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ORIGINAL PAPER

Tree growth, mortality, and above-ground biomass accumulation in a holm oak forest under a five-year experimental field drought

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Abstract A holm oak forest was exposed to an experimental drought during 5 years to elucidate the growth responses of the dominant species *Quercus ilex*, *Arbutus unedo* and *Phillyrea latifolia*. Soil water availability was partially reduced, about 15% as predicted for this area for the next decades by GCM and ecophysiological models, by plastic strips intercepting rainfall and by ditch exclusion of water runoff. The stem diameter increment was highly correlated with annual rainfall in all species, and drought treatment strongly reduced the diameter increment of *Q. ilex* (41%) and specially of *A. unedo* (63%), the species showing higher growth rates. Stem mortality rates were highly correlated with previous stem density, but drought treatment increased mortality rates in all species. *Q. ilex* showed the highest mortality rates (9% and 18% in control and drought plots, respectively), and *P. latifolia* experienced the lowest mortality rates (1% and 3% in control and drought plots, respectively). Drought strongly reduced the increment of live aboveground biomass during these 5 years (83%). *A. unedo* and *Q. ilex* experienced a high reduction in biomass increment by drought, whereas *P. latifolia* biomass increment was insensitive to drought. The different sensitivity to drought of the dominant species of the holm oak forest may be very important determining their future development and distribution in a drier environment as expected in Mediterranean areas for the next decades. These drier conditions could thus have strong effects on structure (species composition) and functioning (carbon uptake and biomass accumulation) of these Mediterranean forests.

Keywords *Arbutus unedo* · Carbon sink · Climate change · Mediterranean forests · *Phillyrea latifolia* · *Quercus ilex*

Introduction

Water availability is a crucial factor determining the diameter increment of trees (Fritts 1976; Orwig and Abrams 1997) and also their height (Koch et al. 2004). Thus, water availability has a strong influence in the plant carbon sequestration, and in the role of the forests as a carbon sink. The improvement of our knowledge of tree responses to changes in water availability is essential to improve predictions of changes in forests posed by the new climatic constraints predicted for next decades (IPCC 2001; Kramer and Mohren 2001; Kramer et al. 2002; Peñuelas et al. 2004b).

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Summer drought has been recognized as the major stress limiting plant species growth and distribution in all Mediterranean regions of the world (Mooney 1983). Therefore, in these regions water availability is a very important factor determining the diameter increment of the stems (Zhang and Romane 1991; Borghetti et al. 1998; Oliveira et al. 1994; Caritat et al. 1996, 2000; Boreux et al. 1998; Costa et al. 2001; Ogaya et al. 2003), very often more important than other factors such as nutrient availability (Cartan-Son et al. 1992; Mayor and Rodà 1994; Mayor et al. 1994). In these Mediterranean regions, a reduction in water availability is expected for the near future as a result of decreases of precipitation and of increases of temperatures, and the consequent increases of evapotranspiration rates (IPCC 2001), which are predicted to be greater than those that already occurred in the twentieth century (Piñol et al. 1998; IPCC 2001; Peñuelas et al. 2002; 2004b).

Holm oak (*Quercus ilex* L.) is a widely distributed tree in the Mediterranean basin. There are some species associated with holm oak forest such as *Phillyrea latifolia* L. and strawberry tree (*Arbutus unedo* L.) with different sensitivity to environmental stresses: *P. latifolia* is a tall shrub more tolerant to drought (Lloret and Siscart 1995; Peñuelas et al. 1998, 2000, 2001; Ogaya et al. 2003) and heat conditions (Ogaya and Peñuelas 2003) than *Q. ilex* and *A. unedo* (Ogaya et al. 2003; Ogaya and Peñuelas 2004).

Q. ilex has been reported to experience higher mortality rates during severe drought events than *P. latifolia* (Lloret and Siscart 1995; Peñuelas et al. 2000). Moreover, after severe drought periods, surviving *Q. ilex*trees have been found to experience a decrease in $\Delta^{13}C$ in their leaves (as a result of an increase in water use efficiency) during the two following years, whereas no changes in isotopic discrimination induced by severe drought have been found in *P. latifolia* (Peñuelas et al. 2000).

Few drought experiments have been conducted in natural forests (Borghetti et al. 1998; Hanson et al. 2001; Peñuelas et al. 2004a), and even fewer have manipulated rainfall over multiple years as it is being done in the Prades mountains in Southern Catalonia (Ogaya et al. 2003). Manipulative water availability experiments allow us to obtain accurate information about ecosystem responses, and to provide further knowledge of long-term changes in growth and development of the different species in response to a decrease in water availability. In this experiment, we have seen a decrease in photosynthetic rates in *Q. ilex*, but not in *P. latifolia* (Ogaya and Peñuelas 2003), and also a decrease in flower and fruit production was observed in *Q. ilex* and in *A. unedo* (Ogaya and Peñuelas 2004). It is expected that these changes in photosynthetic activity will be followed by long-term changes in carbon sequestration and biomass accumulation.

We aimed to study the long-term (5 years of continuous rainfall manipulation) changes in stem growth, stem mortality, and the live aboveground biomass accumulation in these three co-occurring Mediterranean evergreen species (*Q. ilex*, *P. latifolia*, and *A. unedo*) induced by an experimental drought simulating the expected decrease in water availability for the next decades in this typical Mediterranean holm oak forest of Prades. Our hypothesis was that drought-tolerant species such as *P. latifolia* will be less affected in their growth and mortality rates than other species more sensitive to water availability such as *A. unedo* and the currently dominant species *Q. ilex*. Our final aim was to use the results to discuss the possible effects on productivity and community composition of Mediterranean forests of a decreased relative soil water availability of 15–20% as the one predicted for the next decades by Global Circulation Models and by ecophysiological models such as GOTILWA (IPCC 2001; Sabaté et al. 2002; Peñuelas et al. 2004b).

Materials and methods

Study site

The study was carried out in a holm oak forest in the Prades Mountains in Southern Catalonia (NE Spain) (41°13′ N, 0°55′ E), on a south-facing slope (25% slope) at 930 m a.s.l. The soil is a Dystric Cambisol over Paleozoic schist, and its depth ranges from 35 to 90 cm. Mean annual temperature during the study period was 12.4°C and the mean rainfall was 655 mm with a pronounced summer drought during approximately 3 months. This traits, including the steep slope, are typical in Mediterranean forests distributed in the Mediterranean basin which is characterized by a complicated orography (mostly mountainous region).

This holm oak forest has a very dense multistem crown (16616 trees ha^{-1}, and 115 Mg ha^{-1}) and it is dominated by *Quercus ilex* L. (8633 trees ha^{-1}, and 89 Mg ha^{-1}), *Phillyrea latifolia* L. (3600 trees ha^{-1}, and 14 Mg ha^{-1}) and *Arbutus unedo* L. (2200 trees ha^{-1}, and 9 Mg ha^{-1}) with abundant presence of other evergreen species well adapted to dry conditions (*Erica arborea* L., *Juniperus oxycedrus* L., *Cistus albidus* L.), and occasional individuals of deciduous species (*Sorbus torminalis* (L.) Crantz and *Acer monspessulanum* L.). This forest has not been perturbed for the last 60 years.

Experimental design and methodological monitoring

Eight 15 × 10 m plots were delimited at the same altitude along the slope. Half the plots (randomly selected) received the drought treatment since 1999 and the other half were considered control plots. The drought treatment consisted of partial rain exclusion by suspending PVC strips and funnels at a height of 0.5–0.8 m above the soil. Strips and funnels covered approximately 30% of the total plot surface. Moreover, a 0.8 m deep ditch was excavated along the entire top edge of the upper part of the treatment plots to intercept runoff water supply. Water intercepted by strips, funnels, and ditches was conducted outside the plots, below the bottom edge of the plots. Rainfall exclusion by plastic strips does not affect the light interception by the trees because the whole tree canopies are located above the plastics. Litterfall fallen over the plastic strips was regularly (approximately every month) placed below them, and all nutrient differences between below and outside the strips are apparently only due to the change in water availability for decomposition of this litterfall.

An automatic meteorological station installed between the plots monitored temperature, photosynthetic active radiation, air humidity, and precipitation each half-hour. Soil moisture was measured every 2 weeks throughout the experiment by time domain reflectometry (Tektronix 1502C, Beaverton, Oregon, USA) (Zegelin et al. 1989; Gray and Spies 1995). Three stainless steel cylindrical rods, 25 cm long, were vertically installed into the upper 25 cm of the soil at four randomly selected places in each plot. The time domain reflectometer was manually attached to the ends of the rods for each measurement.

Growth, mortality and aboveground biomass increase

The stem circumference was measured annually since 1999 each winter throughout the study until winter 2004. The measurements were conducted with a metric tape at 50 cm height in all living stems of all the species with a diameter larger than 2 cm at 50 cm height. The stem annual mortality rate (m) was calculated as: $m = 1 - (1 - (N_o - N_t)/N_o)^{1/t}$ as described in Sheil et al. (1995), where N_o and N_t are live stem counts at the beginning and end of this 5-year (t) experimental drought.

Aboveground biomass in the plots was estimated by allometric relationships between tree aboveground biomass (AB) and the stem diameter at 50 cm height (D50). Outside the plots, 12 *Q. ilex* and 13 *P. latifolia* trees were harvested, their perimeter at 50 cm height was measured and all their aboveground biomass was weighed after drying them in an oven to reach constant weight. To estimate the aboveground biomass of *Q. ilex* and *P. latifolia* we used the calculated allometric relationships (lnAB = 4.9 + 2.3 lnD50; $R^2 = 0.98$; $n = 12$: $P < 0.001$ for *Q. ilex*, and lnAB = 4.3 + 2.5 lnD50; $R^2 = 0.97$; $n = 13$; $P < 0.001$ for *P. latifolia*), and to estimate the aboveground biomass of *A. unedo* we used the allometric relationship calculated few years ago on the same area by Lledó (1990) (lnAB = 3.8 + 2.6 lnD50; $R^2 = 0.99$; $n = 10$; $P < 0.001$).

Statistical analyses

An analyses of covariance (ANCOVA) was performed with treatment application and species as independent factors, annual precipitation as covariant, and the mean of stem diameter increment in each plot as dependent variable. Another ANCOVA was performed with species and treatment application as independent factors, stem density in each plot as covariate, and the stem annual mortality rate in each plot as dependent variable. Data of annual mortality rate (p) was transformed to arcsin $(p)^{1/2}$ to reach the normality assumptions of the ANCOVA. Finally, another ANCOVA was also conducted with treatment application and species as independent factors, initial biomass in each plot as covariate, and the percentage of biomass increment in each plot as dependent variable. Data of percentage of biomass increment (p) was transformed to sin (p) to reach the normality assumptions of the ANCOVA. All analyses were performed with the Statistica software package (StatSoft Inc. 2001).

Results

Meteorological data and soil water status

Climatic data was typical for Mediterranean sites. During the experimental period, mean annual temperature was similar in all years (Fig. 1). It ranged between 12.2°C (in 1999) and 12.6°C (in 2003). Annual rainfall was more variable and ranged between 464 mm (in 2001) and 899 mm (in 2003). The mean annual rainfall was 655 mm during the overall studied period (Fig. 1).

Soil moisture experienced important fluctuations depending on rainfall periodicity. Minimum values (about 10% v/v) were reached in summer seasons, coinciding with drought conditions, and maximum values (about 30% v/v) were reached in spring and autumn seasons, coinciding with heavy rainfall periods. Drought plots had lower soil moisture (on average 15% relative reduction) than control plots (Fig. 1).

Stem diameter increment

Stem diameter increment was on average 22% smaller in drought plots than in control ones ($P < 0.01$) during the overall studied period. Although stem diameter increment showed a great inter-annual variability (Fig. 2), in all the studied years it was lower in the drought plots than in the control plots (Fig. 2). Stem diameter increment and its reduction induced by drought were not the same for the different species (interaction species·treatment, $P = 0.05$), *A. unedo* had the highest stem diameter increment rates but also experienced the highest decrease (63%) in drought conditions, whereas *Q. ilex* had lower decrease in drought plots (41%), and *P. latifolia* did not experience any decrease (Fig. 3). Stem diameter increment was highly correlated with total annual rainfall ($P < 0.01$) (Fig. 4).

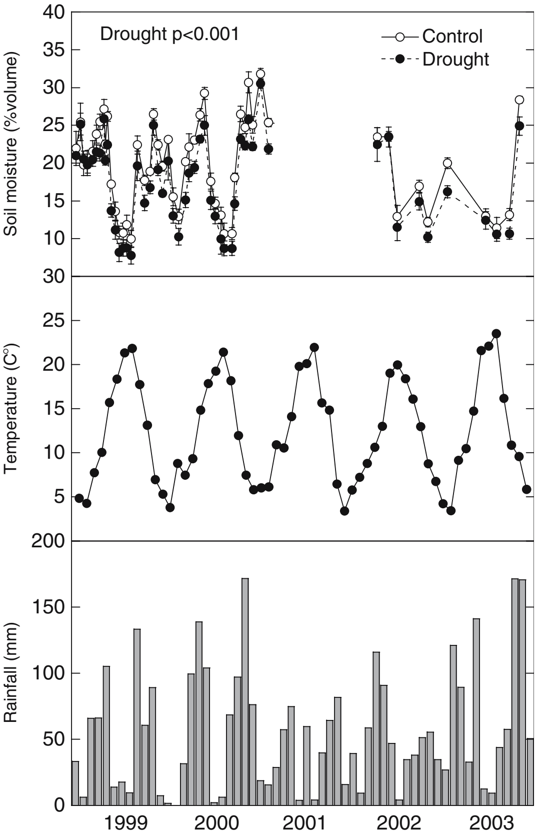

Fig. 1 Seasonal course of soil moisture, monthly temperatures, and monthly rainfall at the study site during the overall studied period

Mortality rates

The annual stem mortality rate was highly correlated with tree density in each plot, and quite high during these 5 years of study (Fig. 5). There

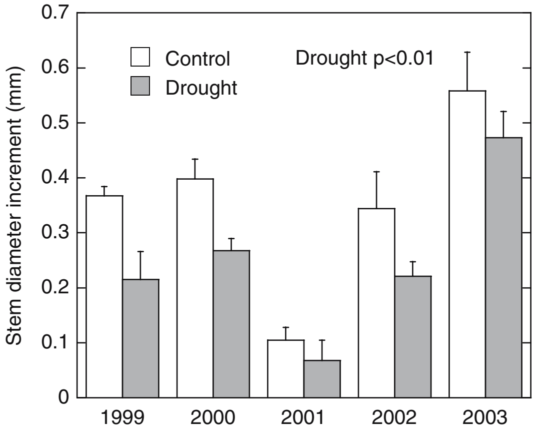

Fig. 2 Annual stem diameter increment of all species in control and drought plots during the overall studied period. Vertical bars indicate standard errors ($n = 4$ plot averages of 172–332 individuals each one)

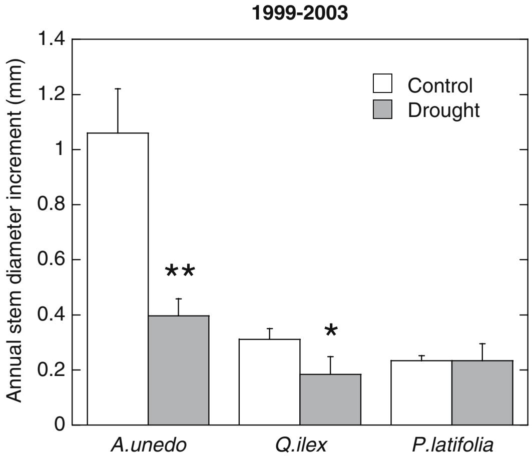

Fig. 3 Mean annual stem diameter increment of *A. unedo*, *Q. ilex*, and *P. latifolia* in control and drought plots during the overall studied period. Vertical bars indicate standard errors ($n = 4$ plot averages of 15–221 individuals each one), the asterisk indicates $P < 0.05$, and the two asterisks indicate $P < 0.01$ (significance levels in the ANCOVA post-hoc tests)

were more dead stems in drought than in control plots (approximately the 8.5% and 5.8% of all stems in drought and control plots, respectively) (Fig. 5). So the annual rate of dead stems was on average 46% higher in drought plots than in control plots ($P = 0.02$). *Q. ilex* showed higher stem mortality rate than the two other species ($P = 0.03$) (Fig. 6).

Aboveground biomass

During these 5 years of study, live aboveground biomass increment (biomass of live trees in January 2004 minus biomass of live trees in January 1999), highly dependent on the initial aboveground biomass in each plot ($P < 0.01$), was about 6.0 Mg ha^{-1} and 1.0 Mg ha^{-1} in control and drought plots, respectively) (Fig. 7).

The relative increment of live aboveground biomass to previous aboveground biomass was

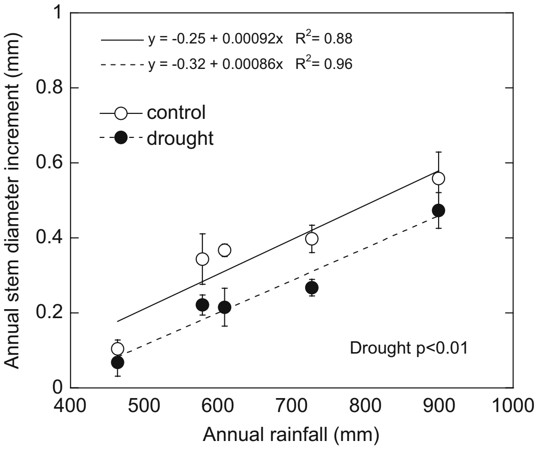

Fig. 4 Relationship between annual stem diameter increment of all species and annual rainfall in control and drought plots during the overall studied period. Vertical bars indicate standard errors ($n = 4$ plot averages of 172–332 individuals each one)

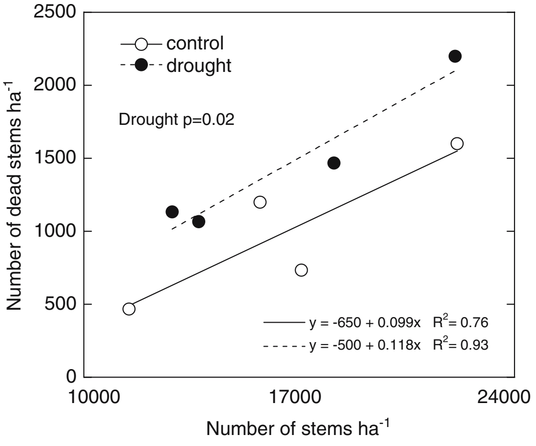

Fig. 5 Relationship between the number of dead stems and the stem density of all species in each plot in control and drought conditions during the overall studied period (each point corresponds to one plot)

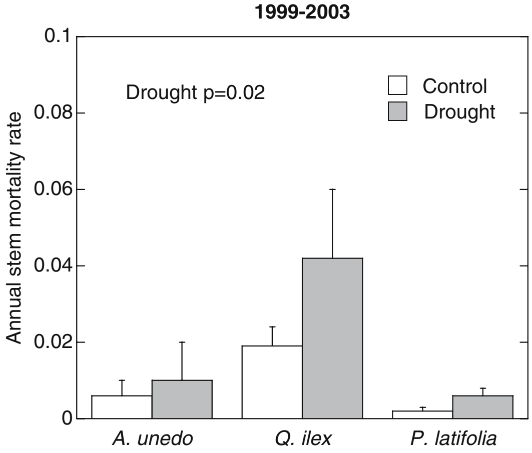

Fig. 6 Mean annual stem mortality rates (calculated as $m = 1 - (1 - (N_o - N_t/N_o)^{1/t}$; see text) of *A. unedo*, *Q. ilex*, *P. latifolia* in control and drought plots during the overall studied period. Vertical bars indicate standard errors ($n = 4$ plot averages of 15–332 individuals each one)

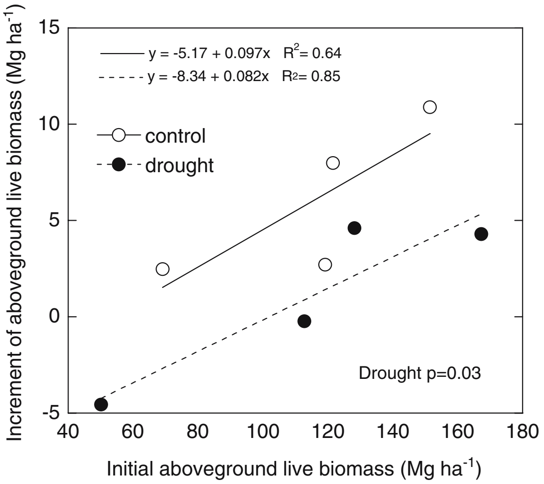

Fig. 7 Relationship between the increment of aboveground live biomass and initial aboveground live biomass of all species in each plot in control and drought conditions during the overall studied period (each point corresponds to one plot)

higher in *A. unedo* than in *P. latifolia*, and higher in *P. latifolia* than in *Q. ilex* ($P < 0.01$) which did not accumulate live aboveground biomass after these 5 years of drought treatment (Fig. 8). *P. latifolia* was the species that presented less changes in relative increment of aboveground live biomass in the drought plots (Fig. 8).

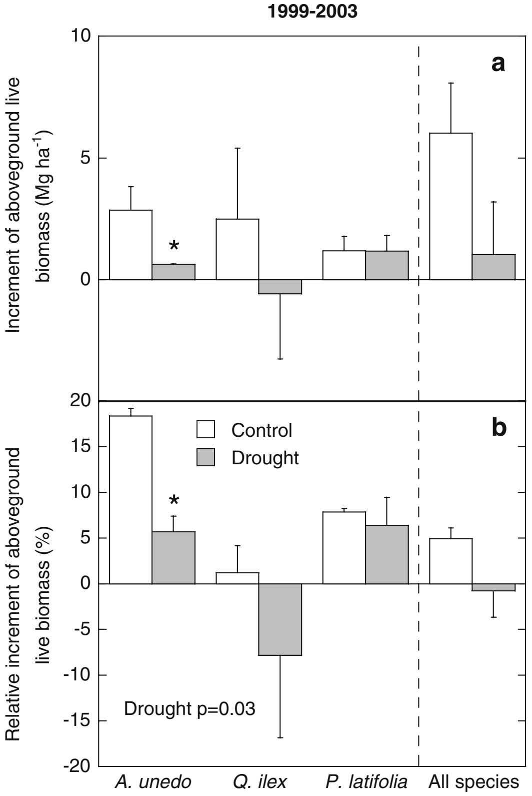

Fig. 8 Increment of aboveground live biomass (**a**), and relative increment of aboveground live biomass (**b**) of *A. unedo*, *Q. ilex*, *P. latifolia*, and all species together in control and drought plots during the overall studied period. Vertical bars indicate standard errors ($n = 4$ plot), one asterisk indicates $P < 0.05$ (ANCOVA post-hoc tests)

Discussion

The stem diameter increment was highly correlated with annual rainfall, and the number of dead stems was strongly correlated with stem density in agreement with previous studies indicating that growth rates in the studied forest are highly constrained by water availability and the elevated stem density (Ibáñez et al. 1999). The mean species response showed higher growth in wet years, and the drought treatment reduced stem growth and increased mortality rates.

However, not all species experienced the same sensitivity to drought. *A. unedo* was the species with the highest growth reduction induced by drought treatment, but it was *Q. ilex* the species that reached the lowest growth rates and the highest mortality rates. Both species presented strong relationships between diameter increment and annual rainfall, showing an important dependence on water availability. *P. latifolia* experienced the lowest mortality rates and did not experience any growth reduction under drought treatment. This gradient in moisture dependence from *Q. ilex* to *P. latifolia* is in agreement to previous studies of stem diameter increment (Ogaya et al. 2003) and of phenological patterns (Ogaya and Peñuelas 2004) conducted in the same area with these three species. It could be explained by higher photosynthetic rates and water use efficiencies observed in *P. latifolia* than in *Q. ilex* (Peñuelas et al. 1998), and lower sap flux reduction observed in *P. latifolia* than in *A. unedo* and *Q. ilex* (Martínez-Vilalta et al. 2003) during summer drought.

Low water availability exerted direct effects on the stem growth. But water availability has also indirect effects on plant growth such as those linked to nutrient availability, which is under soil water control (Chapin 1980). In the studied area, drought treatment has been reported to decrease the soil availability of phosphorus and the foliar phosphorus concentration of the dominant species *Q. ilex* (Sardans and Peñuelas 2004).

The aboveground biomass increment rates obtained in our study are similar to those estimated in other holm oak forests from nearby regions (Ibáñez et al. 1999; Hoff et al. 2002), but our rates are low when compared to those obtained in moist temperate forests from nearby regions (Rodríguez-Murillo 1997). The annual aboveground biomass increment in each plot was dependent on their previous aboveground biomass, but drought treatment reduced biomass increment in all plots. The live aboveground biomass increment in drought plots was on average 83% lower than in control plots. This strong reduction induced by drought had many causes depending on the species. The strong decrease in relative aboveground biomass increment in *A. unedo* was produced principally by a strong reduction in stem diameter increment, but in *Q. ilex* the loss of biomass induced by stem mortality accounts for the negative values in relative aboveground biomass increment reached under drought conditions. *P. latifolia* was the species less affected by drought showing similar aboveground biomass increment in drought plots than in control plots.

Our slight water exclusion (about 15% relative reduction in soil moisture) produced a strong decrease in the total amount of carbon fixed by this forest due to lower growth rates and to increased mortality rates. The holm oak forest represents an important sink of carbon emissions, but the capacity of carbon sequestration of these forests could be highly reduced in the near future with the decrease in water availability predicted for the next decades in Mediterranean areas (IPCC 2001; Peñuelas et al. 2004b).

It has been stated that climate change conditions predicted for the Mediterranean region may decrease tree growth, and lead to a decline of forests or to a decline of particular species within forests (Kirschbaum 2000). The results of this field study show that in effect a decrease in stem growth and carbon allocation was induced by the predicted drought. They also show that not all the species developed the same response under these drought conditions. The more drought-tolerant species such as *P. latifolia* showed a good adaptability to the drier conditions but the more mesic species such as *Q. ilex* and *A. unedo* strongly decreased their growth rates under these drought conditions. If climate becomes drier in Mediterranean areas, and in addition to an important decrease in wood productivity and carbon sequestration, partial species replacement could occur since drought-tolerant species could be favored in detriment of more mesic species.

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