Contrasting impacts of continuous moderate drought and episodic severe droughts on the aboveground-biomass increment and litterfall of three coexisting Mediterranean woody species

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Abstract

Climate change is predicted to increase the aridity in the Mediterranean Basin and severely affect forest productivity and composition. The responses of forests to different timescales of drought, however, are still poorly understood because extreme and persistent moderate droughts can produce nonlinear responses in plants. We conducted a rainfall-manipulation experiment in a Mediterranean forest dominated by *Quercus ilex*, *Phillyrea latifolia* and *Arbutus unedo* in the Prades Mountains in southern Catalonia from 1999 to 2014. The experimental drought significantly decreased forest aboveground-biomass increment (ABI), tended to increase the litterfall and decreased aboveground net primary production throughout the 15 years of the study. The responses to the experimental drought were highly species-specific. *A. unedo* suffered a significant reduction in ABI, *Q. ilex* experienced a decrease during the early experiment (1999-2003) and in the extreme droughts of 2005-2006 and 2011-2012 and *P. latifolia* was unaffected by the treatment. The drought treatment significantly increased branch litterfall, especially in the extremely dry year of 2011, and also increased overall leaf litterfall. The drought treatment reduced the fruit production of *Q. ilex*, which affected seedling recruitment. The ABIs of all species were highly correlated with SPEI in early spring, whereas the branch litterfalls were better correlated with summer SPEIs and the leaf and fruit litterfalls were better correlated with autumn SPEIs. These species-specific responses indicated that the dominant species (*Q. ilex*) could be partially replaced by the drought-resistant species (*P. latifolia*). However, the results of this long-term study also suggest that the effect of drought treatment has been dampened over time, probably due to a combination of demographic compensation, morphological and physiological acclimation and epigenetic changes. However, the structure of community (e.g. species composition,

dominance and stand density) may be reordered when a certain drought threshold is reached.

Introduction

The climate changes resulting from anthropogenic activities have already influenced global water cycle, involving changes in precipitation mounts, timing and variability and reductions in water availability since the middle of last century (Beier *et al.*, 2012; Dai, 2012). Water availability is a crucial factor determining global plant distribution and the diversity of terrestrial ecosystems (Lloret *et al.*, 2004; Carnicer *et al.*, 2011; Wu *et al.*, 2011; Vicente-Serrano *et al*, 2013). Climate change in recent decades produced by the continued emission of carbon has included temperature increases, precipitation decreases and more frequent extreme droughts in the Mediterranean Basin (Dai, 2012; Ji *et al.*, 2014; IPCC, 2014). Mediterranean ecosystems have thus already been disturbed by the frequencies and intensities of droughts (Ogaya & Peñuelas, 2007a; Misson *et al.*, 2011; Doblas-Miranda *et al.*, 2015). The magnitude of the effects have largely depended on the initial species composition (Lloret *et al.*, 2004; Ruiz-Labourdette *et al.*, 2012; Peñuelas *et al.*, 2013a; Doblas-Miranda *et al.*, 2015) and successional trajectories of the ecosystems (Breshears *et al.*, 2005; Mueller *et al.*, 2005; Peñuelas *et al.*, 2013b; Carnicer *et al.*, 2014). Droughts can lead to reductions in primary productivity (Ciais *et al.*, 2005; Boisvenue & Running, 2006; Peñuelas *et al.*, 2007; Wu *et al.*, 2011; Ivits *et al.*, 2014) and the ability of forests to sequester carbon and can thus alter regional carbon budgets (Ogaya & Peñuelas, 2007a; Zhao & Running, 2010; Carnicer *et al.*, 2011; van der Molen *et al.*, 2011; Peñuelas *et al.*, 2013a). Widespread forest declines, die-offs, species shifts and phenological changes (Peñuelas *et al.*, 2004a, 2013a; Carnicer *et al.*, 2011; Misson *et* *al.*, 2011; Ivits *et al.*, 2014) have also been observed in more extreme cases (Lloret *et al.*, 2012; Reyer *et al.*, 2013).

Aboveground net primary production (ANPP) is generally assessed as the amount of carbon incorporated into new organic matter produced aboveground over a specified interval (Clark & Brown, 2001; Chapin *et al.*, 2006; Malhi *et al.*, 2011; Clark *et al.*, 2013; Talbot *et al.*, 2014). ANPP consists of several components: aboveground-biomass increment (ABI), fine litterfall, emissions of biogenic volatile organic compounds (BVOCs) and the loss due to consumers. BVOCs and the loss due to consumers are difficult to measure and are of secondary importance, but the assessment of the main components of ANPP, ABI and litterfall (branch, leaf and fruit litterfall), has received considerable attention for many forest ecosystems (Clark & Brown, 2001; Malhi *et al.*, 2011; Talbot *et al.*, 2014). The cumulative evidence suggests that increasing droughts would have negative effects on forest ANPP, reducing stem growth and increasing defoliation (Ogaya & Peñuelas, 2006; Carnicer *et al.*, 2011; Limousin *et al.*, 2012; Reyer *et al.*, 2013). Information for the magnitude of these effects on ANPP, however, is still scarce, because their quantification requires more field data not usually available due to methodological limitations (Boisvenue & Running, 2006; Beier *et al.*, 2012).

Field manipulation experiments can impose continuous and quantitative disturbance in natural ecosystems and shed light on forest changes induced by reductions in water availability (Peñuelas *et al.*, 2004b, 2007; Wu *et al.*, 2011; Beier *et al.*, 2012; Ivits *et al.*, 2014). Compared to observational studies that depend on the occurrence of natural extreme weather events to disturb the forest ecosystem and carbon budget, experiments that manipulate precipitation can simulate rapid and strong drought perturbations and can thus offer an opportunity to study forest ecosystems under water deficits (Leuzinger *et al.*, 2011; Reyer *et al.*, 2013). Many precipitation-exclusion experiments have been conducted in natural or semi-natural ecosystems around the world and have illustrated the effects of altered precipitation regimes on ecosystem functioning (Wu *et al.*, 2011; Beier *et al.*, 2012). Numerous experiments suggest that the variation of effect sizes is unstable, which is a dynamic process followed by periods of potential stability (Leuzinger *et al.*, 2011). The magnitude and stability of the responses for long-lived species to drought, though, may vary at long timescales (Leuzinger *et al.*, 2011; Beier *et al.*, 2012; Barbeta *et al.*, 2013). Recent studies have reported dampening effects on the response to drought over time (Leuzinger *et al.*, 2011; Barbeta *et al.*, 2013). These dampening effects include epigenetic changes (Rico *et al.*, 2014), physiological changes (Martin-Stpaul *et al.*, 2013; Ogaya *et al.*, 2014), morphological adjustments (Misson *et al.*, 2011), functional changes in roots (Barbeta *et al.*, 2015) and reductions in stand density (Lloret *et al.*, 2004; Grimm *et al.*, 2013). These adjustments to drought, however, may not be sufficient to cope with future droughts that may ultimately produce widespread tree mortality and vegetational shifts favoring the most drought-resistant species.

Holm oak (*Quercus ilex* L.) is an intermediate drought-tolerant species widely distributed in the western Mediterranean Basin. This species is usually accompanied by other Mediterranean woody species with more (*Phillyrea latifolia* L.) or less

(*Arbutus unedo* L.) drought tolerance (Ogaya & Peñuelas, 2003, 2006, 2007a, 2007b, 2007c; Barbeta *et al.*, 2012, 2013, 2015; Ogaya *et al.*, 2014). The varying ecophysiological responses to drought of these tree species have been reported in previous studies (Ogaya & Peñuelas, 2003, 2007a; Ogaya *et al.*, 2014). For example, drought decreased the photosynthetic rate in *Q. ilex* but not in *P. latifolia* (Ogaya & Peñuelas, 2003) and greatly reduced the increase in biomass in *Q. ilex* and *A. unedo* but not in *P. latifolia* after five years of experimental drought in the same site (Ogaya & Peñuelas, 2007a). Barbeta *et al.* (2013) reported a temporal dampening of the treatment effect on stem growth and mortality during the first 13 years of an experimental drought. Some of these studies have focused on long-term (more than 10 years) growth and mortality rates, but there is still a lack of information on the long-term evolution of aboveground biomass, litterfall and net primary production for forests subjected to moderate but persistent drought and to episodic severe droughts as projected for the Mediterranean regions in the coming decades (IPCC, 2014).

Our general objective was to study the ecological effects of the increasing intensity, frequency and duration of droughts predicted for the coming decades in a Mediterranean holm oak forest. Our initial hypotheses were that forest ANPP could significantly decrease under the moderate and persistent experimental drought and that extreme droughts would exacerbate this effect. We also hypothesized species-specific responses to drought, and different responses of ABI than branches, leaves and fruit litterfall, decreasing and increasing respectively in response to drought, and especially to severe episodes. We also monitored the responses of individuals and the entire community to the drier environmental conditions of the long-term (15 years) experimental drought to identify the detailed hierarchical mechanisms underlying transitions in the ecosystem state and to gain knowledge about the responses of the species and the community when tolerance thresholds (or tipping points) are exceeded by severe droughts. We were thus interested in determining whether long-term experimental and extreme natural droughts would accelerate acclimation and resilience of the Mediterranean forest ecosystem or would increase vegetation shifts toward reverse succession (forest to shrubland).

Materials and methods

Experimental site

The experiment was conducted on a south-facing slope (25%) in the Prades Holm oak forest in southern Catalonia (northeastern Iberian Peninsula) (41°21′N, 1°2′E; 930 m a.s.l.). This forest is widely distributed at 400-1200 m a.s.l., with closed canopies 3-10 m in height, depending on the site microclimate and topography. The vegetation is largely dominated by a dense overstory of the evergreen species *Q. ilex* (5258 stems ha^{-1} and 93 Mg ha^{-1}), *P. latifolia* (7675 stems ha^{-1} and 17 Mg ha^{-1}) and *A. unedo* (1100 stems ha^{-1} and 11 Mg ha^{-1}), accompanied by other Mediterranean woody species that usually do not reach the upper canopy (*Erica arborea* L., *Juniperus oxycedrus* L. and *Cistus albidus* L.) and occasional individuals of deciduous species (*Acer monspessulanum* L. and *Quercus* × *cerrioides* Wilk. & Costa). The understory vegetation is very sparse, with abundant litter accumulation. The forest structure consists of a high density of small stems, mostly stump resprouts after a selective thinning, but the forest has not been disturbed for the last 70 years.

This study site has a Mediterranean climate, with 80% of the rain falling in spring (March, April and May) and autumn (September, October and November). Summer drought is common, usually lasting 3-5 months (Dai, 2012; Lopez-Bustins *et al.*, 2013). The annual amount of summer (June, July and August) precipitation averaged 59.2 mm for 1999-2013, less than 10% of the mean annual precipitation (616.1 mm). Summer precipitation was irregular during this period, ranging from 22.0 mm in 2011 to 112.0 mm in 2000. The average summer temperature was 20.5 °C, which was ca.

8.0 °C higher than the mean annual temperature of 12.2 °C. Parent material of the Prades mountain is Jurassic limestone bedrock, which is overlaid by Paleozoic schist and Dystric Cambisol soil and ranges in depth from 30 to 110 cm. The soil is fully covered by litterfall. The climatic, edaphic and physiographic characteristics of this site are archetypical of forests of the Mediterranean Basin, which mostly occur in mountainous areas with shallow soils that exacerbate water deficits in plants.

Experimental design

Eight 15×10 m plots were established in January 1999 at the same altitude (930 m a.s.l.) along the south face of the mountain where the experiment is located. Four randomly selected plots received a drought treatment, and the other four served as control plots. The drought treatment partially excluded throughfall by PVC strips (0.5×18 m^2/strip), which are suspended at a height of 0.5-0.8 m above the ground, and cover approximately 30% of the plot surface. A ditch 0.8-1.0 m deep was excavated across the upper margin of the treatment plot to intercept runoff water. The water intercepted by the strips and ditches was drained outsides of the plots, below their lower margins. The strips were installed under the canopy and did not affect the amount of incident light reaching the leaves. Any litter falling on the PVC strips was regularly (approximately every month) placed below the strips to avoid differences in litter decomposition between the treatment and control plots due to factors other than the availability of water. The forest structure and species composition for all plots was undifferentiated at the start of the experiment.

Measurement of meteorological data and environmental indexes

An automated meteorological station (Campbell Scientific Inc., Logan, USA) was installed at a central point within the experimental system. Air temperature, relative humidity and precipitation were recorded every 30 minutes. Monthly precipitation and temperature data was available from 1975 at a nearby meteorological station (Poblet Monastery). Soil-water content was measured each season throughout the experiment by time-domain reflectometry (Model 1502C, Tektronix, Inc., Beaverton, USA) (Zegelin *et al*., 1989; Whalley, 1993). Three stainless steel cylindrical rods (25 cm long) were permanently installed in the soil at four randomly selected locations in each plot. The time-domain reflectometer was manually connected to the ends of the rods for determining the soil-water content. The Standardized Precipitation-Evapotranspiration Index (SPEI) based on continuous monthly differences between precipitation and potential evapotranspiration (P-PET; D) was used to evaluate drought severity throughout the study period (Vicente-Serrano *et al*., 2010; 2013). We built a database of the D values (1975-2013) and used the SPEI package (version 1.6) to create different timescales (from 1-month to 36-month) of SPEI. We selected SPEIs at different timescales to best fit the values to forest growth and community dynamics, as described in detail by Barbeta *et al.* (2013). We calculated the SPEI for the drought treatment to evaluate the actual drought conditions in the plots, adjusting for a 13% decrease in precipitation in the drought plots (see Results).

ABI, litterfall and ANPP

All living tree stems with diameters >2 cm at a height of 50 cm (D_{50}) were marked with tags and identified to species in January 1999, and their stem diameters were measured using a metric tape. Stem diameter (D_{50}>2cm) for all trees in the plot was re-measured each year. Aboveground biomass (AB) at the plot level was estimated by allometric relationships from the stem diameters (Ogaya & Peñuelas, 2007a). ABI was calculated annually as the difference in AB between years. Trees that died were not measured or further considered for ABI calculations. New stems were added when their diameters reached the threshold (D_{50}≥2cm). The ABs of the three dominant species were estimated from the allometric relationships between stem diameter and AB (Ogaya & Peñuelas, 2007a).

Aboveground litter production (litterfall) was collected seasonally from January 1999 to December 2013 with twenty traps (27 cm in diameter with 1.5-mm mesh) randomly distributed in each plot. We estimated the annual mass of litterfall as the sum of the litters collected every three months during the study period. Litter was separated in the laboratory into leaves, branches and fruits. Leaves and fruits were characterized to species (*A. unedo*, *Q. ilex* and *P. latifolia*). The dry weights of the samples were then obtained by oven-drying the litter to a constant weight at 70 °C.

ANPP was calculated each year during the study period as the sum of the ABIs (no dead stems) and litterfalls for all species in the plot (Clark & Brown, 2001). The litterfall data for 2009 were lost, so we could not calculate the ANPP for that year. A severe drought in 2011 produced an atypically large litterfall, so this litterfall were not included in the ANPP calculation. Losses to herbivores and the emission of volatile organic compounds (VOCS) were not quantified and were considered negligible relative to the ABI and litterfall.

Statistical analysis

Differences in ABI and litterfall (expressed as a percentage of AB) among the species and the entire forest community were analyzed using repeated-measures analyses of variance (ANOVAs), with treatment as the independent factor and year as the repeated measure. These analyses were performed using Statistica 10.0 (StatSoft Inc., Tulsa, USA). Branch litterfall could not be separated by species, so we calculated the total branch litterfall in each plot. The fruit litterfalls for *A. unedo* and *P. latifolia* were also excluded because of their low abundance. Depending on drought treatments, allometric relationships between SPEI and ABI, litterfall and ANPP were tested by standardized major-axis regression. To compare fitted bivariate slopes of the allometric relationships between treatments, we tested the homogeneity of the slopes and intercepts with the smatr R package (version 3.4-3, Warton) described by Warton, *et al* (2012). The relationship was determined with one regression if the control and treatments did not differ.

Results

Environmental conditions

The mean annual temperature during this 15-year experiment period (12.2 °C) was slightly higher than the average for 1975-2013 (11.8 °C) (Fig. 1). In the study period, there were two hottest years in 2006 (13.0°C) and 2011 (13.1°C). The mean annual precipitation for this period (616.1 mm) was lower than the average for 1975-2013 (662.4 mm), which varied greatly from 379.8 mm in 2006 to 926.7 mm in 2010 (Fig. 1). Soil moisture fluctuated with the evaporative demand and precipitation periodicity (Fig. 1). Mean soil moisture throughout the study period was decreased by 13.0% in drought when compared with control plots. However, both control and drought plots reached the lowest soil-moisture contents in summer (14.9±1.2% and 13.0±1.1%, respectively). In this study period, the amount of soil moisture decreased substantially in the summers of 2006 and 2011. May SPEI-6 demonstrated that the periods of 2000-2001, 2005-2006 and 2011-2012 were the driest records for the growing seasons of the study period.

ABI

The ABI of the three dominant tree species was correlated with the inter-annual fluctuations of precipitation, but the species differed in their sensitivity to the variation (Fig. 2). *A. unedo* was the most sensitive to water shortages, with a significantly lower ABI in the drought than the control plots for the entire study period (control=0.4±0.1 and drought=0.1±0.1 Mg ha^{-1}, $p<0.001$). *Q. ilex* had a marginally lower ABI in the drought than the control plots (control=0.5±0.2 and drought=0.2±0. 3 Mg ha^{-1}, $p<0. 1$); the ABIs differed more during the first five years and the extreme episodes of 2005-2006 and 2011-2012. *P. latifolia* ABIs were not affected by the drought treatment during the study period.

ABI was positively correlated with the SPEI drought index in these species (Fig. 3). *A. unedo* ABI was correlated with April SPEI-1 ($R^2=0.16$), *Q. ilex* ABI with May SPEI-6 ($R^2=0.39$, $p<0.05$ and $R^2=0.61$, $p<0.001$ for the control and drought plots, respectively) and *P. latifolia* ABI with May SPEI-3 ($R^2=0.62$). *Q. ilex* was the most sensitive species to natural drought (Fig. 3).

Litterfall

The experimental drought significantly increased branch litterfall throughout the study period ($p<0.01$) (Fig. 4a), especially in the severely dry year of 2011 ($p<0.001$). The relative branch litterfall was also negatively correlated with SPEI; the best fit was with September SPEI-3 ($R^2=0.28$, $p<0.05$ and $R^2=0.32$, $p<0.05$ for the control and drought plots, respectively). Branch litterfall was most sensitive to water availability in the dry summer months (July, August and September). The drought treatment significantly increased this sensitivity (SMATR, common slope=-1.96, $p<0.05$) (Fig. 4b).

The interannual fluctuations of the relative leaf litterfall in these species indicated the different sensitivities to drought (Fig. 5). Leaf litterfall was higher in the drought than the control plots for *A. unedo*, *Q. ilex* ($p<0.05$) and *P. latifolia* ($p<0.05$) during the experimental period. Defoliation rates were significantly higher in the drought than the control plots in 2007 ($p<0.001$) and 2011 ($p<0.001$) for *Q. ilex* and in 2004

($p<0.05$) and 2007 ($p<0.001$), but not 2011, for *P. latifolia*. The relative leaf litterfall for these species was negatively correlated with SPEI; *A. unedo* and *Q. ilex* depended on October SPEI-3 ($R^2=0.19$ and 0.25, respectively), whereas *P. latifolia* was most dependent on November SPEI-3 ($R^2=0.41$) (Fig. 5). Relative leaf litterfall did not differ between the control and drought plots for these species (Fig. 6).

The drought treatment significantly decreased the fruit litterfall for *Q. ilex* ($p<0.05$), especially in 2000 ($p<0.05$) and 2003 ($p<0.01$). The relative fruit litterfall decreased in both the control and drought plots during extreme droughts, indicating less fruit maturation (Fig. 7a). December SPEI-6 was positively correlated with the relative fruit litterfall ($R^2=0.27$).

ANPP

ABI of the entire forest community was lower in the drought than the control plots throughout the study period (control=1.1±0.3 and drought=0.4±0.3 Mg ha^{-1}, $p<0.01$) (Fig. 8). Minimum ABIs occurred during the extreme droughts in 2000-2001, 2005-2006 and 2011-2012. The drought treatment increased forest litterfall (control=2.4±0.3 and drought=2.6±0.4 Mg ha^{-1}, $p<0.1$), and the extreme drought of 2011 triggered a heavy litterfall (control=5.5±0.5 and drought=7.2±0.7 Mg ha^{-1}, $p<0.001$). ANPP estimated from the sum of ABI and litterfall consequently only tended to be higher in the control plots (control=3.8±0.3 and drought=3.4±0.3 Mg ha^{-1}, $p<0.1$), despite a clearly higher ABI than in the drought plots. ANPP was even minimal in the dry years of 2001, 2005, 2010 and 2012. Our 15-year drought treatment demonstrated a dampening effect, and ANPP decreased by 10% throughout the experiment.

The best fits with the SPEI indices were with May SPEI-6 (R^2=0.52) for ABI, with September SPEI-1 (R^2=0.24) for litterfall and with May SPEI-3 (R^2=0.55) for ANPP. The drought treatment slightly increased these trends toward lower ABIs and ANPPs and higher litterfalls in the years with lower SPEIs (Fig. 9). ABIs were positive only when May SPEI-6 was >0. ABI reached its maximum of 2.6 Mg ha^{-1} when May SPEI-6 was >1 and its minimum of -2.0 Mg ha^{-1} when May SPEI-6 was <-1. Litterfall reached its maximum of 7.0 Mg ha^{-1} when September SPEI-1 reached its extreme value of -2. ANPP reached its maximum of ca. 5.8 Mg ha^{-1} at a May SPEI-3 of 2.

Discussion

Effects of experimental and extreme natural droughts on ABI, litterfall and ANPP

Both experimental and extreme natural droughts reduced the forest ABI. Sensitivity to the drought conditions, however, varied among the three dominant species. *A. unedo* was the most sensitive species to the drought treatment, with a significantly lower ABI in the drought than the control plots, but *Q. ilex* was the most sensitive species to extreme natural droughts, with severe reductions in ABI in the three extreme episodes, especially in the drought plots (Fig. 2). The species-specific drought vulnerability is consistent with that of previous studies conducted in the same Mediterranean forest (Ogaya & Peñuelas, 2003, 2007a; Barbeta *et al.*, 2013) and demonstrates that a reduction in soil moisture produces great disparity in the responses depending on species-specific hydraulic conductivity in stems (Barbeta, et al., 2012) or leaf physiological traits (Ogaya & Peñuelas, 2003; Ogaya et al., 2014). *Q. ilex* is more vulnerable to water shortage than *P. latifolia* due to more sensitive foliar photosynthesis (Ogaya & Peñuelas, 2003; Ogaya et al., 2014), aboveground growth (Ogaya & Peñuelas, 2007a; Barbeta et al., 2013) and stem hydraulic conductivity (Martínez-Vilalta et al., 2002; Barbeta et al., 2012). Therefore, this holm oak forest may experience a vegetation shift involving reverse succession (forest to shrubland) under future drier and warmer scenarios, including more frequent extreme droughts.

Litterfall was a 10% higher in the drought treatment plots than in control ones throughout the study period and increased up to 32% more than control following the extreme drought of 2011 (Fig. 4a), a likely consequence of drought-induced xylem cavitation accelerating branch and leaf senescence, which may eventually lead to tree mortality (Ogaya & Peñuelas, 2006; Misson *et al.*, 2011; Choat *et al.*, 2012). Drought-induced litterfall may also result from the reduction in leaf area as a conservative strategy to reduce transpiration and maintain hydraulic conductance under water stress, a response that has been observed under extreme drought conditions (Limousin *et al.*, 2009; Barbeta *et al.*, 2015). Leaf litterfall in all three species was higher in the drought than in the control plots. *P. latifolia*, however, was less affected than the other species, which could be attributed to its hydraulic architecture (the conduit diameter of roots and stems) (Martínez-Vilalta *et al.*, 2003) and its capacity to maintain higher hydraulic conductivity during dry periods (Barbeta *et al.*, 2012). Our results were also consistent with the higher crown defoliation and stem mortality in *Q. ilex* than in *P. latifolia* under severe drought (Ogaya & Peñuelas, 2006, 2007b; Barbeta *et al.*, 2013, 2015)

The drought treatment decreased the long-term relative production of fruit in *Q. ilex*, in agreement with shorter term observations at an earlier stage of the same experiment (Ogaya & Peñuelas, 2007c). Some studies have reported negative effects of drought on flower and fruit development (Pérez-Ramos *et al.*, 2010; Sanchez-Humanes & Espelta, 2011), on the phenology of reproduction (Peñuelas *et al.*, 2004a) and on the sex ratio (Misson *et al.*, 2011). It has been reported that Q. ilex can adapt to the limited conditions by adjusting carbon allocation to growth and reproduction (Pulido *et al.*, 2014). Nonetheless, in our study, both the ABI and the fruit production were lower under dry condition, which was also found by previous studies conducted in the same type of forest (Pérez-Ramos *et al.*, 2010; Limousin *et al.*, 2012).

The responses of forest productivity to water limitation are highly dependent on the vegetation types and species interactions (Peñuelas *et al.*, 2007; Kreyling *et al.*, 2008; McDowell *et al.*, 2008; Wu *et al.*, 2011). Most studies indicate that experimental or natural droughts cause lower productivity (Ciais *et al.*, 2005; Peñuelas *et al.*, 2007; Luyssaert *et al.*, 2010; Wu *et al.*, 2011; Tilman *et al.*, 2012; Reyer *et al.*, 2013), but other studies have reported no significant changes (Kreyling *et al.*, 2008; Jentsch *et al.*, 2011). A review of 34 precipitation experiments ranging in duration from 1 to 11 years reported that decreased precipitation significantly reduced ANPP by an average of 37% (Wu *et al.*, 2011). In our study, forest ANPP decreased by an average of only 10%, substantially lower ($p<0.1$) than expected and a likely consequence of a dampening of the effect of the treatment as the duration of the experiment increased (Barbeta *et al.*, 2013).

Litterfall should not be ignored when estimating ANPP. A large increase in litterfall coincided with water shortage in our study in the dry year of 2011 (Fig. 8). The forest ANPP estimated by the sum of ABI and litterfall would consequently not represent the response of plant production when the water deficit exceeded a determinate threshold. The estimation of ANPP thus remains methodologically difficult in Mediterranean evergreen forests, and caution is recommended when using litterfall to calculate ANPP, because litterfall does not necessarily correspond to annual production.

The duration of natural droughts impacts the increase in forest biomass

The ABIs of the three species were highly correlated with SPEI in spring (April and May) (Fig. 3), indicating that the water balance in spring was particularly important for growth. The relationships with SPEI, however, were species-specific. The ABI of *Q. ilex* was the most sensitive to natural drought (May SPEI-6), and *Q. ilex* was also the only species with different relationships in the control and drought treatments (Fig. 3). The drought treatment thus increased the dependence of *Q. ilex* ABI on water availability. The ABI of *Q. ilex* was best correlated with a longer timescale than the other two species (May SPEI-6), suggesting that water reserves stored during wet and cold seasons may be used later during the growing season (Barbeta et al., 2013; 2015). SPEI is a good predictor of radial tree growth and ANPP for forests across all biomes, and longer SPEI timescales correlate better in seasonally dry environments (Vicente-Serrano *et al.*, 2013). As with *Q. ilex* in our study, accumulated precipitation from the previous autumn and the current spring may be particularly beneficial for tree-ring growth and the features of wood anatomy (Martin-Benito *et al.*, 2012; Drew *et al.*, 2013). Forests in Mediterranean ecosystems may thus undergo significant decreases in ABI if lower precipitation and higher evapotranspiration reduce the autumn, winter and spring water recharge.

This Mediterranean forest suffered frequent natural droughts in summer, which increased branch withering and defoliation (Fig. 4a). Relative branch litterfall was negatively correlated with September SPEI-3 and thus depended on the summer water balance (July, August and September). High intensities of summer droughts could promote hydraulic failure at the branch level and increase branch withering. A previous study at this site emphasized that *Q. ilex* and *P. latifolia* stem mortality depended on the water balance over longer periods (Barbeta *et al.*, 2013). Branch withering would thus represent a response to shorter droughts that do not induce widespread stem mortality. Defoliation may be another short-term adjustment to drought. Indeed, plants adjust to drought by reducing the lifespan of leaves and by increasing turnover rate (Bussotti *et al.*, 2003; Ogaya & Peñuelas, 2006; Limousin *et al.*, 2009, 2012). The accumulated effect of drought in the long-term would substantially reduce crown condition and transpiration, eventually modifying the carbon and water cycles and the ecosystem services.

Fruit production and December SPEI-6 were positively correlated in *Q. ilex* in our 15-year moderate experimental drought, indicating higher fruit production with higher water availability in summer and autumn (Fig. 7b), consistent with a study at this site reporting a strong correlation between fruit production and precipitation in *Q. ilex* 10 months prior to fruit maturation (Ogaya & Peñuelas, 2007c). Drier summer and autumn in the future would thus decrease fruit production. These results also support SPEI as an effective tool to assess the impacts of drought on agricultural and ecological production (Potop, 2011; Vicente-Serrano *et al.*, 2013).

The water balance in March, April and May may be critical for the ANPP of this forest (Fig. 8). The response of ANPP to drought varies among forest types and drought severity and duration, but dry forests, shrublands and steppes with low ANPPs have the highest correlations with the SPEI (Vicente-Serrano *et al.*, 2013).

The response to drought also depends on the characteristic drought timescale; arid and humid biomes respond to water deficits of shorter duration than do semiarid and subhumid biomes (Vicente-Serrano *et al.*, 2012; 2013). Robust observational studies have highlighted that drought is a main driver of reduced forest ANPP and that drought can be amplified by warmer temperatures (Breshears *et al.,* 2005; Mueller *et al.*, 2005; Adams *et al.*, 2009; Wu *et al.,* 2011; Anderegg *et al.*, 2012).

Long-term experimental drought is driving Mediterranean forests to acclimate to extreme conditions

The forest in this study experienced three extreme dry periods during this 15-year study, in 2000-2001, 2005-2006 and 2011-2012. Both the experimental and natural droughts decreased the ABI of the forest. Leaf litterfall was highly variable inter-annually, with higher values in the drought than the control plots throughout the study period and a peak of defoliation in the extreme drought in 2011. Extreme droughts provoked higher tree mortality but also activated adaptive responses linked to forest structure and species composition (Mueller *et al.*, 2005; Ruiz-Labourdette *et al.*, 2012; Grimm *et al.*, 2013). The effects of drought on forest community were gradually attenuated at our experimental site. ABI and ANPP presented a dampening trend that is likely a result of (i) demographic compensation enhancing recruitment or adult survival due to low competition in the drought plots (Jentsch *et al.*, 2011; Lloret *et al.*, 2012; Barbeta *et al.*, 2013; Peñuelas *et al.*, 2013a), (ii) changes in morphology and function at the individual level (Martin-Stpaul *et al.*, 2013; Barbeta *et al.*, 2015) and (iii) epigenetic modifications (Rico *et al.*, 2014). The results of this study thus show that a partial and gradual acclimation to a drier environment over the long-term is possible if the responses to drought fluctuate below safe thresholds and/or tipping points.

The Mediterranean region is predicted to suffer more rapid and intense climate changes in the coming decades that could severely alter the structure of forests and their capacity to assimilate carbon (IPCC, 2014). Mediterranean forests display tolerance, plasticity and resilience in response to drought, but the progressive increase in aridity combined with extreme droughts will challenge the survival of these forests in their current form. Our 15-year experimental-drought study demonstrated a partial acclimation of a Mediterranean forest to a 13% decrease in soil moisture, but if the effects of chronic and extreme droughts increase beyond a critical threshold, this stabilizing process could be disrupted and produce a shift in the vegetation (a progressive replacement of *Q. ilex* by *P. latifolia*). Future studies should address the complex dynamics (demographical processes and structure and composition changes) underlying the response of ecosystems to extreme droughts and chronically drier conditions.

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Figure Legends

Fig. 1 Mean annual temperature, inter-annual precipitation and May SPEI-6 variables during the study period (1999-2013). The error bars in represent the standard errors of the means (n=4 plots).

Fig. 2 Aboveground biomass increment (ABI) of the three dominant species in the controls and drought treatments. The bars represent the best-fitted SPEI timescale for *Arbutus unedo* (April SPEI-1), *Quercus ilex* (May SPEI-6) and *Phillyrea latifolia* (May SPEI-3). Significant differences are marked with asterisks (*, $p<0.05$; **, $p<0.01$; ns, not significant). The vertical bars represent the standard errors of the means (n=4 plots).

Fig. 3 Multiple-slope comparisons between the controls and drought treatments of the above-ground biomass increment (ABI) for *Arbutus unedo*, *Quercus ilex* and *Phillyrea latifolia* during 1999-2013. The error bars represent the standard errors of the means (n=4 plots).

Fig. 4 (a) Relative branch litterfall of all species in the controls and drought treatments (n=4 plots). Significant differences are marked with asterisks (***, *p*<0.001). (b) The standardized major axis regression between relative branch litterfall and September SPEI-3 in the controls and drought treatments.

Fig. 5 Relative leaf litterfall to biomass of *Arbutus unedo*, *Quercus ilex* and *Phillyrea latifolia* throughout the study period (1999-2013). Significant differences are marked with asterisks (*, *p*<0.05; **, *p*<0.01; ***, *p*<0.001). The error bars represent the standard errors of the means (n=4 plots).

Fig. 6 Allometric relationships between the relative leaf litterfall and October SPEI-3 for *Arbutus unedo*, October SPEI-3 for *Quercus ilex* and November SPEI-3 for *Phillyrea latifolia*. The error bars represent the standard errors of the means (n=4 plots).

Fig. 7 (a) Relative fruit litterfall to biomass in the control and drought treatments for *Quercus ilex*. The error bars represent the standard errors of the means (n=4 plots). (b) Relationship between the relative fruit litterfall and December SPEI-6 for *Q. ilex*.

Fig. 8 Mean aboveground biomass increment (ABI) for May SPEI-6, total litterfall for September SPEI-1 and aboveground net primary production (ANPP) for May SPEI-3 of the forest community in the control and drought treatments. Significant differences are marked with asterisks (***, *p*<0.001). The error bars represent the standard errors of the means (n=4 plots). The vertical bars represent the best-fitted SPEI time-scale.

Fig. 9 Relationships between aboveground biomass increment (ABI) and May SPEI-6, total litterfall and September SPEI-1 and aboveground net primary production (ANPP) and May SPEI-3 for the entire forest community. The error bars represent the standard errors of the means (n=4 plots).

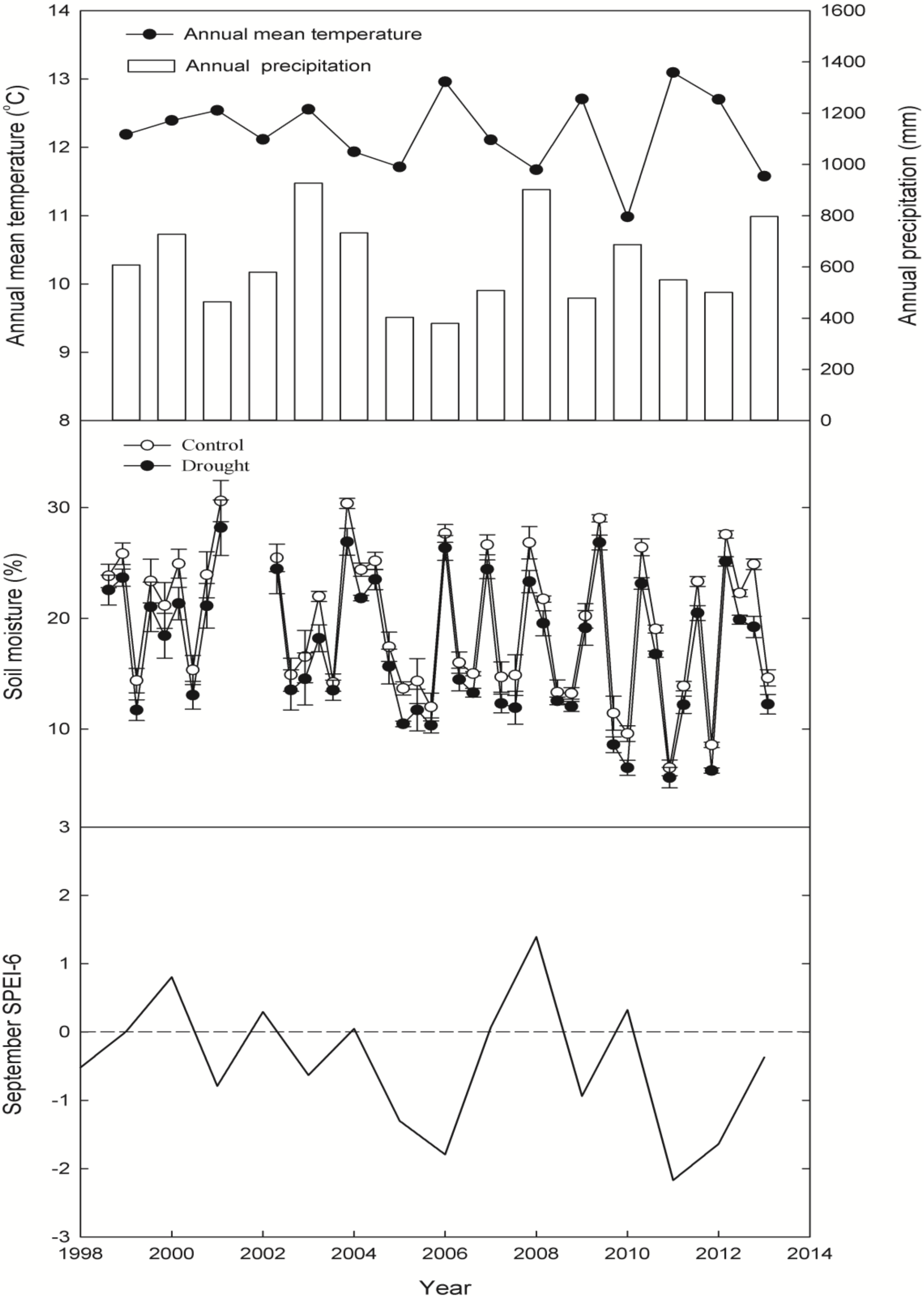

Annual mean temperature
Annual precipitation
Annual mean temperature (°C)
Annual precipitation (mm)
14
13
12
11
10
9
8
1600
1400
1200
1000
800
600
400
200
0
Control
Drought
Soil moisture (%)
30
20
10
3
September SPEI-6
2
1
0
-1
-2
-3
1998
2000
2002
2004
2006
2008
2010
2012
2014
Year

Fig. 1

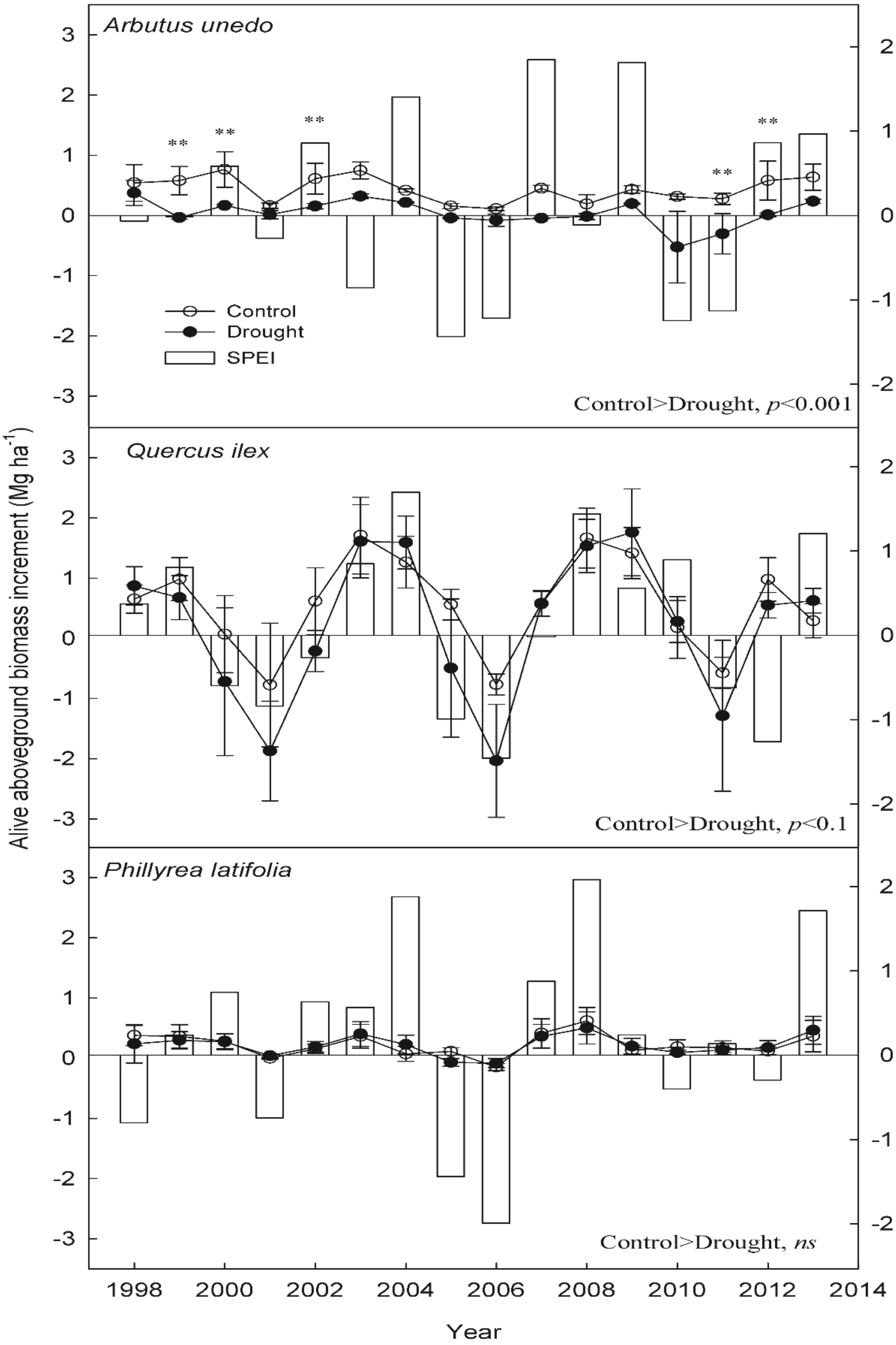

Arbutus unedo
Quercus ilex
Phillyrea latifolia
Control
Drought
SPEI
**
Control>Drought, p<0.001
Control>Drought, p<0.1
Control>Drought, ns
Alive aboveground biomass increment (Mg ha-1)
April SPEI-1
May SPEI-6
May SPEI-3
Year
1998
2000
2002
2004
2006
2008
2010
2012
2014
3
2
1
0
-1
-2
-3

Fig. 2

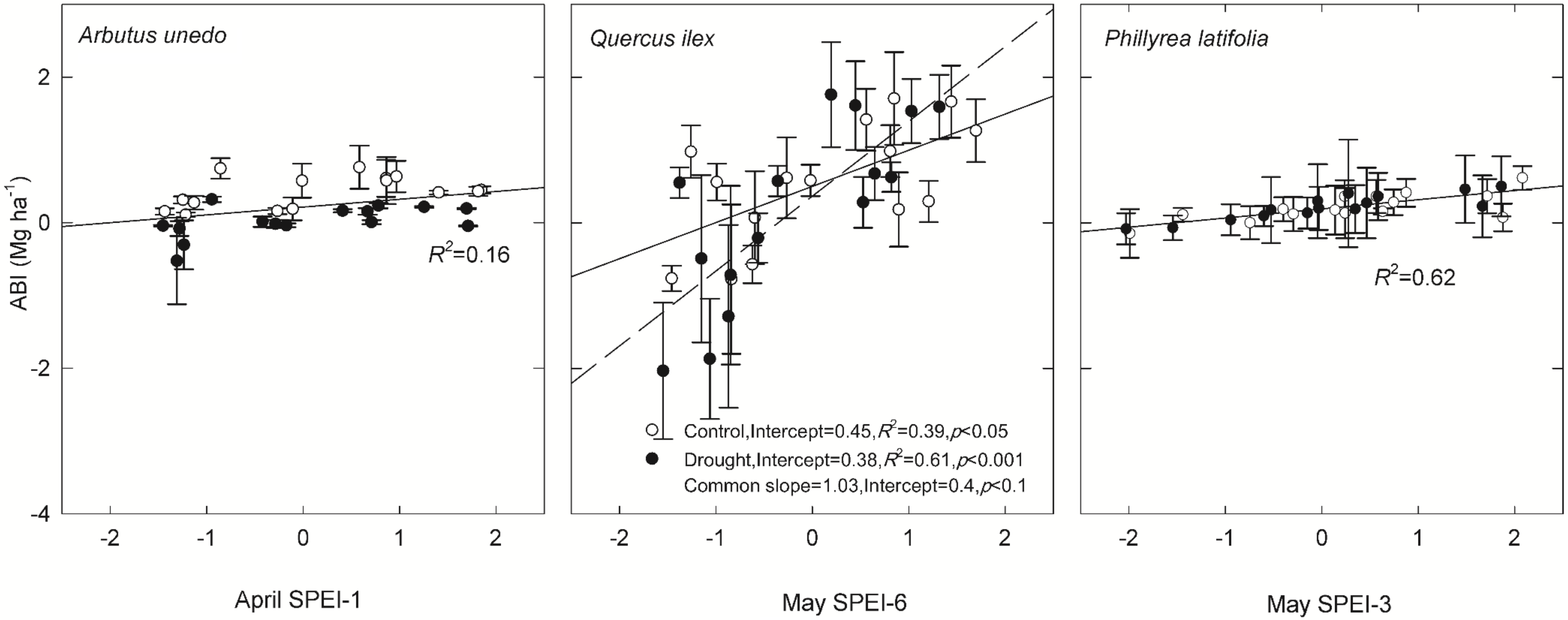

Arbutus unedo
Quercus ilex
Phillyrea latifolia
ABI (Mg ha^{-1})
2
0
-2
-4
-2
-1
0
1
2
R^2=0.16
R^2=0.62
○ Control,Intercept=0.45,R^2=0.39,p<0.05
● Drought,Intercept=0.38,R^2=0.61,p<0.001
Common slope=1.03,Intercept=0.4,p<0.1
April SPEI-1
May SPEI-6
May SPEI-3

Fig. 3

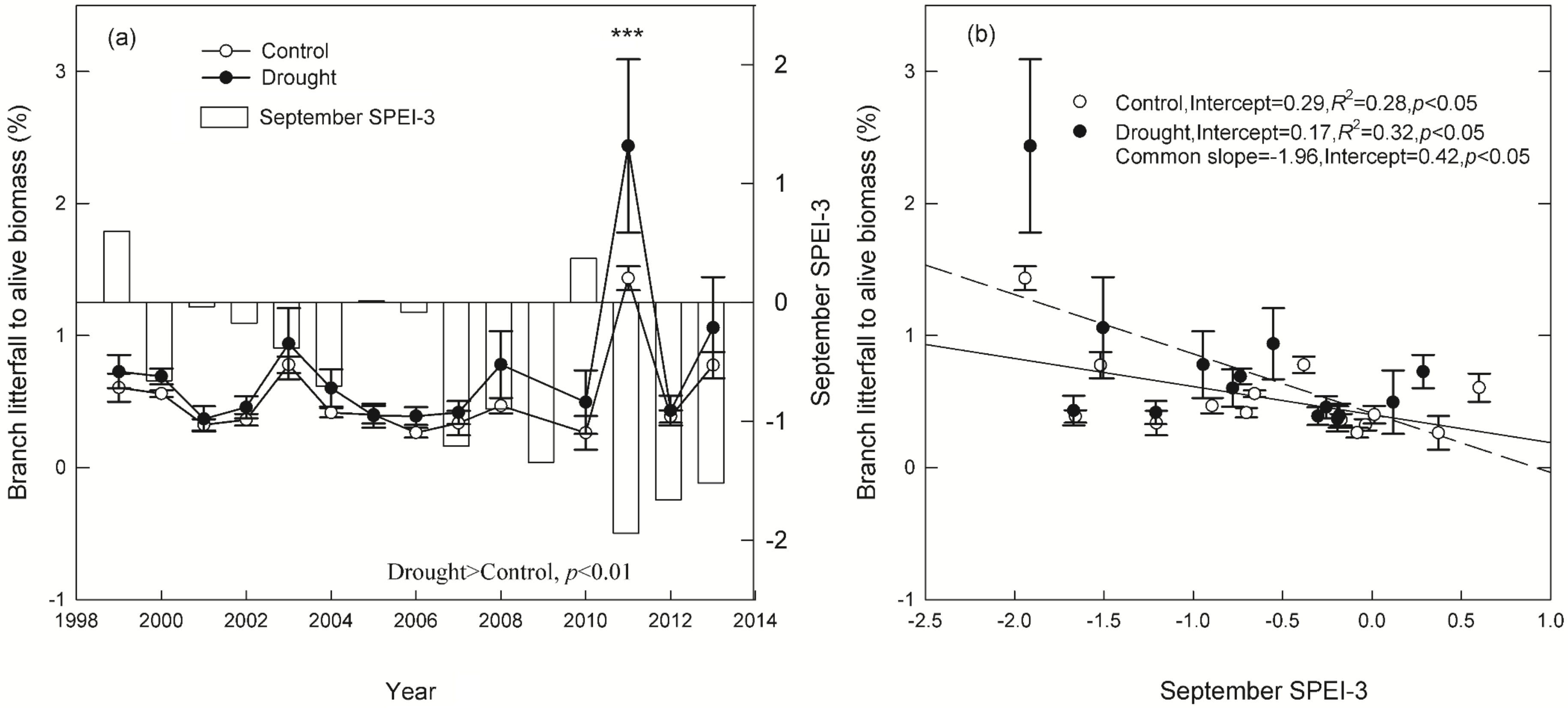
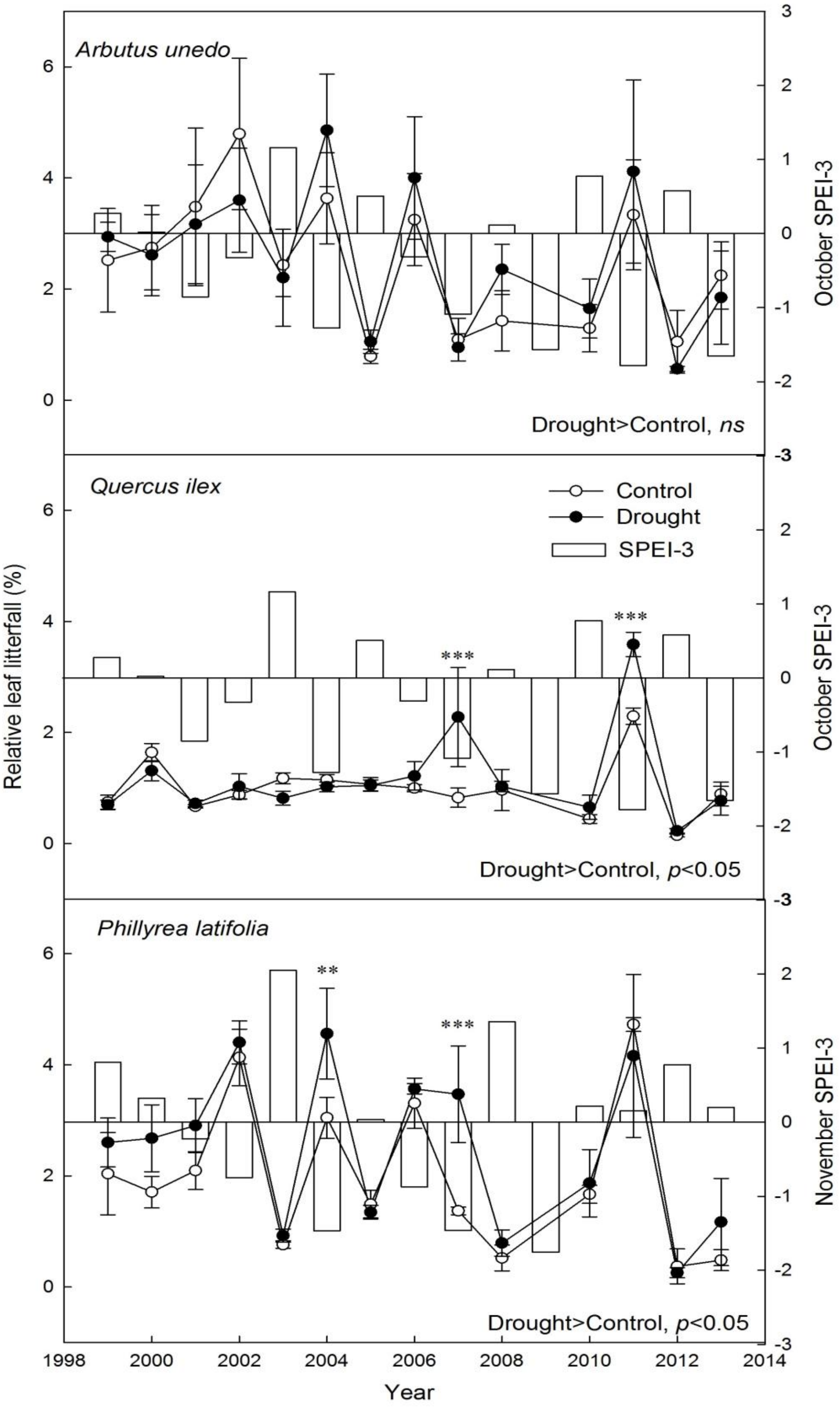

(a)
Control
Drought
September SPEI-3
***
Drought>Control, p<0.01
Branch litterfall to alive biomass (%)
September SPEI-3
Year
1998
2000
2002
2004
2006
2008
2010
2012
2014
-1
0
1
2
3
-2
-1
0
1
2
(b)
Control,Intercept=0.29,R2=0.28,p<0.05
Drought,Intercept=0.17,R2=0.32,p<0.05
Common slope=-1.96,Intercept=0.42,p<0.05
Branch litterfall to alive biomass (%)
September SPEI-3
-2.5
-2.0
-1.5
-1.0
-0.5
0.0
0.5
1.0

Fig. 4



Arbutus unedo
Drought>Control, ns
Quercus ilex
Control
Drought
SPEI-3
***
***
Drought>Control, p<0.05
Phillyrea latifolia
**
***
Drought>Control, p<0.05
Relative leaf litterfall (%)
October SPEI-3
October SPEI-3
November SPEI-3
Year
0
2
4
6
-3
-2
-1
0
1
2
3
1998
2000
2002
2004
2006
2008
2010
2012
2014

Fig. 5

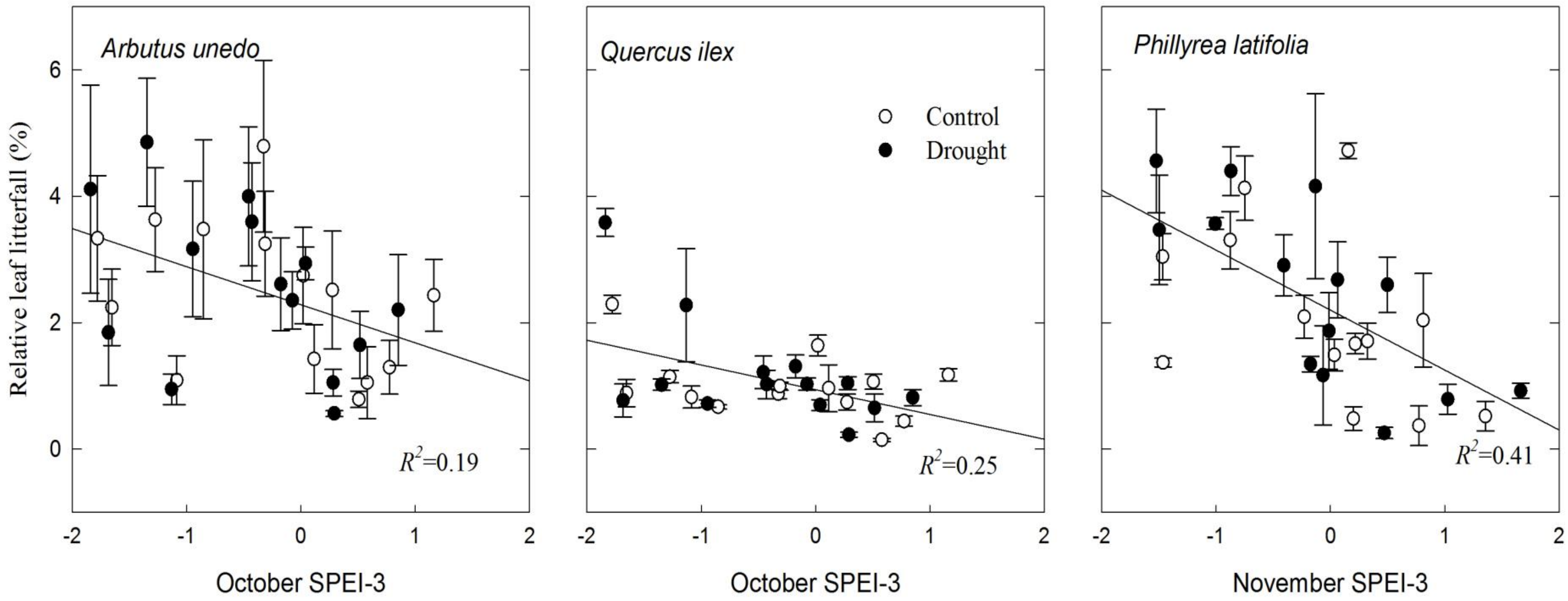

Arbutus unedo
Quercus ilex
Phillyrea latifolia
Relative leaf litterfall (%)
○ Control
● Drought
R^2=0.19
R^2=0.25
R^2=0.41
0
2
4
6
-2
-1
0
1
2
October SPEI-3
October SPEI-3
November SPEI-3

Fig. 6

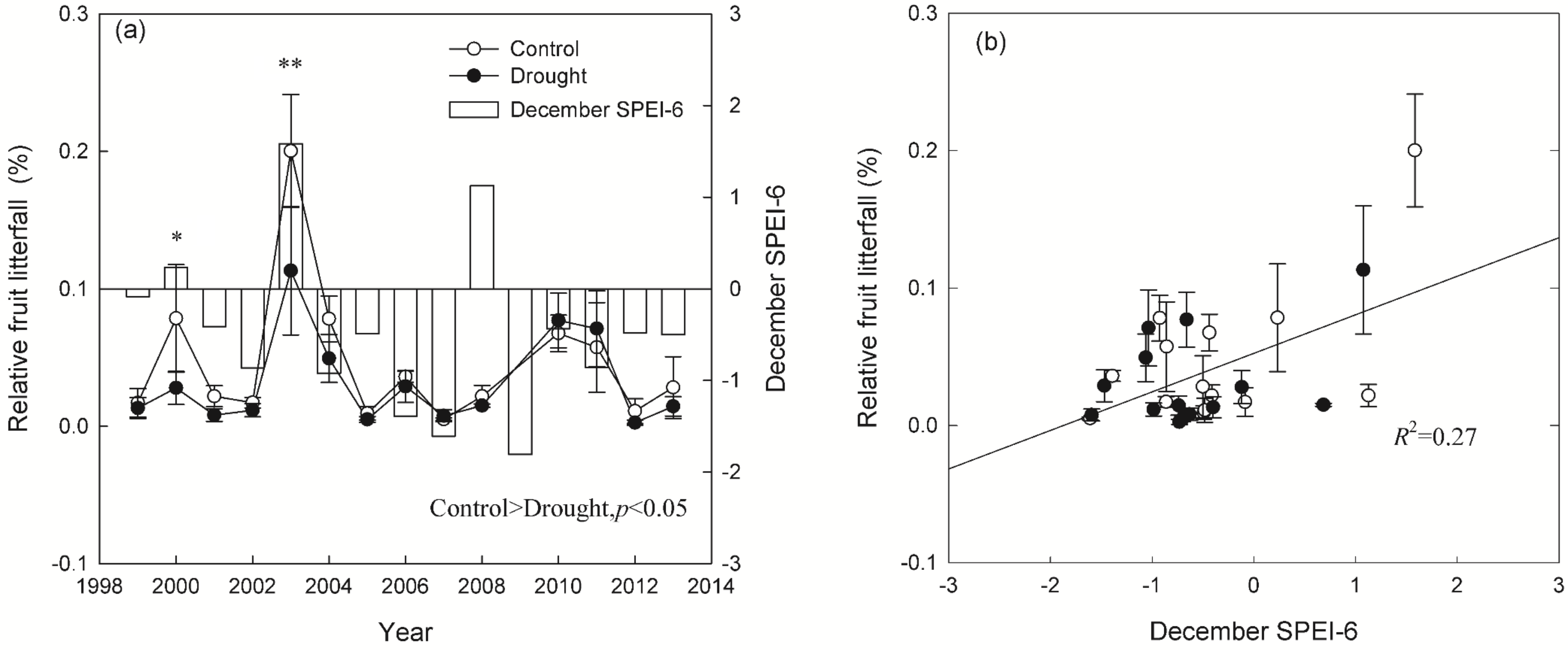

(a)
Control
Drought
December SPEI-6
*
**
Control>Drought,$p<0.05$
Relative fruit litterfall (%)
December SPEI-6
Year
0.3
0.2
0.1
0.0
-0.1
3
2
1
0
-1
-2
-3
1998
2000
2002
2004
2006
2008
2010
2012
2014
(b)
$R^2=0.27$
Relative fruit litterfall (%)
December SPEI-6
0.3
0.2
0.1
0.0
-0.1
-3
-2
-1
0
1
2
3

Fig. 7

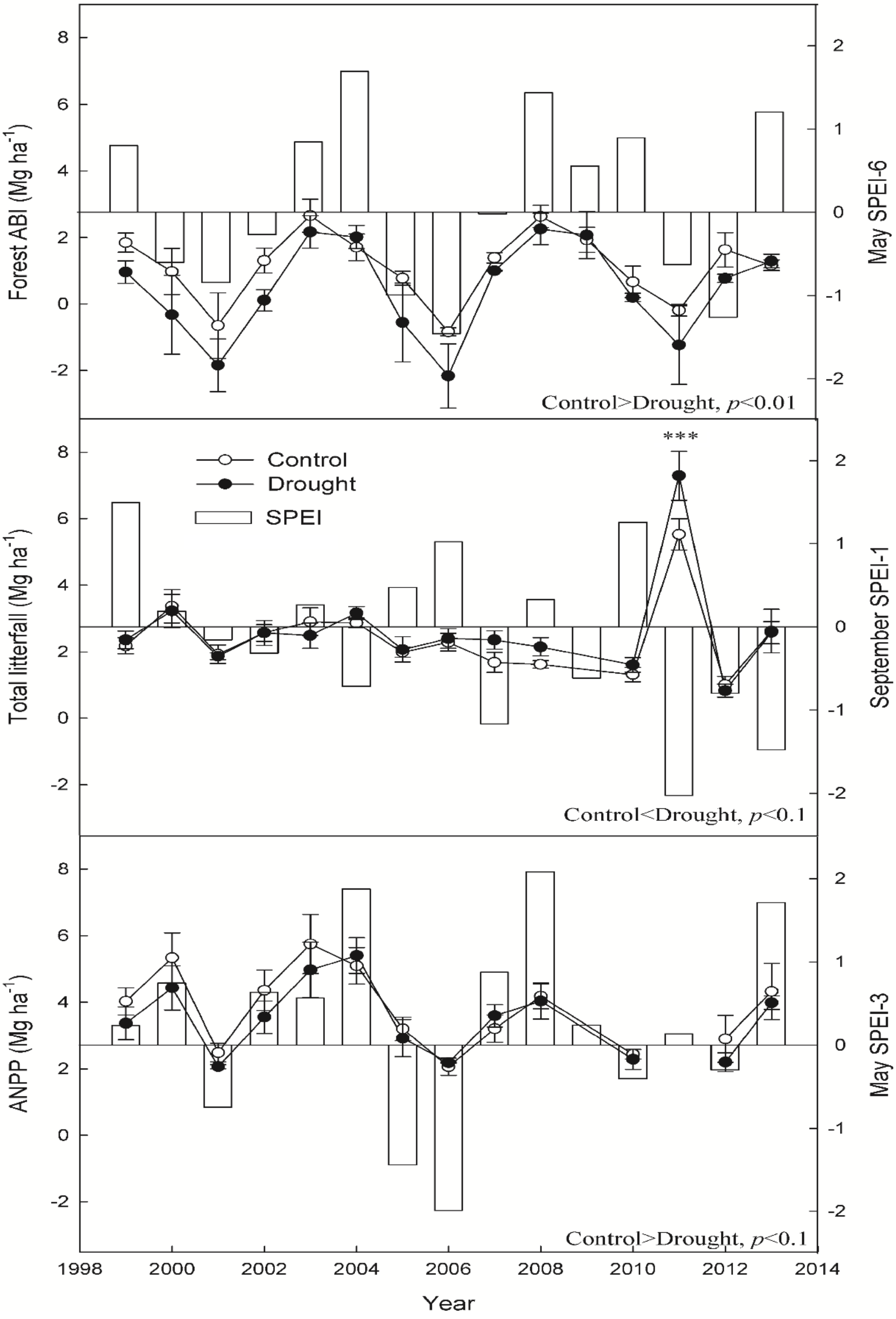

Forest ABI (Mg ha^{-1})
May SPEI-6
Control>Drought, p<0.01
***
Control
Drought
SPEI
Total litterfall (Mg ha^{-1})
September SPEI-1
Control<Drought, p<0.1
ANPP (Mg ha^{-1})
May SPEI-3
Control>Drought, p<0.1
8
6
4
2
0
-2
2
1
0
-1
-2
1998
2000
2002
2004
2006
2008
2010
2012
2014
Year

Fig. 8

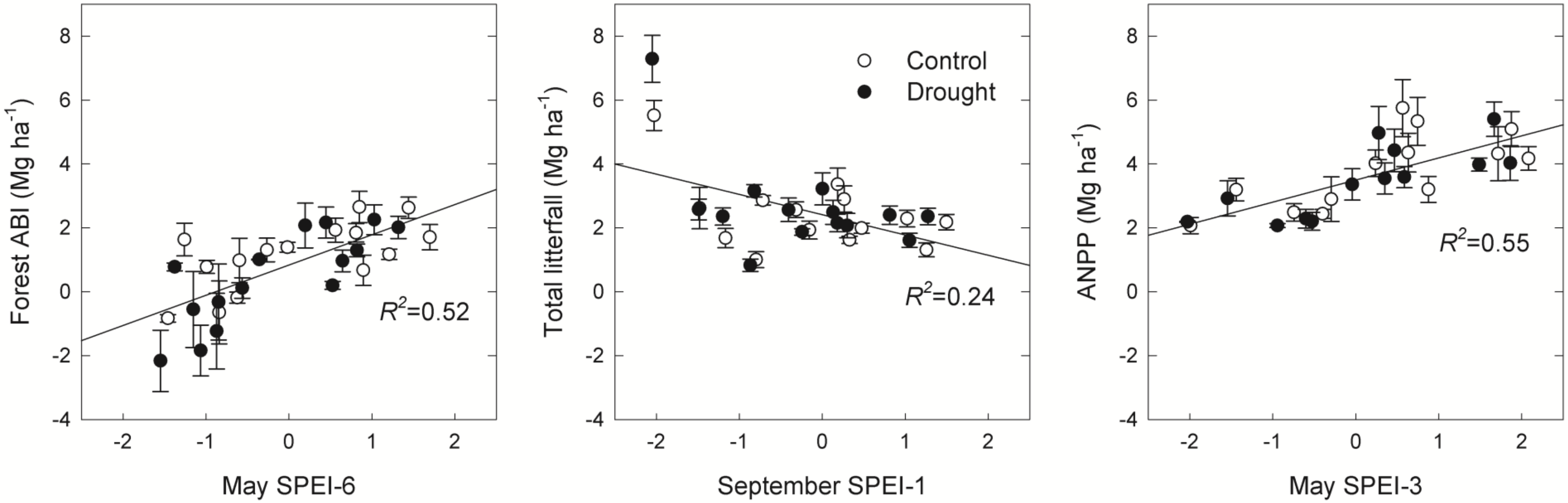

Forest ABI (Mg ha^{-1})
May SPEI-6
R^2=0.52
Total litterfall (Mg ha^{-1})
September SPEI-1
○ Control
● Drought
R^2=0.24
ANPP (Mg ha^{-1})
May SPEI-3
R^2=0.55
8
6
4
2
0
-2
-4
-2
-1
0
1
2

Fig. 9