Species-specific drought effects on flower and fruit production in a Mediterranean holm oak forest

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Summary
A holm oak forest was exposed to an experimental drought (reduction of 15 per cent soil moisture as predicted for this area for the next decades by General Circulation Models and ecophysiological models) during 7 years to elucidate the reproductive responses of the dominant species Quercus ilex L., Arbutus unedo L. and Phillyrea latifolia L. Soil moisture was partially reduced by plastic strips intercepting rainfall and by ditch exclusion of water runoff. During the period studied, meteorological conditions and soil moisture were continuously monitored, together with flower and fruit production in the three dominant species. In Q. ilex and A. unedo, flower and specially fruit production were strongly correlated with annual rainfall, but not in P. latifolia. The experimental drought reduced flower and fruit production in Q. ilex by 30 per cent and 45 per cent, respectively. Reductions in flower and fruit production were not significant in A. unedo and were not observed in P. latifolia. A decrease in production of reproductive structures and the different response of the species studied to a decrease in water availability could induce important changes in the competitive ability of the different species and in the long term in the community species composition and future distribution of these Mediterranean species.

Introduction
An increase in air temperatures is predicted for the Mediterranean basin during the next decades. Higher evapotranspiration is thus expected and lower water availability for vegetation is also predicted by General Circulation Models and ecophysiological models (IPCC, 2001; Sabaté et al., 2002; Peñuelas et al., 2005). A decrease in water availability (currently already the most important factor limiting plant development in Mediterranean areas) could induce important changes in plant reproductive phenology (Peñuelas et al., 2002, 2004) and affect other species interacting with these plants (Fitter et al., 1995; Peñuelas and Filella, 2001). But, reproductive phenology alone is not likely to change. Flower and fruit production and the consequent seed dispersion, which are crucial processes for the establishment of new individuals and a very important factor determining future species distribution, are also likely to be altered by climate change.

The climate of the Mediterranean basin is characterized by moderately low temperatures in winter and high temperatures in summer, whereas rainfall periods are more frequent in spring and autumn (Di Castri and Mooney, 1973; Mitrakos, 1980; Mooney, 1983). Some Mediterranean plants
flower during spring, coinciding with a great vegetative development and avoiding summer drought and winter cold. Other Mediterranean species flower during autumn, when temperatures are not cold and rainfall is usually abundant (Orshan, 1989). Fruit development starts just after flowering, but the duration of fruit development and the maturation period are highly variable depending on the species (Orshan, 1989).

Holm oak (Quercus ilex L.) is a drought-tolerant tree widely distributed in the Mediterranean basin. Phillyrea latifolia L. is a small tree associated with holm oak forests and more resistant to drought and high temperatures than Q. ilex (Peñuelas et al., 1998; Ogaya and Peñuelas, 2003). Arbutus unedo L. is another small tree typical of holm oak forests that in some areas has shown greater drought sensitivity than P. latifolia (Ogaya and Peñuelas, 2007).

The reproductive phenologies of Q. ilex and P. latifolia are typical for Mediterranean species. Flowering takes place in spring, fruit development in summer and fruit maturation and seed dispersal in autumn (de Lillis and Fontanella, 1992; Castro-Diez and Montserrat-Martí, 1998). In A. unedo, flower bud formation occurs in spring, but flowering takes place in the following autumn, and fruit development continues over a prolonged period until fruit matures in the autumn of the following year (de Lillis and Fontanella, 1992).

We aimed to study the reproduction of the three dominant species in Mediterranean holm oak forests, their dependence on climatic conditions and the variations produced by the decrease in water availability expected for Mediterranean areas during the next decades.

Materials and methods

The present study was carried out in the Prades holm oak forest in Southern Catalonia (NE Spain) (41° 21′ N, 1° 2′ E, 950 m) on a south-facing slope (25 per cent slope). The soil is a Dystric Cambisol over Paleozoic schist, and its depth ranges from 35 to 90 cm. This holm oak forest has a very dense multi-stem canopy (16 616 stems ha⁻¹) and it is dominated by Q. ilex (8633 stems ha⁻¹), P. latifolia (3600 stems ha⁻¹) and A. unedo (2200 stems ha⁻¹), with an abundance of other evergreen species well adapted to dry conditions (Erica arborea L., Juniperus oxycedrus L. and Cistus albidus L.) and occasional individuals of deciduous species (Sorbus torminalis (L.) Crantz and Acer monspessulanum L.).

In the study site, eight 15 x 10-m plots were delimited at the same altitude along the slope in 1999. Four of them (randomly selected) received the drought treatment consisting of partial rain exclusion by suspending PVC strips at a height of 0.5–0.8 m above the soil (covering 30 per cent of soil surface), and the excavation of a 0.8-m-deep ditch (reaching the bedrock) at the upper edge of the plots to intercept runoff water supply. Water intercepted by strips and ditches was conducted outside the plots, below the bottom edge of the plots. The other four plots did not receive any treatment and were considered control plots.

An automatic meteorological station (Campbell Scientific Inc., Logan, UT, USA) installed between the plots monitored temperature, photosynthetic active radiation, air humidity and precipitation. Soil moisture was measured each month throughout the experiment by time domain reflectometry (Tektronix 1502C, Tektronix, Beaverton, OR, USA) connecting the time domain reflectometer to the ends of three stainless steel cylindrical rods, 25 cm long, fully driven into the soil (Zegelin et al., 1989). Four sites per plot were randomly selected to install the steel cylindrical rods for soil moisture measurements.

In each one of the eight plots, 20 circular baskets (27 cm in diameter with a 1.5-mm mesh) were randomly distributed on the ground. The fallen litter in the baskets was collected every 2 months from 1999 to 2005 (both included). Flowers and fruits collected in litter were weighed after drying in an oven at 70°C to constant mass. We then calculated the proportion of flower and fruit production in Q. ilex, P. latifolia and A. unedo relative to total above-ground tree biomass. The tree biomass was estimated by allometric relationships with the stem diameter at 50-cm height measured in Q. ilex and P. latifolia trees growing in the area of study (outside the plots) (Table 1). To estimate the biomass of A. unedo we used the allometric relationship calculated for the same forest by Lledó (1990). The stem diameter of all Q. ilex, P. latifolia and A. unedo trees growing in the plots was measured each winter.
A repeated-measures analysis of variance (ANOVA) was performed with soil humidity as the dependent variable and treatment application as independent factors. Other repeated-measures ANOVA were conducted with flower and fruit production in the three species studied as dependent variable and year and treatment application as independent factors. Exponential relationships between flower and fruit production in the three species studied and rainfall were conducted with data for different monthly periods of accumulated rainfall going systematically from the previous month to the whole period of the previous 12 months before flowering and fruiting. We here show the data for the best correlated periods with flower and fruit production for each one of the three species studied. Data of the proportion of flower and fruit biomass production relative to the total above-ground biomass \( p \) was transformed to \( \arcsin(p)^{1/2} \) to reach the normality assumptions of the ANOVA. All analyses were performed with the Statview software package (Abacus Concepts, Cary, NC, USA).

**Results**

Meteorological data for these 7 years of study were typical for a Mediterranean climate; hot and dry summers, relatively cold winters and rainfall periods concentrated in spring and autumn (Figure 1). Mean annual temperature varied from 11.7°C in 2004 to 12.6°C in 2003, and total annual rainfall varied from 403 mm in 2005 to 927 mm in 2003 (Figure 1). Drought treatment decreased soil moisture by ~20 per cent, whereas during dry periods (usually in summer and also in winter) the decrease of soil moisture induced by drought treatment did not exceed 10 per cent.

In both control and drought plots, flower production was correlated with rainfall during the 2 months before flowering in *Quercus ilex* \( (P < 0.01) \).
and with rainfall during the 2 months before flower bud formation in A. unedo (P = 0.04) (Q. ilex flowers during May, and A. unedo develops flower buds during June), whereas no correlation with rainfall was observed in P. latifolia (which flowers during March) (Figure 2). Fruit production was also strongly correlated with rainfall during the 10 months before fruit maturation in Q. ilex (P < 0.001). This relationship was not observed in P. latifolia, and fruit production in A. unedo was more correlated with summer rainfall (P < 0.01) (rainfall during June, July and August) (Figure 2). Quercus ilex and A. unedo were thus the species whose fruit production was more sensitive to accumulated rainfall.

During the total study period (1999–2005), drought treatment decreased flower and fruit production in Q. ilex by 30 per cent and 45 per cent, respectively, but this effect was not observed in P. latifolia or in A. unedo; fruit production of A. unedo was reduced under drought conditions, but differences were not statistically significant (Figure 3).

Discussion

The production of reproductive structures of Q. ilex was more sensitive to drought conditions than those of P. latifolia, as it has also been found for its photosynthetic performance, phenology, primarily productivity and mortality rates so far described in the literature (Peñuelas et al., 1998; Ogaya and Peñuelas, 2004, 2007). Flower and fruit production of Q. ilex were more dependent on water availability than those of P. latifolia, and while drought treatment decreased flower and fruit production in Q. ilex, it had no significant effect on P. latifolia. The dependence of A. unedo on water availability was intermediate and more complex. Our previous studies have shown that A. unedo experienced a delay in flower and fruit formation (Ogaya and Peñuelas, 2004) and lower stem growth (Ogaya and Peñuelas, 2007) under these experimental drought conditions. Fruit production in A. unedo was higher in control plots than in drought plots, but these differences were not significant, probably because the inter-annual variability of fruit production in A. unedo was very high. Particular effects of the meteorological conditions during the overall period of fruit development may also account for these complex responses. For example, spring of 2005 was unusually dry and flower bud formation was very low. As a consequence, it is likely that fruit production in the following year is affected in autumn by this low amount of flowers.

On the other hand, some Mediterranean species have a strong inter-annual variation in flower and especially in fruit production. Some authors have described this event as a masting strategy. The high fruit production avoids total consumption of the fruits by herbivores, avoiding low seed dispersal associated with high predator consumption rates (Herrera et al., 1994; Siscart et al., 1999). These inter-annual fluctuations may not wholly depend on climatic conditions and could be an important problem when estimating the effect of climatic conditions on fruit and fruit production. In addition, climate or drought treatment could influence seed predators, affecting indirectly the amount of fruits collected in the baskets.

Other field manipulations conducted in other forests revealed lower canopy transpiration (Wullschleger and Hanson, 2006) and a decrease in the total amount of flowers (Llorens and Peñuelas, 2005) under experimental drought. The results of this long-term study show that more arid conditions in Mediterranean forests, as those predicted for the following decades (IPCC, 2001; Sabaté et al., 2002; Peñuelas et al., 2005), could decrease the production of plant reproductive structures. The recruitment of new individuals could thus be reduced (Borchert et al., 1989), with important changes in species’ competitive abilities and future species distribution. In addition, lower water availability could also decrease the survival rates of these new individuals (Lloret et al., 2004). The different response observed in the three species studied as also found for many other variables such as photosynthetic performance, growth, phenology or mortality (Peñuelas et al., 1998; Ogaya and Peñuelas, 2004, 2007) suggests long-term changes in the future species’ distributions in Mediterranean forests, with an increase of more drought-resistant species such as P. latifolia to the detriment of less drought-resistant species such as Q. ilex, currently the dominant species in many Mediterranean forests.
Figure 2. Relationships between flower and fruit production of the three species studied and rainfall. The strongest relationships of flower production were those with rainfall during the 2 months before flowering in *Quercus ilex* and during the 2 months before flower bud formation in *Arbutus unedo*. The strongest relationships of fruit production were those with rainfall of the previous 10 months in *Q. ilex* and with summer rainfall in *A. unedo*. Each point corresponds to an annual mean of control or drought treatment during the 7-year study (1999–2005) ($n = 14$).
Figure 3. Annual flower and fruit production of the three species studied in the control and drought plots during the 7-year study period (1999–2005). Vertical bars indicate standard errors of the mean (n = 4). Significance (repeated-measures ANOVA) of the drought treatment is depicted inside the panels for Quercus ilex.

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