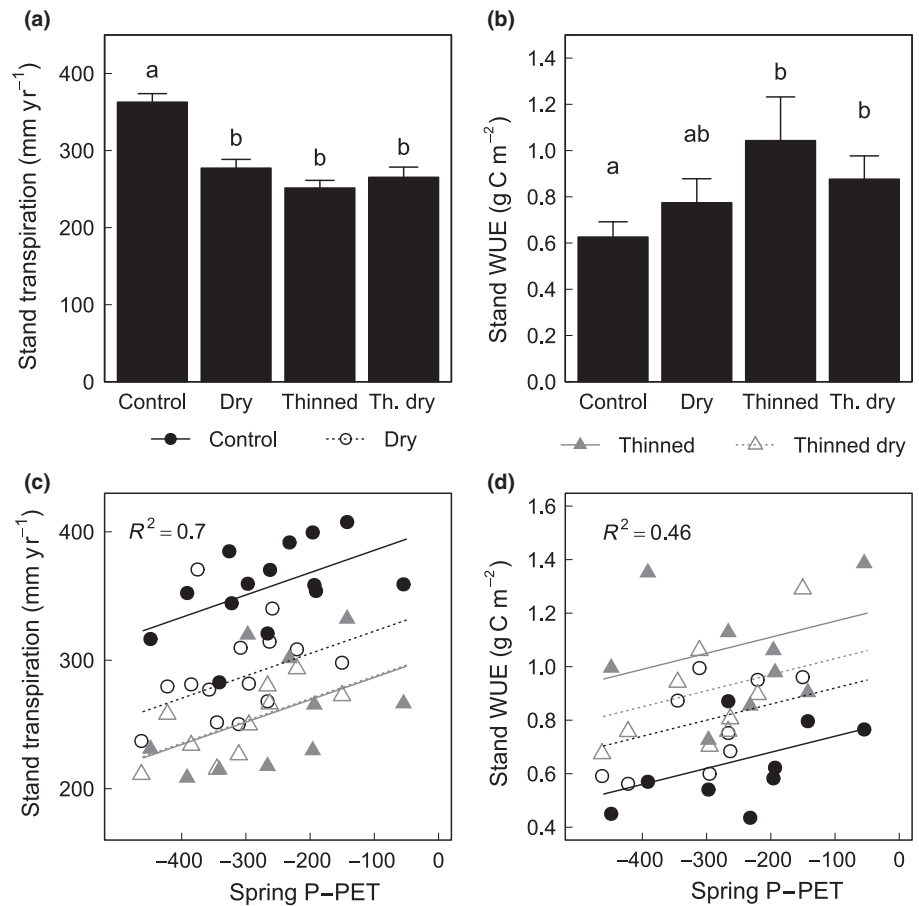


Fig. 5 *Quercus ilex* stand transpiration (a, c) and water-use efficiency (WUE, b, d): 14 yr average according to rainfall exclusion and thinning treatments (a, b) (error bars represent the SE) and relationship with annual drought (c–d). The adjusted R^2 of the full model is shown (see Fig. 3 for variance decomposition and Supporting Information Table S4 for model equations). P – PET, difference between precipitation and potential evapotranspiration calculated with the Priestley–Taylor formula; Th. dry, thinned dry treatment.

Standing wood biomass change ranged from -176 g C m^{-2} in 2006 in the dry treatment to $+353 \text{ g C m}^{-2}$ in the thinned treatments in 2008. A decrease in standing biomass (mortality exceeding tree growth) occurred for the unthinned treatments in 2005, 2006 and 2011, and additionally in 2009 and 2014 in the dry treatment. Rainfall exclusion had a negative but nonsignificant effect (-20% , $P=0.12$) and thinning increased standing wood biomass change by 113% ($P<0.001$), irrespective of the rainfall exclusion treatment (no interaction, $P=0.6$; Table S3; Fig. 6b). Annual standing wood biomass change decreased with spring drought (explained variance of 34%) with no effect of rainfall exclusion, but the slope of this relationship was two-fold lower for the thinned treatments (Table S4; Fig. 6d). Thinning explained 19% of the variance and its interaction with spring drought 3% (Fig. 3). No trend of treatment effects across time was detected for stand mortality or standing wood biomass change (Fig. S8).

Discussion

Experimental drought impacts on ecosystem functioning

Reducing rainfall inputs by 27% led to an 11% decrease of stand ANPP. This is remarkably close to the 10% ANPP decrease found by Liu *et al.* (2015) in response to a similar rainfall exclusion experiment in a holm oak forest in Prades, Catalonia, Spain. In a synthesis of precipitation manipulation experiments, Wu

et al. (2011) found that ANPP reduction mm^{-1} rainfall excluded varied between 0.04 to 0.16 g C m^{-2} . In our experiment, ANPP decrease represented $0.10 \text{ g C m}^{-2} \text{ mm}^{-1}$ excluded, indicating an intermediate sensitivity of holm oak ANPP to precipitation reductions. Negative effects of rainfall exclusion on ANPP increased over time (Fig. 4), suggesting the occurrence of carry-over effects such as progressive depletion of soil moisture, nutrients or tree carbohydrate reserves under persisting drought (van der Molen *et al.*, 2011). A similar trend has been reported in another precipitation reduction experiment in Hungary (Estiarte *et al.*, 2016), which contradicts the view of ecosystem responses to rainfall manipulation dampening over time (Leuzinger *et al.*, 2011; Barbeta *et al.*, 2013). Among the different ANPP components, the strongest effect of rainfall exclusion was observed for leaf production, which was reduced shortly after the rainfall exclusion setup in our study site (Limousin *et al.*, 2009, 2012), as well as in the Prades experiment (Ogaya & Peñuelas, 2006). The dry treatment also reduced acorn production, confirming the sensitivity of *Q. ilex* fructification to water availability (Ogaya & Peñuelas, 2007b; Sánchez-Humanes & Espelta, 2011; Pérez-Ramos *et al.*, 2013). However, we did not observe negative effects of the rainfall exclusion on wood production, standing wood biomass change or tree mortality, in contrast to the results from the Prades forest (Ogaya & Peñuelas, 2007a; Barbeta *et al.*, 2013). On the contrary, wood production for a given drought level was higher in the dry plot (Fig. 2b), which may partly be a

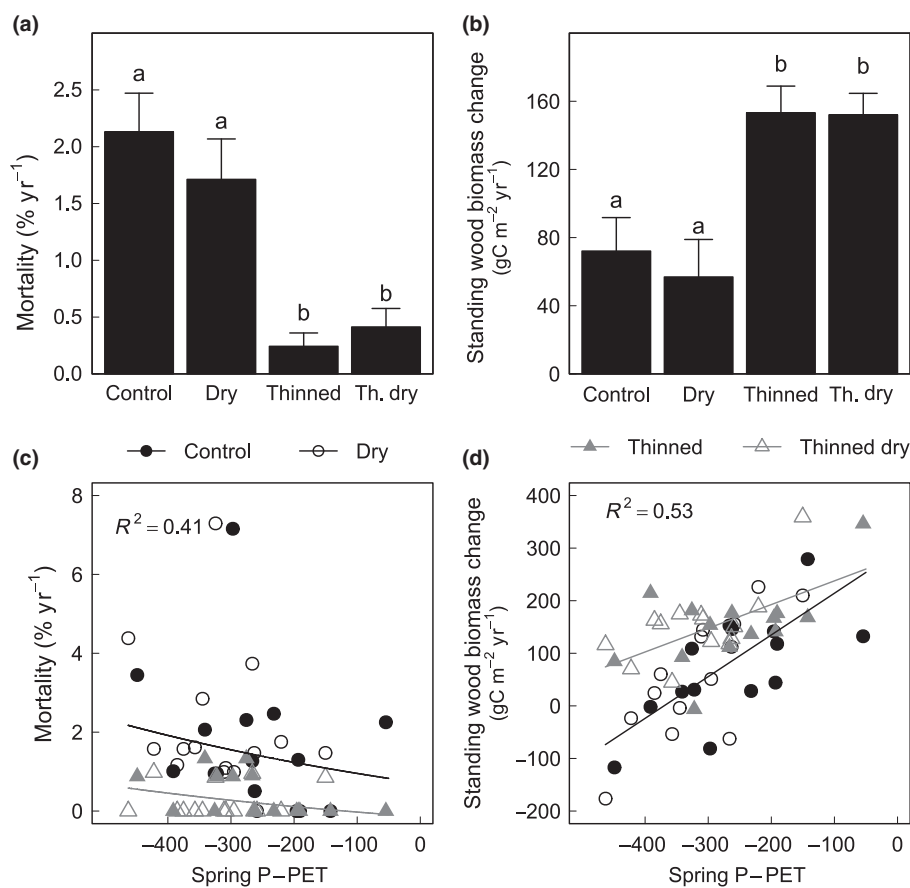


Fig. 6 *Quercus ilex* stand mortality rate (a, c) and wood biomass change (b, d) per yr: 14 yr average according to rainfall exclusion and thinning treatments (a, b) (error bars represent the SE) and relationship with annual drought (c, d). The adjusted R^2 of the full model is shown (see Fig. 3 for variance decomposition and Supporting Information Table S4 for model equations). P – PET, difference between precipitation and potential evapotranspiration calculated with the Priestley–Taylor formula; Th. dry, thinned dry treatment.

result of the higher initial basal area in the dry plot in unthinned stands (Table 1) or of the drought-avoiding stem growth phenology (Lempereur *et al.*, 2015). As stem growth occurs mainly in spring, when P – PET differences between rainfall exclusion treatments were limited (Fig. S2), this ANPP component may be less sensitive to the experimental set-up.

Besides reducing the total stand ANPP, rainfall exclusion affected the ANPP components differentially, thus modifying the stand-level C allocation. In particular, rainfall exclusion decreased the C allocation to leaves but not to stems. Such a shift in C allocation from short-lived leaf tissues to long-lived wood implies a longer C storage, with important consequences for the ecosystem C budget (Friedlingstein *et al.*, 1999). The long-term reduction in leaf litterfall corresponds to an adjustment to the drier conditions, which is a powerful means to balance ecosystem C assimilation and water stress (Eagleson, 1982). Indeed, stand transpiration was strongly reduced in the dry treatment, consistently with the lower transpiring leaf area (Limousin *et al.*, 2009). Lower leaf area reduces rainfall interception and transpiration, which can alleviate the impact of reduced rainfall inputs by slowing the soil water depletion. Only the ANPP was measured here, but increased below-ground allocation is also known to partially alleviate water stress and to occur in response to increased drought (Poorter *et al.*, 2012). Increasing allocation to the stem in response to drought has not been reported previously, but stem growth in dense, ageing oak coppices is already very limited

under ambient rainfall conditions, so that further reduction may not be possible without impairing the formation of functional vessels and the stem water transport capacity (Corcuera *et al.*, 2006). Reducing leaf production while maintaining stem growth decreases the leaf area per sapwood area and helps to maintain the leaf-specific hydraulic conductance (Limousin *et al.*, 2012). Because water availability is more limiting to holm oak stem growth than the C supply from photosynthesis (Lempereur *et al.*, 2015), the lower photosynthetic leaf area in the dry treatment might be more beneficial, by delaying the drought onset in spring, than detrimental, through reduction of C assimilation. The tendency for increased WUE in the dry treatment also indicates that the drought effect on biomass production is dampened compared with the effect on transpiration.

In managed stands, the effects of rainfall exclusion were of similar magnitude to those in the unmanaged stands with regard to total stand ANPP and acorn production, but much less pronounced and never significant with regard to leaf production and stand transpiration. Leaf area reduction owing to the removal of suppressed trees in the thinned plots resembles the natural stand leaf area adjustment in response to increased drought and may have been sufficient to limit water stress, without requiring further adjustment of the thinned dry plot. Indeed, the absence of leaf area and transpiration adjustment in the thinned stands did not translate into a higher vulnerability of production functions. Thinned stands are expected to recover their previous leaf area

over time, which can occur rapidly (1–2 yr) under humid conditions (Bréda *et al.*, 1995; Sohn *et al.*, 2013; Gebhardt *et al.*, 2014). However, in our experiment leaf litterfall was still reduced 15 yr after thinning (Fig. S4). Thinning from below that does not create large gaps in the canopy may have limited the leaf area recovery because understory development and stem resprouting remained limited by canopy shading. In addition, holm oak is a slow-growing species for which stand recovery may be slower.

Thinning impacts on ecosystem functioning

Thinning increased stand ANPP and compensated for increased drought, because higher wood and acorn production compensated for lower leaf and branch production. The thinned stands had higher wood production in spite of a number of trees reduced by almost half, which is a result of the strong stimulation of the stem growth of the remaining trees (Mayor & Rodà, 1993; Rodríguez-Calcerrada *et al.*, 2011; Cabon *et al.*, 2018). Thinning also increased acorn production and mitigated the negative effect of drought on acorn production, as also found by Sánchez-Humanes & Espelta (2011). Because oak sexual regeneration is difficult and limited (Pérez-Ramos *et al.*, 2013), thinning might be a suitable strategy to favor reproduction in a context of climate change. Tree mortality was strongly reduced in thinned treatments because of the removal of the less vigorous trees, which led to a two-fold higher standing wood biomass change at the stand level. Thinning can thus help abandoned coppices to maintain their above-ground productivity and limit the loss of C as a result of tree mortality, particularly under drier conditions. The transpiration of thinned stands was reduced compared with the control because of a lower sapwood area per unit ground area, which was not compensated by an increased individual sap flow rate (Gebhardt *et al.*, 2014; Lechuga *et al.*, 2017). Increased WUE in thinned stands has also been reported at the tree and stand levels in two recent studies (Gebhardt *et al.*, 2014; Fernandes *et al.*, 2016) and suggests that water availability is not the only limiting factor for stand productivity, which also benefits from increased light or nutrient availability after thinning. Alternatively, this increased stand-level WUE may be the result of the selection of the bigger trees by thinning from below, because bigger trees capture a disproportionate amount of light and water resources and convert it more efficiently into biomass (Binkley *et al.*, 2004; Gspaltl *et al.*, 2013). In summary, thinning can thus maintain forest productivity and enhance wood and acorn production while reducing water consumption.

How do experimental drought and thinning impact the ecosystem drought–function relationships?

Most of the ecosystem functions studied here were primarily limited by spring drought (Allard *et al.*, 2008). Spring drought explained high proportions of the variance of stand ANPP and wood production, confirming the previously reported sensitivity of holm oak growth to spring water balance (Gea-Izquierdo *et al.*, 2011; Lempereur *et al.*, 2015). Leaf litterfall, by contrast, was related to the drought stress of the previous year, so that fewer

leaves were shed following dry years (Rambal *et al.*, 2014). This phenomenon might be linked to an increased leaf life span under dry conditions (Ogaya & Penuelas, 2006; Limousin *et al.*, 2012), so that, consistent with the cost–benefit hypothesis, the leaf life span required to pay back the leaf construction costs increases after dry years when leaf photosynthetic activity was reduced. According to our variance partitioning approach, sensitivity to interannual drought varied depending on the ANPP components in the order ANPP > leaf > wood > acorn (Fig. 3), a hierarchy consistent with the results of Rambal *et al.* (2014) using a nearby dataset of holm oak ecosystem productivity. Variable sensitivity to drought among tree organs implies that drought modulates the C allocation by increasing relatively the C allocation to the organs that are less sensitive to drought stress. Consequently, the allocation to wood is less impacted by increasing drought than is the allocation to leaves, either when compared between treatments of the rainfall exclusion or among years with different water deficits. Except for wood production, the relationships between ANPP components and drought were neither modified in slope nor in intercept by the drought treatment (Fig. 2), suggesting that rainfall exclusion did not induce legacy effects or acclimations for most ANPP functions. Similarly, Estiarte *et al.* (2016) found that the relationships between ecosystem ANPP and precipitation did not differ in eight out of 11 rainfall exclusion experiments, and unexpectedly exhibited a higher intercept in two of these experiments. They concluded that most experiments ran for too short a time or were not severe enough to induce strong structural changes and suggested that ecosystem responses to drought were plastic and possibly reversible. In our site, however, the decrease in leaf area in the dry unthinned treatment has been partly attributed to a lower number of ramifications (Limousin *et al.*, 2012). This type of architectural modification could therefore induce a legacy effect on leaf production during subsequent years (Sala *et al.*, 2012). Here, we did not evidence a change in the leaf litterfall–drought relationship in the dry compared with the control treatment, or a temporal increase of the dry treatment effect on leaf litterfall (Fig. S4). This implies that trees are able to compensate for a lower branch ramification induced by the rainfall exclusion through increased leaf production per branch and/or branch ramification following wet years. It remains difficult, however, to draw conclusions on the recovery and reversibility of treatment effects in an experiment where dry plots never experience the same water availability as the control. Experiments submitting trees and ecosystems to a release of drought stress after long-term chronic drought (e.g. by stopping the rainfall exclusion or irrigating the dry plots) are needed to elucidate whether or not acclimation to drought alters the capacity of the ecosystem to fully recover under favorable conditions.

Conversely, thinning effects manifested in a higher intercept of the wood and acorn production relationships with spring drought. These higher intercepts in thinned stands may be related to a higher proportion of gross precipitation reaching the soil as a result of lower interception compared with unthinned stands. However, applying the Gash rainfall interception model to our study site (Gash *et al.*, 1995; Limousin *et al.*, 2008) shows only

an average 6% increase in net precipitation in the thinned stands where the change in leaf area was intermediate between the control and dry treatments. This difference is very limited compared with the rainfall exclusion effect (−27%). The reduced stand transpiration and/or increased availability in other colimiting resources thus probably explain these higher intercepts of the relationships between drought and wood or acorn production. In addition, standing wood biomass change was less sensitive to drought in the thinned than in the unthinned stands, owing to both a lower mortality and the maintenance of stem growth in thinned treatments even during the driest spring of 2006. These results are in line with studies evidencing a higher impact of drought on tree mortality (Linares *et al.*, 2009; Young *et al.*, 2017) and growth in high-density stands, either at the individual tree level (Misson *et al.*, 2003; Martín-Benito *et al.*, 2010; Fernandes *et al.*, 2016) or at the stand level (Bottero *et al.*, 2016; Gleason *et al.*, 2017). We hypothesized that thinning might cause changes in an opposite direction to the response to drought, such as increased transpiration demand or leaf area per basal area (McDowell *et al.*, 2006; Mausolf *et al.*, 2018) and thus increase the stand sensitivity to drought. This was not observed, however, and contrary to this hypothesis, the decrease in leaf litterfall and transpiration was a stand-level response common to both drought and thinning. Hydraulic acclimation to wetter conditions, which is expected to increase drought sensitivity of trees, may thus occur only in response to high thinning intensities where light penetration, air temperature and vapor pressure deficit are strongly increased (Clark *et al.*, 2016), while moderate thinning could lower the drought sensitivity through an increase in water and other resource availability (Warren *et al.*, 2001; Martín-Benito *et al.*, 2010). Moreover, in coppice stands, thinning increases the root : shoot ratio, which may help to sustain growth and functioning during dry events.

Stand transpiration and WUE were poorly related to annual drought indexes, probably because of the predominant influence of stand structure in controlling the forest water balance – as reflected by the higher proportion of variance explained by thinning treatments (Fig. 3). The lower intercept in the dry treatment indicate that water-related functions are more affected by long-term rainfall reduction than could be expected based on their relationship with drought. The reduction in leaf area imposed by both rainfall reduction and thinning, and the reduction in basal area in the thinned stands exert structural constraints on stand transpiration that limit its recovery potential when water availability is not limiting, for instance during the rainy season in autumn (Limousin *et al.*, 2009). Similarly, Grossiord *et al.* (2018) found that sap flux density was less sensitive to daily soil moisture in several precipitation reduction experiments in mature forests, indicating a lower transpiration recovery under well-watered conditions. These two studies point to legacy effects of long-term drought on ecosystem transpiration, leading to new trajectories of the transpiration–drought relationship.

In our study, a 15 yr decrease in precipitation inputs by 27% did not alter the temporal trajectory of the ANPP–drought relationship. However, the effect of rainfall exclusion on ANPP tended to increase over time throughout the study (Fig. 4), which

suggests that a new trajectory of the ANPP–drought relationship is to be expected in the future, although we do not know yet over which time span. In addition, faster structural changes and permanent losses of stand vitality might occur after rare extreme drought events which could become more frequent and intense in the future, especially when they happen in spring, which is a critical period for most ANPP components. Structural adjustments to long-term drought strongly modified forest transpiration, suggesting that climate change impacts on the water budget in Mediterranean forests could be partly decoupled from impacts on the C budget.

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Author contributions

JG analyzed the data and led the writing of the manuscript; J-MO set the experiment up and collected the data; J-ML initiated the ideas for data interpretation; and all authors contributed to discussions and writing of the manuscript.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 ANPP components, mortality and standing wood biomass change relationships with drought and treatment analyzed with linear mixed models, with block as random factor.

Fig. S2 Precipitation – potential evapotranspiration during the years of the experiments.

Fig. S3 ANPP, wood production, leaf litterfall and acorn production according to experimental treatments and years.

Fig. S4 Temporal trends in treatment effects on stand ANPP, wood production, leaf litterfall and acorn production.

Fig. S5 Branch and flower litterfall according to treatments.

Fig. S6 Stand transpiration and water-use efficiency according to experimental treatments and years.

Fig. S7 Stand mortality and wood biomass increment according to experimental treatments and years.

Fig. S8 Temporal trends in treatment effects on stand mortality and standing wood biomass change.

Table S1 Results of the mixed models of annual stand function depending on annual drought, rainfall exclusion and thinning treatment.

Table S2 Results of the mixed models testing for temporal trends in treatment effects on stand ANPP components, mortality and standing wood biomass change.

Table S3 Results of the linear mixed models testing for average treatment effects on stand ANPP components, transpiration, mortality and standing wood biomass change.

Table S4 Selected models of mean stand function depending on annual drought, rainfall exclusion and thinning treatment.

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