Environmental and Experimental Botany 71 (2011) 123–127

Contents lists available at ScienceDirect

Environmental and Experimental Botany

journal homepage: www.elsevier.com/locate/envexpbot

Chlorophyll fluorescence responses to temperature and water availability in two co-dominant Mediterranean shrub and tree species in a long-term field experiment simulating climate change

Romà Ogaya*, Josep Peñuelas, Dolores Asensio, Joan Llusià

Global Ecology Unit CREAF-CEAB-CSIC, CREAF (Center for Ecological Research and Forestry Applications), Universitat Autònoma de Barcelona, E-08193 Bellaterra, Barcelona, Spain

ARTICLE INFO

Article history:
Received 17 February 2010
Received in revised form 18 October 2010
Accepted 26 October 2010

Keywords:
Chlorophyll fluorescence
Climate change
Cold
Drought
Evergreen leaves
Fv/Fm
Heat
Mediterranean forest
Phillyrea latifolia
Quercus ilex

ABSTRACT

A rain exclusion experiment simulating drought conditions expected in Mediterranean areas for the following decades (15% decrease in soil moisture) is being conducted since 1999 in a Mediterranean holm oak forest to study its response to the forecasted climatic changes for the coming decades. The maximum PSII quantum yield of primary photochemistry (Fv/Fm) was measured in *Quercus ilex*, and *Phillyrea latifolia*, the co-dominant species of the studied forest, from 1999 to 2009 in four plots: two of them were control plots and the other two plots received the rain exclusion treatment. In both species, the Fv/Fm values were highly dependent on air temperatures, and in a second term, in water availability. *P. latifolia* was the species with the larger decrease in Fv/Fm values induced by low air temperatures, while in hot seasons, the Fv/Fm values in *P. latifolia* were even higher than in *Q. ilex*. Rainfall exclusion decrease Fv/Fm values significantly only in few monitoring dates. The most drought resistant species *P. latifolia* was more affected by the experimental rainfall exclusion than *Q. ilex* that instead lost number of leaves per tree. There was a synergic effect of drought stress and winter cold in *P. latifolia* not observed in *Q. ilex*, but a more conservative strategy in *P. latifolia* maintaining leaves with a down-regulation of the linear photosynthetic electron transport. These results indicate that, although other physiological and reproductive strategies at whole plant level must be also taken into account, the warmer and drier environment expected for the following decades could favour the species more sensitive to cold and more resistant to drought, the shrub *P. latifolia*, in detriment of the tree *Q. ilex* as already observed in the field after severe heat-drought episodes.

1. Introduction

An increase in air temperatures and a slight decrease in precipitations are forecasted for the Mediterranean Basin by most General Circulation Models (GCMs) (IPCC, 2007). Lower water availability is also projected for this region by ecophysiological models such as GOTILWA (Sabaté et al., 2002; Peñuelas et al., 2005). In fact, increased temperatures and lower water availability have been already experienced in the last decades (Le Houérou, 1996; Piñol et al., 1998; De Luis et al., 2001; Peñuelas et al., 2002, 2005; Peñuelas and Boada, 2003).

Several studies have described restricted plant activity in the Mediterranean area in summer months due to heat and drought stress (Tenhunen et al., 1990; Filella et al., 1998; Peñuelas et al., 1998, 2007; Larcher, 2000; Llusià and Peñuelas, 2000; Yordanov et al., 2000; Ogaya and Peñuelas, 2003a,b). But warming may alleviate the plant stress produced by minimum temperatures in colder seasons to which some Mediterranean species are sensitive (Mitrakos, 1980; Oliveira and Peñuelas, 2000, 2001, 2004; Ogaya and Peñuelas, 2003a,b, 2007),

The maximal photochemical efficiency, Fv/Fm ratio, is the most common measurement of chlorophyll *a* fluorescence, and it is inversely proportional to damage in the PSII reaction centres (Farquhar et al., 1989). Reductions in photochemical efficiency in Mediterranean species have been detected in summer in response to drought but also in winter in response to cold stress (Karavats and Manetas, 1999; Gratani et al., 2000; Larcher, 2000; Oliveira and Peñuelas, 2000, 2001, 2004; Llorens et al., 2003a,b; Ogaya and Peñuelas, 2003a,b; Bellot et al., 2004; Prieto et al., 2009).

Quercus ilex L. (holm oak) and *Phillyrea latifolia* L. are plant species frequently co-occurring in the Mediterranean forests. In particular, *Q. ilex* is a tree widely distributed in the sub-humid areas of the Mediterranean Basin, whereas *P. latifolia* is a tall shrub distributed in warmer and drier areas (Tretiach, 1993; Lloret and Siscart, 1995; Peñuelas et al., 1998, 2000).

Our aim was to study the effect of a long-term experimental drought on maximal of PSII of two dominant woody species of Mediterranean forests in order to elucidate how do these two

* Corresponding author. Tel.: +34 935814036; fax: +34 935814151.
E-mail address: r.ogaya@creaf.uab.cat (R. Ogaya).

0098-8472/$ – see front matter
doi:10.1016/j.envexpbot.2010.10.016

dominant species respond to increasing drought and to the interacting effects with heat in summer and cold in winter. We also aim to study the possible advantage of photochemical efficiency in *P. latifolia* compared to the actual dominant species *Q. ilex* under these drier conditions, as observed in other parameters such as gas exchange (Ogaya and Peñuelas, 2003b) and leaf demography (Ogaya and Peñuelas, 2006). The experimental period covered 10 years (1999–2009) and the four seasons of the year, so as to include inter-annual and inter-seasonal variability in the study of the plants' responses to drought treatment.

2. Materials and methods

2.1. Study site

The present study was carried out in Prades holm oak forest in Southern Catalonia (NE Spain) (41°21′N, 1°2′E), at 950 masl and on a south-facing slope (25% 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 multistem crown (16,616 stems ha^{-1}) and it is dominated by *Q. ilex* (8633 stems ha^{-1}), *P. latifolia* (3600 stems ha^{-1}) and *Arbutus unedo* L. (2200 stems 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 is non-perturbed since 60 years, and the maximum height of the dominant species is about 6–10 m tall.

2.2. Experimental design

In the study site, four 15 m × 10 m plots were delimited at the same altitude along the mountain face. Two of them (randomly selected) received the treatment consisting of partial rain exclusion by suspending PVC strips at a height of 0.5–0.8 m above the soil (covering 30% of the soil surface), and the excavation of a 0.8 m deep ditch at the upper part of the plots to intercept runoff water supply. The rain exclusion treatment started in January 1999. Water intercepted by strips and ditches was conducted outside the plots, below their bottom edge. The other two plots did not receive any treatment and were considered control plots.

An automatic meteorological station 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, 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.

2.3. Chlorophyll fluorescence

The maximum PSII quantum yield of primary photochemistry (Fv/Fm) was measured in each one of the 4 annual seasons under clear-sky conditions during the overall studied period (11 years). Fv/Fm was measured with a PAM-210 fluorometer (Walz, Effeltrich, Germany) in sunlit leaves at the top of the canopy of the two most abundant species of this forest, *Q. ilex* and *P. latifolia*. Before each measurement, the leaves were dark-adapted for 20 min with leaf clips. In each plot, two trees per species were randomly selected and five current-year leaves in each tree were measured during midday solar time.

2.4. Statistical analyses

Simple linear regressions were conducted to examine the relationships between Fv/Fm values and air temperature (during the measurement, mean temperature of the day of measurement, and minimum temperature of 1, 3, or 5 days before measurement), soil moisture, and rainfall (of the 1, 2, 3, or 4 months before measurement). Later, multiple linear regressions were conducted to test the meteorological influence on the maximal photochemical efficiency of PSII. Fv/Fm was the dependent variable and air temperature, and soil moisture or rainfall the predictor variables. In these multiple regressions the forward stepwise regression technique was used. Repeated measurements analysis of variance (ANOVA) was conducted with soil moisture values in each plot as dependent variable and treatment as independent factor. Another ANOVA was conducted with Fv/Fm values as dependent variable and season of measurement, species, and treatment as independent factors. Fv/Fm values were arcsin transformed to reach the normality assumptions of the ANOVAs and regression analysis. All analyses were performed with the Statistica software package (Statsoft Inc., Tulsa, OK, USA).

3. Results

The climate of the area studied is of mountain mesic Mediterranean type. During the study, the mean annual temperature was 12.3 °C, and the mean annual rainfall 668 mm (Fig. 1). Rainfall was concentrated in spring and autumn seasons, whereas the summers were the driest periods coinciding with higher air temperatures (Fig. 1). The drought treatment reduced about 13% soil moisture of drought plots compared to control plots (Fig. 1), but this reduction was larger during rainfall seasons and lower during dry seasons ($P < 0.01$).

The highest values of the maximal photochemical efficiency of PSII (Fv/Fm) were measured in spring, under the optimum combination of air temperature and water availability (Fig. 2); the lowest Fv/Fm values were reached in winter when air temperatures were the lowest ones (Fig. 2); and intermediate values were measured in summer and autumn, either because of low water availability or low air temperature, respectively (Fig. 2). The Fv/Fm values ranged from 0.8 in warm and humid periods to 0.2 in winter 2005, when an exceptional cold and dry period occurred (Fig. 3). These results and those obtained by the regression analyses showed clearly that the Fv/Fm values were dependent on air temperature and water availability, decreasing in parallel with the temperature and water availability. Air temperature was a more important factor determining Fv/Fm values than water availability as shown by the semi-partial correlation values for these two variables in the multiple regressions (Table 1).

Table 1
Multiple linear regression equations for Fv/Fm values in *Q. ilex* and *P. latifolia* as a function of different climatic variables: "T_{min}" is the minimum temperature of the preceding 24 h of measurement, and "SM" is the soil moisture (%, v/v) measured with TDR method. Semi-partial correlations of these two variables are also depicted.

Species	Multiple regression	R^2 value	P value	Semi-partial correlations T_{min}	Semi-partial correlations SM
Q. ilex	$Fv/Fm = 0.449 + 0.0148T_{min} + 0.0082SM$	0.32	<0.001	0.53	0.43
P. latifolia	$Fv/Fm = 0.445 + 0.0157T_{min} + 0.0062SM$	0.25	<0.001	0.50	0.29
Both species	$Fv/Fm = 0.447 + 0.0152T_{min} + 0.0072SM$	0.28	<0.001	0.51	0.35