

Physiology

Highlighting the differential role of leaf paraheliotropism in two Mediterranean *Cistus* species under drought stress and well-watered conditions



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ABSTRACT

The differential degree by which paraheliotropism may counterbalance the deleterious impact of high irradiance between congeneric species in relation to different water availabilities has been poorly investigated. We followed the evolution of gas exchange, quenching analysis and OJIP parameters in restrained (R) and free (F) to move leaves of *Cistus monspeliensis* (CM) and *Cistus salvifolius* (CS) under drought stress (WS) and well-watered conditions (WW). Concerning gas exchange parameters, leaf restriction effect was overall not significant in CM except in apparent carboxylation efficiency (C_e) under WS, while CS showed a significant sensitivity of maximum net photosynthetic rate (A_{max}), stomatal conductance (g_s) and C_e even under WW. The recovery analysis highlighted also a faster g_s recovery in F leaves. Furthermore, in both the species, restriction affected photon allocation pathways especially in terms of light-regulated and light-independent constitutive non-photochemical energy dissipation under WW, ultimately affecting electron transport rate (ETR). Nevertheless, the OJIP analysis provided us evidences that CM was characterized by a down-regulation of ETR while an impairment occurs in CS. In CM this was due to its ability to modify a certain fraction of reaction centers thus resulting in a higher capability for dissipation of excess light energy under well-watered conditions, not affecting electron transport efficiency. This response was not observed in CS. Overall, we demonstrated that congeneric species, even mostly sharing the same physiological targets, differ in the degree by which leaf movements help to counterbalance the negative effect of the high irradiance in relation with the amount of water available.

1. Introduction

Photoinhibition occurs in environments with high radiation fluxes, and its deleterious effects become harsher when plants are exposed to others environmental stresses (Werner et al., 2002). It has been widely considered that leaves can prevent photoinhibition by energy dissipation through the electron transport system together with thermal energy dissipation in PSII antennae (Kitao et al., 2006). In addition to these photoprotective mechanisms, the avoidance mechanisms resulting from leaf or chloroplast movements (i.e. ‘paraheliotropism’) cannot be disregarded (Chaves et al., 2009). Drought stress is one of the main environmental constraints limiting the capacity for CO₂ assimilation and favoring photoinhibition (Pastenes et al., 2005). Under the Mediterranean type of climate, plant species have to withstand severe water stress, high temperatures and high irradiance during summer (Flexas et al., 2014). In fact, in Mediterranean ecosystems the distribution of the dominant growth form and habitus is related to water

availability (De Micco and Aronne, 2009). According to a gradient of increasing aridity, there is a decrease in the transpiring surfaces up to the complete lack of leaves in drought deciduous shrubs, associated with drought-evading annual species. An intermediate form between evergreen and drought deciduous species is represented by seasonally dimorphic species (De Micco and Aronne, 2009). Among them, seasonal dimorphic *Cistus* spp. are representative of the earlier successional stages in shrublands of the Mediterranean Basin (Correia et al., 1992) showing enhanced germination and populations regeneration just after fire (Saura-Mas et al., 2009) which constrains their growth during the favorable period, be it before winter or the onset of summer drought (Puglielli et al., 2017). Given their post-fire regeneration strategy, *Cistus* seedlings and saplings are often exposed to harsh environmental conditions. Overall, the species of this genus have been widely investigated in term of its responsiveness to drought (e.g. Harley et al., 1987; Zunzunegui et al., 2009; Grant et al., 2014) and several reports have highlighted the role of paraheliotropism as an effective

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way to avoid photoinhibition in different *Cistus* spp. (e.g. Gratani and Bombelli 1999; Werner et al., 1999, 2002; Oliveira and Peñuelas 2002). In any case, these authors compared such responses to that of other leaf habits, such as evergreen sclerophyllous, and in adult plants under field conditions by analyzing mainly F_v/F_m , Φ_{PSII} , ETR or just gas exchange responses in relation to leaf paraheliotropisms in *Cistus* species. This results in the lack of knowledge on the different extent by which leaf paraheliotropisms may be involved in protecting leaves of different *Cistus* species as well as of a detailed photochemical analysis of such a response. Moreover, even though the phenomenon has been mainly associated with water-stressed plants, it also occurs in well-watered plants but to a lesser extent (Pastenes et al., 2005). Therefore, this study was designed and conducted to contribute to the filling of these gaps of knowledge. In particular, we asked the following questions: (i) May congeneric species differ in the extent by which they are affected by leaf restriction? (ii) Do the species share the same physiological targets of leaf restriction? (iii) Can leaf movements restriction affect carbon assimilation also in well-watered plants? To answer these questions we followed the evolution of gas exchange, quenching analysis and the fast chlorophyll a fluorescence induction parameters in one-year old *C. salvifolius* L. and *C. monspeliensis* L. during drought stress and recovery and under well-watered conditions.

2. Materials and methods

2.1. Study site and plant material

The role of paraheliotropism in leaves protection from photoinhibition under drought stress and recovery was assessed during the summer of 2015 in one-years-old plants of *Cistus monspeliensis* and *Cistus salvifolius* growing outdoors in the installations of the University of Seville (37°17'; 5°59'W, altitude 0 m a.s.l.; Seville, SW Spain). This site is located in the Mediterranean climate region with Atlantic Ocean influence, being the summer characterized by high temperatures, irradiance, evapotranspiration and absence of rainfall (García-Novo et al., 2007). *Cistus* plants were obtained from a forest nursery located in Granada (37°15'; 3°44'W, altitude 576 m a.s.l.; Granada, SE Spain). These plants were grown in 5 l pots containing an organic commercial substrate:perlite mixture (3:1). Hereafter *C. monspeliensis* and *C. salvifolius* are referred as CM and CS, respectively.

2.2. Microclimate measurements

Microclimate environmental variables in the study site were measured with an automatic weather station (Agrocomponentes, Murcia, Spain) installed at canopy level and located 20 m away from the experimental pots. Measurements of air temperature, relative humidity, wind speed and photosynthetically active photon flux density (PPFD) during the experimental period were made every 10 s and data were averaged and recorded every 30 min.

2.3. Experimental procedure

A potted trial (48 pots) was established in a split plot arrangement on a randomized complete block with three replications (three blocks) and with four plots per block. Each plot in a block corresponded to a water regime, with or without restraining of the leaves: well-watered free (WWF) and restrained (WWR) and water-stressed free (WSF) and restrained (WSR). Each sub-plot corresponded to a species, with two plants (pots) per species, per sub-plot. The choice of two plants per sub-plot was related to the necessity to exclude any differential effect of plant position.

At the beginning of the experiment all plants were watered to field capacity and then were divided in two water treatments. One group was subjected to drought by withholding water until severe water stress was reached. Severe water stress was considered to have occurred when

stomatal conductance to CO_2 (g_s) dropped below $50 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ (Medrano et al., 2002). The other group was maintained under well-watered conditions throughout the entire experimental period by adding the amount of water they lost during the day. Soil water content (SWC) was calculated in both treatments by weighing each pot every day at midday and comparing pots mass with the corresponding mass at field capacity (Gallé et al., 2007). Moreover, after the severe stress achievement, plants were consecutively re-watered to field capacity as control plants and maintained in this condition along all the recovery period. Also, in order to avoid the direct soil water evapotranspiration during the experiment, an upper layer of 2 cm of perlite was placed in each of the pots (Galmés et al., 2007).

On the other hand restriction treatment was developed following the methodology employed by Oliveira and Peñuelas (2002). Thus twenty-five fully developed leaves of similar age per plant were experimentally restrained with thin wire loops of $0.7 \times 0.3 \text{ cm}$ (length \times width) that held them in an horizontal position. In order to avoid the interference of wire loops on leaves gas exchange they were placed in the basal part of the leaves exactly in the portion of insertion with the shoot (Fig. 1). Before the beginning of the physiological measurements, leaves were restrained for 48 h according to Pastenes et al. (2005).

The first measurements of leaves water status, gas exchange and chlorophyll fluorescence were taken after 24 h from the onset of the water stress treatment at least in three randomly selected restrained and non-restrained leaves per plant and per plot. Then, subsequent measurements were carried out every two days. Additionally, the recovery was followed for 2 weeks after rewatering. Measurements were taken at midday since *Cistus* spp. adjust leaf inclination depending on the hour of the day (Gratani and Bombelli, 1999) and leaf age (Oliveira and Peñuelas, 2002). This procedure let us exclude measurements of leaf angle variations by assuming a cumulative effect of daily leaf movements in free to move leaves throughout the experiment.

2.4. Plant water status

Leaf total water potential, Ψ_{leaf} and relative water content, RWC were measured at pre-dawn (Ψ_{pd} and RWC_{pd}) and at midday (Ψ_{md} and

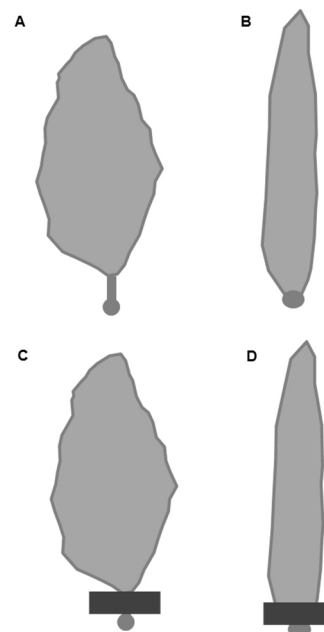


Fig. 1. Schematic representation of *C. salvifolius* and *C. monspeliensis* leaves without (A,B) and with (C,D) restriction treatments. Black lines represent the thin wire loops ($0.7 \times 0.3 \text{ cm}$, length \times width) used to hold leaves in an horizontal position.

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