

Linking photosynthetic performances with the changes in cover degree of three Mediterranean shrubs under climate manipulation

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Decision date: 21-May-2018

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: [10.1111/oik.05263].

ABSTRACT

Understanding how different combinations of plant functional traits contribute to species fitness is a question of considerable ecological interest, that can give insights into the mechanisms controlling community assembly, and into the processes by which climate change can modify plant community structure and composition.

We investigated the changes in cover degree of three shrubs (*Cistus monspeliensis*, *Dorycnium pentaphyllum* and *Helichrysum microphyllum*) growing in a Mediterranean garrigue subjected for 11 years to a reduced rainfall regime, following a conceptual framework based on the two-phase resource dynamic model: considering the seasonal drought typical of the Mediterranean climate, the two-phases were identified based on high (pulse phase) and low (interpulse phase) soil water availability.

We developed a parameter proportional to the whole plant photosynthesis (plant photosynthetic index, PPI), scaling up the leaf photosynthesis to canopy level, taking into account the different canopy densities and the fluctuations in leaf biomass due to summer leaf shedding. PPI was used to derive plant performance estimators for both pulse (maximum value reached by PPI, PPI_{max}) and interpulse phase (duration of the exhaustion phase, Dur_{ep} , when drought constrains PPI below the plant carbon compensation point determining carbon starvation). For each species the ratio between PPI_{max} and Dur_{ep} (named PPI_{red}) was used as an index of plant performance.

The reduced rainfall regime mainly decreased the performances of the dominant species *C. monspeliensis*, both limiting PPI_{max} and extending Dur_{ep} . Under both natural and the manipulated rainfall regime, PPI_{red} was proportional to plant success, measured as the cover degree variation rate of the species.

This result suggests that a mechanistic approach using functional traits to quantify the different performance of co-occurring species can be used to investigate 1) the drivers of the medium-term changes in species abundance and 2) the processes responsible for change in plant community composition under climate change.

Keywords: plant species reordering under climate change, photosynthetic performances under drought stress, functional traits related to plant growth/survival

INTRODUCTION

Understanding the processes that govern species assembly in plant communities represent a central goal of comparative ecology. During ecological successions the differences in performances of co-occurring species drive change in species abundance (Pickett et al. 1987), and several studies have been carried out with the aim of providing a mechanistic and predictive framework to better understand the mechanisms driving these changes (Rees et al. 2001; Angert et al. 2007; Smith et al. 2009; Kimball et al. 2012; Sterck et al. 2014). The comprehension of these mechanisms is particularly relevant to predict the effect of climate change on plant communities composition. For the Mediterranean Basin, IPCC models predict a decline in soil moisture (Kirtman et al. 2013) as a consequence of an increase of temperature and a decrease in precipitation in spring and summer (Christensen et al. 2013). An extended drought stress period can affect the performance of co-occurring species in different ways, triggering changes in their relative abundance, and determining a new community assembly. This species reordering can also modify ecosystems processes, like the carbon uptake and storage (Peñuelas et al. 2000; Ogaya and Peñuelas 2003; Ogaya and Peñuelas 2007; Serrano-Ortiz et al. 2014) Considering that the projections of future atmospheric CO₂ concentration rely on the role of terrestrial ecosystems as carbon sinks (Higgins and Harte 2012; Ciais et al. 2013), it is crucial to improve the understanding of the mechanisms determining the changes in species abundances (de Graaff et al. 2014) and their feedbacks with the carbon cycle.

The construction of a predictive theory of vegetation dynamics can be set up in different ways, and a trait-based approach is widely used in ecological research to this purpose. Following the classification proposed by Violle et al. (2007), functional and performance traits can be defined. A functional trait is any morphological, physiological or phenological feature measurable at the individual level that impacts fitness via its effect on growth, reproduction and survival: performance traits are direct measure of fitness, like plant growth, reproductive output and plant survival (Arnold 1983; Violle et al. 2007). Several works relate functional traits, like leaf photosynthesis (Oechel et al. 1981; McAllister et al. 1998; Throop et al. 2012), leaf nitrogen content (Turner et al. 1995; Gulías et al. 2003), leaf morphology (Gulías et al. 2003) and plant morphology (de la Riva et al. 2016) to the abundance of the species within a community. Other works explore the link between functional and performance traits of the species, such as leaf physiology - survival and fecundity (Kimball et al. 2012), water use efficiency - growth (Angert et al. 2007), leaf and plant morphology -

growth and survival (Sterck et al. 2014; Greenwood et al. 2017), leaf morphology and water use efficiency - survival and recruitment (Lloret et al. 2016).

Another possible method for the study of vegetation dynamics is based on the “two-phase resource dynamics” approach (Goldberg and Novoplansky 1997; Schwinning and Kelly 2013). It suggests that two different factors affect plant fitness, the capacity to grow during periods of optimal resource availability (*pulse phase*) and the capacity to survive during periods of resources shortage (*interpulse phase*). In regions with discontinuous resources availability, such as the Mediterranean area (reduced water availability during summer drought), the two-phase resource dynamic allows us to take into account the effect of the stressful conditions on species performance. In fact, after the spring season, the progressive reduction of soil water availability affects plant functionality imposing cycles of stress phases: 1) response - the stress is detected; 2) resistance - mechanisms are activated to avoid and to cope with the loss of functionality; 3) exhaustion - the functionality is progressively lost (Lichtenthaler 1996). The exhaustion phase can be followed by a recovery phase or by the mortality of the plants. Recent studies suggest that the main mechanism driving tree mortality in forests is plant hydraulic failure (Anderegg et al. 2016). However, it has been reported that shrubs are more resistant to cavitation than trees, whatever the leaf habit is (winter deciduous, drought deciduous, evergreen, and conifer species) (Maherali et al. 2004). For shrubs carbon starvation can be therefore a relevant cause of mortality. The carbon-starvation hypothesis (McDowell et al. 2008) predicts that stomatal closure to prevent hydraulic failure causes photosynthetic carbon uptake to diminish to near zero (= carbon compensation point, CO₂ photosynthetic uptake equal to the respiratory CO₂ loss on daily basis); if this phase lasts longer than the carbon reserve, plant starvation and mortality can occur; hydraulic failure can in any case occurs if the drought is sufficiently long or intense to force whole-system cavitation via xylem equilibration with extremely dry soil (McDowell et al. 2008).

Within this context, we developed estimators for the plant performance in both *pulse* and *interpulse phases*, accounting for plant physiology (photosynthetic activity), morphology (plant leaf biomass) and phenology (seasonal variation in the leaf biomass). Based on these functional traits, we obtained a parameter proportional to whole plant photosynthesis (Plant Photosynthetic Index, PPI), and we used it to develop two plant performance indices: the maximum Plant Photosynthetic Index (PPI_{max}) and Duration of the exhaustion phase (Dur_{ep}). PPI_{max} is an estimator of the growth capacity during the resource *pulse phase*. Dur_{ep} is an estimator of survival during the *interpulse-phase*, based on the duration of the period when reduced water availability constrains plant photosynthesis (PPI) below the carbon

compensation point (the longer the period, the lower the survival). Experimental evidences suggest that plants reach the carbon compensation point when plant-level photosynthesis drop below one third of the optimal conditions (McDowell et al. 2011; Hartmann et al. 2013; Zhao et al. 2013; Li et al. 2015, see materials and methods for further details). According to this threshold, Dur_{ep} was computed as sum of the days when PPI was lower than 1/3 of PPI value recorded under optimal environmental conditions (PPI_{max}).

The estimators of the pulse-growth (PPI_{max}) and interpulse-survival capacity (Dur_{ep}) were finally combined in a synthetic index of plant performance (Reduced Plant Photosynthetic Index, PPI_{red} , with $PPI_{red} = PPI_{max} / Dur_{ep}$). In this index, the growth capacity during *pulse-phase* (positive effect on plant performance) is counterbalanced (reduced) by the factor Dur_{ep} , proportional to the probability that plant mortality can occur *during interpulse-phase* (negative effect on plant fitness).

The object of the present work was to test a mechanistic framework for the analysis of the changes in shrub species cover degree observed in a 11 year old rainfall reduction field experiment (Beier et al. 2004). We hypothesize that, because of their higher growth and survival capacity, species showing higher PPI_{red} will increase their abundance and cover degree over time. This hypothesis was tested deriving for each species, for both natural and manipulated rainfall regime, the PPI_{red} index of plant performance, along with other plant performance descriptors. Then, the observed changes in species cover degree were used to validate the ability of these performance indices to explain the species dynamic under different environmental conditions.

MATERIALS AND METHODS

Site description

The study area is in the Regional Park of Porto Conte - Capo Caccia, in north-western Sardinia, Italy (40° 37 N, 8° 10 E). The climate is semi-arid, characterized by a mean annual rainfall of 640 mm and a mean temperature of 16.8 °C. Rainfalls mainly occurs in autumn and spring, with a long dry period from May to August. At the beginning of the experiment (2001), the experimental site was covered by a shrubland community (*garrigue*), an open and scattered low scrub formation with a major incidence of drought-deciduous species (Di Castri

1981). In the present study we investigated the three shrub species dominating the plant community in 2001 (*Cistus monspeliensis* L., *Dorycnium pentaphyllum* Scop. and *Helichrysum microphyllum* subsp. **tyrrhenicum** Bacch., Brullo & Giusso)..

Microclimate manipulation and climate monitoring

A rainfall reduction experiment has been running at the study area since July 2001, with the aim of simulating an extension of the summer drought: treated plots (drought plots) were covered with waterproof plastic curtains (20 m²) only during rain events that occurred in spring and autumn (Beier 2004) and the responses to the treatment were compared to control plots. Control and drought plots were replicated three times. In each plot the soil water content (expressed as a percent of the yearly maximum value, Soil Relative Water Content, SRWC) at 10 cm depth was monitored continuously by soil moisture probes (ECH₂O probe model EC-20, Decagon Devices, Inc.) and recorded on a half hourly basis (due to malfunctioning of the probes during 2009, the data of this year were excluded from the dataset). A meteorological station recorded the climate of the experimental site.

In the period from 2001 to 2012, the rainfall inputs in the drought plots were 19% lower than control plots in spring (April and May) and 34% lower than control plots in autumn (October and November).

Species abundance

We monitored species abundance inside the experimental plots using the pinpoint method (Troumbis and Memtsas 2000). In each plot a sharpened pin was lowered through the vegetation along four different transects; the measurements were arranged at 5 cm intervals along each transect, collecting 300 hits per plot. Considering that the vegetation in the plots is mainly structured in a single layer, only the first hit of the pin with the vegetation was counted; plant species and hit type (with living and dead parts) were also recorded; the number of hits with living parts of each species expressed as percentage of total hits was used as an estimate of its cover degree. We carried out pin point measurements during the late spring, in the years 2001 (pre- treatment sampling), 2002, 2003, 2004, 2010, 2011 and 2012.

Canopy morphology

We determined the total leaf biomass per canopy projected area (g m⁻²) through a destructive sampling carried out on the experimental plots in September 2010, during the dry season,

when the summer leaf shedding was completed. Furthermore, we estimated the seasonal variations of leaf biomass (relative to September 2010) inside the experimental plots using a ceptometer (in *C. monspeliensis*) and a canopy images analysis technique (in *D. pentaphyllum* and *H. microphyllum*). The seasonal trend of leaf biomass was then obtained multiplying the value measured at September 2010 for the relative variations. See Supplementary Material Appendix 1 for the detailed methodology.

Gas exchange and leaf water status

Gas exchange measurements were carried out in eleven sampling campaigns from March 2010 to November 2011, monitoring two individuals per species in each plot. All measurements were carried out in the field from 11:00 a.m. to 1:00 p.m. using a LI-6400 portable photosynthesis system equipped with the 6400-22L Lighted Conifer Chamber (Li-Cor Bio-sciences, Lincoln, Neb., USA). When measuring, we set temperature and photosynthetic active radiation intensity inside the leaf chamber according to the values measured at the same time in the outer environment (under cloudless sky conditions). CO₂ concentration was set at 400 ppm. Flow rate was set at 500 $\mu\text{mol s}^{-1}$ for most of the measurement data, and reduced to 300 $\mu\text{mol s}^{-1}$ during extreme drought (September 2010 and July 2011) to increase the accuracy of the measure at low photosynthetic rates. Due to the small size of the leaves of the species analyzed, and in order not to alter the self shading conditions usually experimented by the leaves inside the canopy, we enclosed an entire branchlet inside the chamber. After each measurement, the branchlet was collected and the leaf dry mass determined; the leaf level net assimilation rate (A_{leaf}) was expressed on dry leaf mass basis ($\mu\text{mol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$).

After the robust assumptions that each leaf inside the canopy is subjected to the same light environment imposed inside the chamber (including self-shading in the diverse species), we multiplied A_{leaf} ($\mu\text{mol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$) by plant leaf biomass (g m^{-2}) obtaining PPI (Plant level Photosynthetic Index, PPI, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). We considered PPI a proxy of the photosynthesis at the plant scale, and we used it to compare species performance during the year.

Finally, pre-dawn leaf water potential (ψ_{pd} , MPa) was determined before sunrise on branchlets collected from the same specimens chosen for gas exchange measurements, using a Scholander pressure chamber (SKPM 1400, Skye Instruments LTD, UK).

Estimate of the duration of the exhaustion phase

The duration of the exhaustion phase was defined as the period during which plant photosynthesis is below the plant carbon compensation point. An estimate of the plant-level photosynthesis corresponding to the plant compensation point was obtained from the literature. In an experiment investigating the physiological responses of *Ulmus minor* to flooding, photosynthesis was progressively limited by stomatal closure, and the whole plant carbon balance approached to the carbon compensation point at photosynthesis rates below 31 % of the value recorded before stomatal conductance reduction (Li et al. 2015). In *Thuja occidentalis* under drought stress the carbon compensation point was reached at photosynthesis rates corresponding to $32\% \pm 12$ (average of value determined at 15°C, 25°C and 35 °C, similar to the range of daily temperatures occurring at the experimental site in summer, data not shown) of the value recorded under optimal water availability (Zhao et al. 2013). In *Picea abies* the balance between photosynthesis and respiration was reached when photosynthesis was between 37 and 4% (the exact value was not determined) of the value recorded in control plants kept under optimal water availability (Hartmann et al. 2013). Furthermore, in the conceptual model proposed in McDowell et al. (2011), although representing a general plant response to drought not referred to any specific plant species, respiration equals plant photosynthesis when plant photosynthesis is around 28% of the values recorded before stress: taking into account these information, we considered the 33% of photosynthetic rates registered under full resource availability (PPI_{max} in our study) a suitable generic threshold indicating the upper limit of the carbon starvation zone. We used this threshold ($PPI_{max}/3$) to estimate Dur_{ep} in the species investigated.

To this aim, two different periods were considered: i) the reduction period, which included the plant responses to drought from spring (highest photosynthetic rates) to summer drought (lowest photosynthetic rates); ii) the recovery period, which included the plant response to the autumn rainfall occurring from summer drought to the following spring. For each species, period and treatment, we fitted the ψ_{pd} -PPI and the SRWC- ψ_{pd} relationships with an exponential and logarithmic function, respectively. The ψ_{pd} -PPI relationship was used to determine the threshold value of ψ_{pd} (ψ^*_{pd}) beyond which PPI falls below the plant carbon compensation point during summer and returns above this threshold in autumn. The SRWC- ψ_{pd} logarithmic relationship was used to identify, based on the daily SRWC values recorded in the period 2002-2011, the days with ψ_{pd} lower than ψ^*_{pd} : by doing so, we determined the number of days with PPI below the plant carbon compensation point (Dur_{ep}). The average duration of the exhaustion phase in the period 2002-2011 (expressed as a percentage of the

total number of days in this period) was used as a reduction factor for PPI_{max} , to obtain a new parameter, PPI reduced (PPI_{red}) given by the ratio between PPI_{max} and Dur_{ep} ($PPI_{red} = PPI_{max} / Dur_{ep}$). Following the same procedure, A_{leaf} reduced ($A_{leaf red}$) was also calculated ($A_{leaf red} = A_{leaf max} / Dur_{ep}$).

These indices increase linearly with increasing PPI_{max} (or $A_{leaf max}$) and decrease exponentially with increasing Dur_{ep} . The indices sensitivity to an increase of Dur_{ep} is therefore high for species that in natural conditions experience a short exhaustion phase, and low for species that in natural conditions experience a long exhaustion phase. See Supplementary Material Fig. A1 for visual representation of PPI_{red} sensitivity to PPI_{max} and Dur_{ep} .

Statistics

To test the seasonal variability of the physiological and morphological parameters, we applied the analysis of variance for repeated measures (repeated measures ANOVA; Proc GLM, STATISTICA, ver. 7.0; Statsoft), assuming that no temporal autocorrelations occurred between the instantaneous processes recorded in subsequent measurement campaigns. Species and treatments were introduced as a between subject factor, and sampling date was introduced as a within subject factor. In addition, for each sampling date, analyses of variance (ANOVAs) followed by a LSD post hoc test, were used to test the differences among species and between treatments.

Before performing the regression analysis between PPI and leaf water potential, PPI values of each specimen were normalized by the maximum value recorded during the study period (PPI_{max}) for the same individual.

Within each species, we compared the nonlinear responses of PPI to ψ_{pd} between different datasets using the Akaike's information criteria (Graph Pad Software Inc., San Diego, CA, 2007), that selects the model that most likely have generated the data: one curve for different datasets (no differences) or different curves for each datasets (significant differences). We used the same approach to compare the responses of ψ_{pd} to SRWC among species.

Differences between non-linear equation parameters relative to diverse species, phases and treatments were considered significant when their 95% confidence intervals did not overlap. When no significant differences were found between species, periods and treatments, the pooled data was used.

Data deposition

Data available from the Figshare Repository: <https://figshare.com/s/f5f42105dbf6ff034903>

RESULTS

Plant cover dynamics

At the beginning of the experiment (2001) the whole study area was covered by a plant community dominated by the shrubs species *C. monspeliensis*, *D. pentaphyllum*, and *H. microphyllum*, accounting together for 73% of the total plant cover and for 77% of the total shrub cover. During the following 11 years, the overall shrub cover increased in the control plots and decreased in the rainfall reduction treatment (Fig. 1a).

The study species showed different dynamics: *C. monspeliensis* significantly increased its cover degree in the control plots (+0.6 % of the total cover per year), while a reduction was observed in the drought plots (-1.0 %) (Fig. 1b).; no significant variation was observed in *D. pentaphyllum* cover (Fig. 1c). *H. microphyllum* showed a decrease of cover degree in both control (-2.5 %) and treated plots (-1.9%) (Fig. 1d). More sporadic shrub species not present in all plots (mainly *Cistus incanus* and *Pistacia lentiscus*) increased their cover under drought.

Seasonal trend of morphological and physiological parameters

The leaf biomass (g m^{-2}) significantly differed among species, showing in addition significant seasonal trends (Fig. 2a). Leaf biomass peaked in spring, with the highest values recorded in *C. monspeliensis* ($468 \pm 46 \text{ g m}^{-2}$), followed by *H. microphyllum* ($208 \pm 15 \text{ g m}^{-2}$) and *D. pentaphyllum* ($64 \pm 9 \text{ g m}^{-2}$). During summer drought, leaf shedding reduced the leaf biomass in all species; with respect to the spring maximum value, at the end of the dry season (September 2010) leaf biomass was reduced by 48% in *C. monspeliensis*, by 30% in *D. pentaphyllum* and by 26% in *H. microphyllum*. Leaf biomass recovered in autumn, and in *C. monspeliensis* this recovery was faster than in the other two species (Fig. 2a). During the period of leaf biomass monitoring, the rainfall reduction treatment did not significantly affect this parameter.

In all species, the pre-dawn shoot water potential (ψ_{pd} , Fig. 2b) showed values close to zero during the wettest months, decreasing progressively in summer; during summer drought, *D. pentaphyllum* kept its water potential higher than the other two species (Fig. 2b).

Leaf level gas exchange rates peaked in all species in May (Figs. 2c and 2d), reached minimum values during summer drought (September) and recovered in autumn after the first rain events: in spring both *H. microphyllum* and *D. pentaphyllum* showed the largest values of

stomatal conductance (g_s , Fig. 2c) and leaf photosynthesis (A_{leaf} , Fig. 2d) compared to *C. monspeliensis*; differently, during the recovery period following the autumn rains (October and November), the recovery of photosynthetic spring rates was delayed in *D. pentaphyllum* and *H. microphyllum* (Fig. 2d). At plant level, PPI of *D. pentaphyllum* was always below the other two species (Fig. 2e), due to the lowest leaf biomass value. In spring, *C. monspeliensis* and *H. microphyllum* showed similar PPI_{max} values, achieved through a different combination of A_{leaf} (low in *C. monspeliensis*, high in *H. microphyllum*) and leaf biomass (high in *C. monspeliensis*, low in *H. microphyllum*). In autumn *C. monspeliensis*, due to the fast recovery of both leaf biomass and leaf gas exchange rates, was instead the species with the highest PPI. Rainfall reduction affected ψ_{pd} and A_{leaf} mainly in spring and in autumn, with significant differences recorded in autumn, when the first rainfalls after the summer drought were cut off (Fig. 3). In this period significant reductions of ψ_{pd} and A_{leaf} were observed in all studied species. In the control plots, *D. pentaphyllum* and *H. microphyllum* showed a delayed recovery after the summer drought, and the effect of the rainfall reduction treatment was also shifted to the late autumn (November 2010) (Figs. 3c and 3d); in this phase the photosynthetic activity resulted uncoupled from the plant water status, signalling the permanence of stressful conditions or structural changes in leaf functionality. In autumn 2011, due to a longer dry season, the recovery period resulted shifted towards a colder period; under these conditions, rainfall reduction did not affect A_{leaf} .

Impact of summer drought on carbon gain

To evaluate the effect of plant water status on plant carbon gain, we estimated the relationship between PPI and leaf water potential by nonlinear exponential fitting. The ψ_{pd} -PPI exponential relationship showed significant differences among species, periods and treatment, determining different ψ_{pd}^* thresholds (the ψ_{pd} value corresponding to $\frac{1}{3} \text{PPI}_{\text{max}}$) (Fig. 4, Table1). In the control plots, during the reduction period, *H. microphyllum* reached the threshold of $\text{PPI}_{\text{max}}/3$ at ψ_{pd} values higher (less negative) than *C. monspeliensis* and *D. pentaphyllum* (Figs. 4a, 4b and 4d, Table 1). These differences were not significant in the drought plots, because of the different ψ_{pd} -PPI response observed in *H. microphyllum* (Fig. 4d). During the recovery period no differences between treatments were recorded, and *H. microphyllum*, due to the delayed recovery of photosynthesis, showed a ψ_{pd}^* value considerably higher than those derived for *C. monspeliensis* and *D. pentaphyllum*.

To estimate the impact of these different drought responses on carbon gain over the entire study period, the dependence of ψ_{pd} on relative soil water content (SRWC) was approximated

by a logarithmic function (Fig. 5): the different ψ_{pd} -SRWC relationship in *D. pentaphyllum* indicates a slower reduction of ψ_{pd} in response to the soil drying. Neither periods (reduction and recovery) nor treatments affected these responses. According to the drought responses of the species under investigation, we found significant differences among species in Dur_{ep} (Table 2).

Due to high ψ_{pd}^* values, *H. microphyllum* was the species with the longest Dur_{ep} (i.e. the longest period with low photosynthetic rates). *D. pentaphyllum* and *C. monspeliensis* presented similar ψ_{pd}^* values, but because of the different SRWC- ψ_{pd} responses (Fig. 5), *D. pentaphyllum* reached this leaf water potential threshold at lower SRWC values than *C. monspeliensis*. This different response to the soil drying was responsible for the shorter Dur_{ep} of *D. pentaphyllum* (Table 2).

To evaluate the ability of the different performance estimators calculated in this study to describe the species success, we plotted the $A_{leaf\ max}$, $A_{leaf\ red}$, PPI_{max} , PPI_{red} values for the three species against their cover degree variation rate (Fig. 6): despite the variations of the absolute value of these two variables determined by rainfall reduction, only the species rank based on PPI_{red} (a plant performance estimator) corresponded in both treatments to the species' rank based on cover degree variation rate (a plant success measure) (Figs. 6g-h) Contrarily, a similar correspondence does not exist if we consider simpler descriptors of plant performance, such as maximum leaf level photosynthesis ($A_{leaf\ max}$, Figs. 6a-b), reduced leaf level photosynthesis ($A_{leaf\ red}$, Figs 6c-d) or maximum plant photosynthetic capacity (PPI_{max} , Figs. 6c-f).

DISCUSSION

According to Goldberg and Novoplansky (1997), the different changes in species cover degree observed from 2001 to 2011 can be analyzed using the “two-phase resource dynamics” approach, evaluating the species responses to optimal and stressful environmental conditions.

Pulse growth phase

Under the *pulse-phase* the photosynthetic activity of a specimen provides carbon resources for growth, and therefore for competition with other individuals; production, functioning, and maintenance of the resource uptake systems (leaves, stem, and roots) rely in fact on the availability of photosynthetic resources to be invested in these apparatuses (Solbrig and

Orians 1977; Pearcy et al. 1981; Fu et al. 2011). We used PPI_{\max} to represent the amount of carbon available for growth and resources acquisition during the *pulse-phase* (Angert et al. 2007), that is related to both canopy (leaf biomass) and leaf (leaf photosynthesis, A_{leaf}) traits. Considering the plant performance at best resource availability, *C. monspeliensis* and *H. microphyllum* (higher PPI_{\max}) should have an advantage over the species with a lower PPI_{\max} , like *D. pentaphyllum*, leading to a progressive replacement of the latter. However, it must also be considered the response to the stressful conditions that occur in summer, during the *interpulse-phase* (Craine et al. 2012).

Interpulse survival phase

After drought detection, stress coping mechanism are activated to limit the loss of plant functionality (Lichtenthaler 1996). Stomatal closure and partial leaf shedding are the main mechanism used by the species under investigation to reduce canopy conductance during drought. These responses prevent leaf water potential falling below the threshold determining xylem hydraulic failure, and avoid plant desiccation. However, both involve a reduction of CO_2 assimilation, with the risk of plant starvation occurrence and mortality (McDowell et al. 2008; Mitchell et al. 2014). Carbon starvation is therefore tightly interdependent on both the avoidance and the occurrence of plant hydraulic failure, and it can reduce plant performances impacting on maintenance metabolism, phloem transport, defence mechanisms, and on the dynamics of hydraulic conductance and refilling (McDowell 2011). The length of the period when a species is unable to keep a positive carbon balance (approximated by Dur_{ep}) can be used therefore to represent their *interpulse survival* capacity, and depend on the adaptive strategy adopted to face summer drought and to prevent xylem embolism.

In species such as *C. monspeliensis* the main adaptation to drought is the reduction of the transpiring surface, achieved through the shedding of about half of the leaves (Aronne and de Micco 2001). If from one hand this drought avoidance strategy strongly reduces PPI , on the other it improves the water status of the plant, prevents a rapid stomatal closure of the leaves remaining on the branches, and allows this species to avoid a significant reduction in leaf photosynthesis for most of the summer. The maintainance of active summer types leaves can be promoted by the low vulnerability to cavitation shown by the xylem of this species (de Micco et al. 2008). After the first autumn rains these leaves provide the resources for the flushing of new shoots, facilitating the fast recovery of plant photosynthetic functionality, and constraining Dur_{ep} .

The high amount of leaf biomass displayed under optimal condition (responsible for the high PPI_{max}) combined with the leaf exchange strategy and the rapid autumn recovery (that limit Dur_{ep}) give to *C. monspeliensis* a high PPI_{red} score, i.e. the best capacity to acquire resources when they are available without risking carbon starvation when they are not. This strategy is however not more effective under the climate change simulation: rainfall reduction tends to lower PPI_{max} (-16%) and to increase the Dur_{ep} (+6%), limiting in this way the species performances in the drought plots (22% reduction of the PPI_{red} value) (Fig. 3a, Table 2).

Compared to *C. monspeliensis*, *D. pentaphyllum* follows, in relation to its morphology, a different adaptive strategy to cope with drought: in addition to the desiccation avoidance (obtained through a moderate leaf shedding, Fig. 2a), it adopts a “morphological” avoidance of water stress (Ackerly 2004). This is achieved through a deep root system, that enables the access to water at deeper soil layers (Bhaskar et al. 2007; Signarbieux and Feller 2012), and limits the tissue water deficit in summer, as attested in this study by the highest pre-dawn leaf water potentials at the peak of drought.

During stressful conditions occurring in summer, *D. pentaphyllum* is therefore able to avoid the massive leaf shedding displayed by *C. monspeliensis*, and the almost total stomatal closure observed in the other species. The decline of PPI during summer was therefore less pronounced in this species, with a short Dur_{ep} and a reduced risk of carbon starvation. The maintenance of a significant summer transpiration observed in this species is associated with the anisohydric response to drought, which involves the tolerance of low leaf water potentials, with a higher risk of xylem embolism during intense drought (McDowell et al. 2008). Rainfall reduction did not affect PPI_{max} in *D. pentaphyllum*, reducing instead photosynthetic rates in the late autumn, without increasing Dur_{ep} (Fig. 3); only a small reduction of PPI_{red} was therefore observed in response to the drought treatment. This delayed autumnal depression of photosynthetic activity can likely be related to interference of the rainfall reduction with the nutrient cycle (Sardans and Peñuelas 2007).

H. microphyllum is a shallow rooted species (personal observation), and in spring shows high values of PPI_{max} , similar to *C. monspeliensis*. The response to drought is however different. This species does not seem able to effectively avoid drought stress through leaf shedding (Fig. 2a), and without a deep root system and an effective phenological avoidance mechanism, during summer it avoids desiccation through an early stomatal closure (Flexas and Medrano 2002) (Fig. 2b). This mechanism explains the steepest reduction of the leaf level photosynthesis as water potential decreases (Fig. 2d), and the early beginning of the exhaustion phase. After the summer dry period, the incomplete A_{leaf} recovery extends Dur_{ep}

until the late autumn: this functionality loss can depend on the decrease in plant hydraulic conductivity due to xylem cavitation (Pou et al. 2008; Quero et al. 2011), or on the accumulation of abscisic acid in the leaves, that can induce a persistent stomatal closure (Takahashi et al. 2018). The reduced desiccation tolerance of this species, along with the slow autumn recovery of optimal CO₂ assimilation rates, determines the longest Dur_{ep}, amounting to about half of the year (Table 2), and the very low PPI_{red} value.

The rainfall reduction treatment tends to reduce the maximum spring rates of photosynthesis (Fig. 3c), but did not increase Dur_{ep}; in fact, during summer, the PPI decay was slower in drought plots (Fig. 5d), counteracting the effect of the earlier decline of the soil moisture due to the spring rainfall reduction: this phenomenon could reflect an acclimation process involving both plant adaptations (change in leaf morphology and physiology) (Walter et al. 2013; Backhaus et al. 2014) and ecosystem processes (lower competition for resources in drought plots). This acclimation has, however, negligible impact on PPI_{red}, that resulted lower in drought plots.

PPI_{red} as index of plant success

Several studies stressed the importance of different plant traits in determining the success of a species within a community, such as leaf level photosynthetic rates (Zhang et al. 2005; Angert et al. 2007; Fu et al. 2011; Yu and Gao 2011), canopy morphology (Knapp et al. 2008) and plant phenology (Throop et al. 2012; Limpens et al. 2014). The method followed in this work combined all these variables and their responses to environmental constraints in a synthetic index (PPI_{red}) of plant performance.

In the dynamic context of an ecological succession, the species with higher PPI_{red} (i.e. with high PPI_{max} and short Dur_{ep}) are expected to outperform over time those with lower values of this performance index: a low PPI_{max} limits in fact the resources available for growth and competition, while a long Dur_{ep} increase the risk of carbon starvation and plant hydraulic failure (Mcdowell et al. 2008, Mcdowell et al. 2011).

This approach can also be useful to explain the mechanisms by which the shift in resources availability due to climate change affects species performances: in fact the adaptations that confer to species a given level of fitness are competitively superior only over a narrow range of environmental conditions. Under climate change these environmental conditions can result altered, with a consequent modification of the relative performance of the co-occurring species. At our experimental site, under the manipulated rainfall regime we observed an inversion of the cover trend of the dominant species *C. monspeliensis* (Fig. 1) (de Dato et al.

2008). The quantitative application of the two-phase resource dynamic proposed in this work allows us to identify the main processes responsible for this different dynamic under rainfall manipulation: because of PPI_{max} reduction (-16%) and Dur_{ep} elongation (+6%), *C. monspeliensis* moved from first to the second place in the PPI_{red} rank.. The decline of this species in the drought plots can be therefore attributed to the competition of species maintaining their performance also under rainfall reduction, such as *D. pentaphyllum*, (in which no PPI_{red} reduction was observed in response to the rainfall reduction treatment), and secondary to an increase of drought induced mortality.

This differential response to climate change simulation of the species investigated triggered a species reordering within the plant community in the drought plots (de la Riva et al. 2016). Considering that among the species considered in this study *C. monspeliensis* showed the highest carbon assimilation capacity, its progressive reduction can alter the carbon balance of the entire ecosystem; furthermore, in several Mediterranean habitats *C. monspeliensis* is the first species that colonize the soil after fires (Clemente et al. 1996), and its abundance reduction under future climate could lead to changes in post fire succession trajectories (Johnstone and Chapin III 2006).

In conclusion the work tested a process-based ecophysiological approach for the analysis of the changes in species cover degrees during ecological succession in a Mediterranean *garrigue* community, and it represents an attempt to provide a tool to analyze the mechanisms by which the chronic resource alteration due to the climate change can modify the plant community structure (Chang et al. 2015; Lloret et al. 2016). Finally, considering that there is an increasing need to develop approaches able to quantify the plant and ecosystem processes under future climatic variables (Alexander et al. 2016), the present work can indicate a methodology useful to inform ecological models about the capacities of the plants species to withstand the new environmental conditions, improving the estimates of species distributions and their dynamics under climate change.

FUNDING – ACKNOWLEDGEMENTS

This work was supported by the European Commission under the FP7-Research Infrastructures Program [Grant Agreement No. 227628] as a part of the Integrated Network on Climate Research Activities on Shrubland Ecosystems (INCREASE) project. We thank the anonymous reviewers that helped to improve the manuscript.

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Figure Legends

Figure 1:

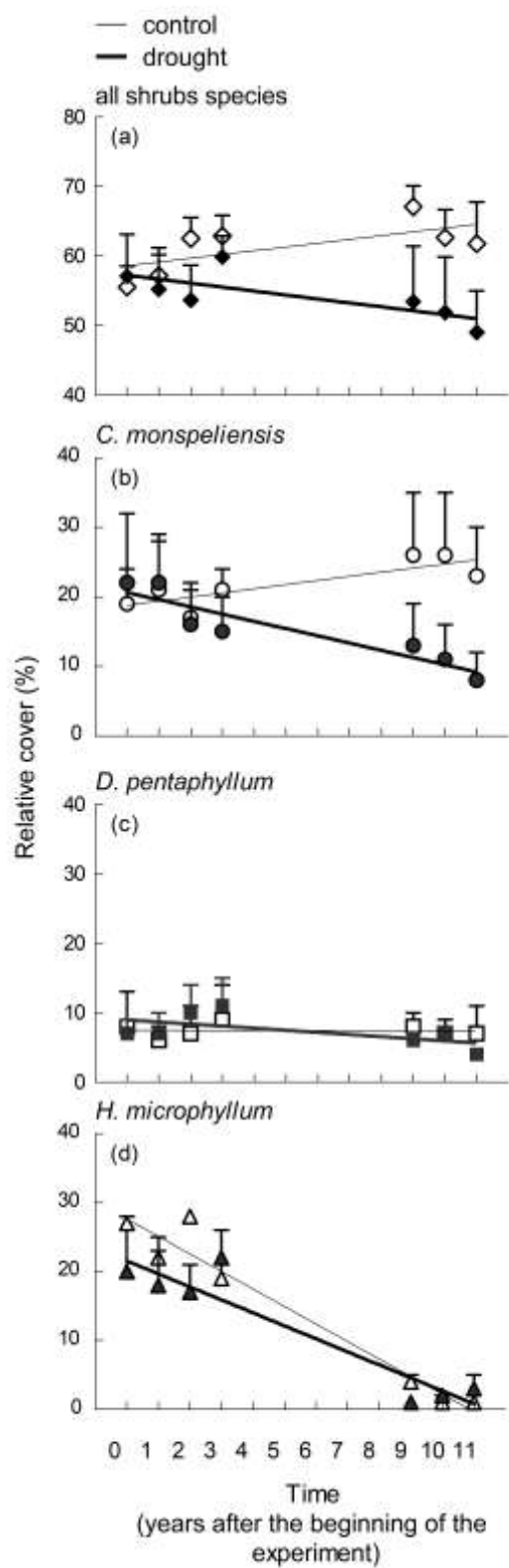


Figure 2: Seasonal trend (lines) and distribution (box plots) of a) plant leaf biomass, b) pre-dawn shoot water potential, c) stomatal conductance, d) leaf photosynthesis expressed per leaf weight unit and e) Plant level Photosynthetic Index (PPI) expressed per projected canopy area unit during 2010 in *Cistus monspeliensis*, (circles) *Dorycnium pentaphyllum* (squares) and *Helichrysum microphyllum* (triangles). The data refers to control plots. When present, different capital letters indicate, for each sampling date, significant differences among species; different lower-case letters indicate, within each species, significant differences among sampling dates; x-coordinate values are slightly offset to facilitate visual interpretation of the data. Mean \pm SE, n=6.

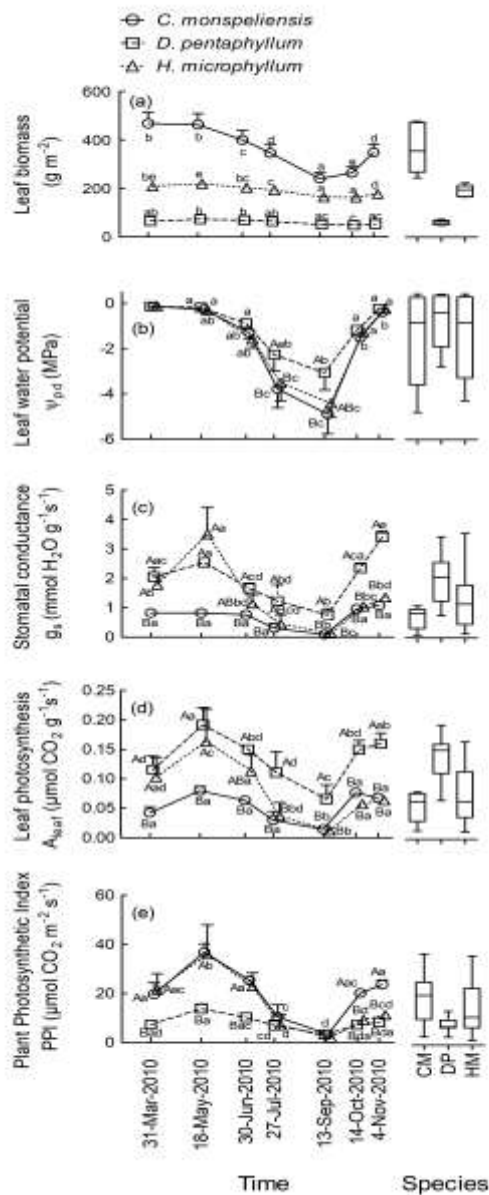


Figure 3 : Leaf photosynthesis (lines, left axis) and leaf water potential (bars, right axis) during the entire period of physiological monitoring in control treatment (open bars and symbols) and rainfall reduction treatment (filled bars and symbols) in a) *Cistus monspeliensis* b) *Dorycnium pentaphyllum* and c) *Helichrysum microphyllum*. d) relative soil water content in control treatment (thin line) and rainfall reduction treatment (thick line); arrows indicate the end of the drought period in 2010 and 2011. * indicates significant differences between control and rainfall reduction treatment. Mean \pm SE, n=3.

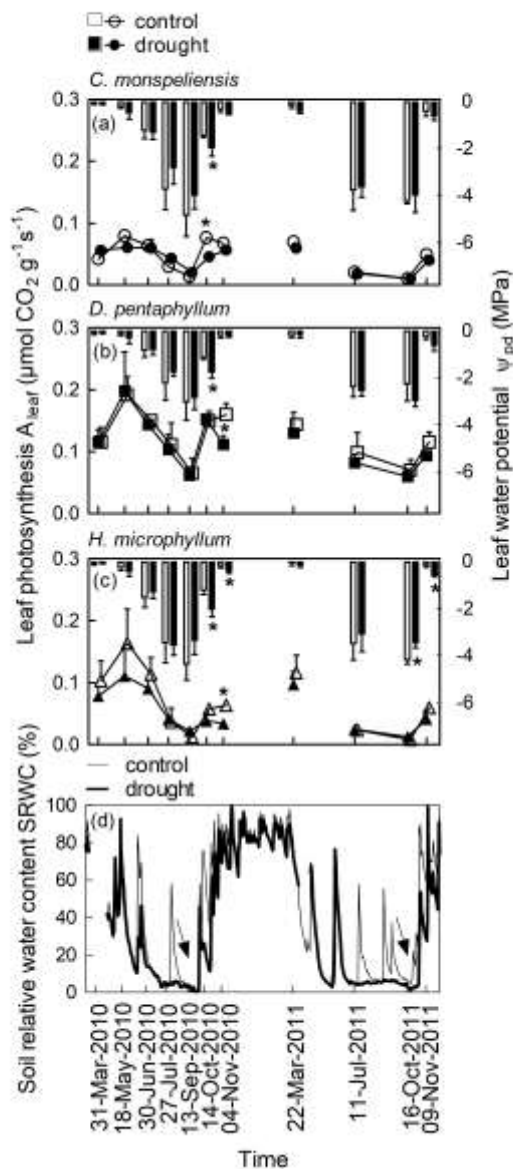


Figure 4: Responses of Plant level Photosynthetic Index (PPI, expressed as percent of the maximum value) to the leaf water potential variations in the different species, periods and treatments. Lines represent the exponential fitting of the data in a) *Cistus monspeliensis*, reduction and recovery period, control and rainfall reduction treatments b) *Dorycnium pentaphyllum*, reduction period, control and rainfall reduction treatments, c) *Dorycnium pentaphyllum*, recovery period, control and rainfall reduction treatments, d) *Helichrysum microphyllum*, reduction period in control treatment (thin line) and reduction period in rainfall reduction treatment (thick line) and e) *Helichrysum microphyllum*, recovery period in control and rainfall reduction treatments. The horizontal dotted lines identify the leaf water potential threshold corresponding to one third of the maximum PPI (ψ^*_{pd}). Open and filled symbols indicate respectively control and drought treatments. To facilitate the visual interpretation of the data, the x axis direction was inverted in the graphs showing the recovery period. See Supplementary Material Table A2 for the equations parameters and the fitting statistics.

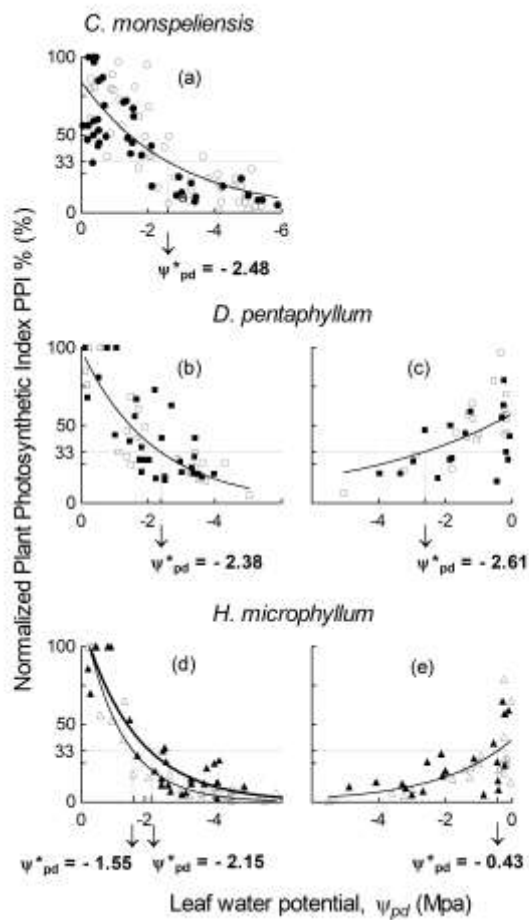


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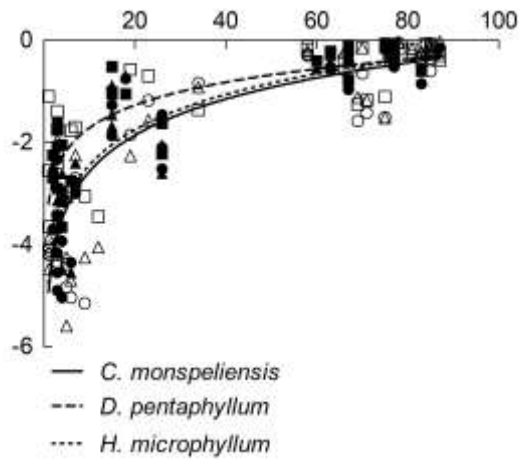


Figure 6:

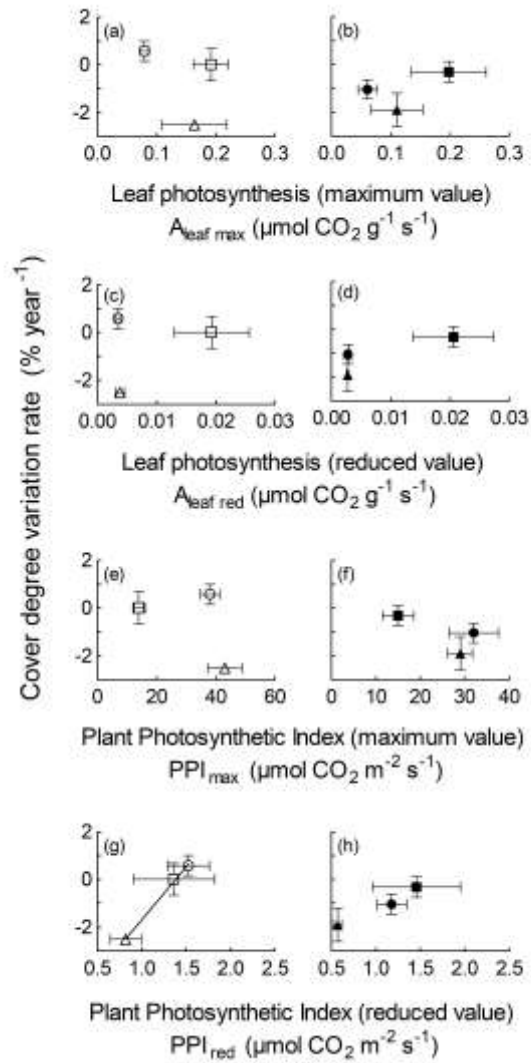


Table Legends

Table 1 Parameters indicating the different responses of Plant level Photosynthetic Index (PPI) (expressed as percent of the maximum value) to the leaf water potential variations in *Cistus monspeliensis*, *Dorycnium pentaphyllum* and *Helichrysum microphyllum*. k , absolute value of the decay constant relative to exponential relationship between PPI and leaf water potential; ψ^*_{pd} water potential value corresponding to one third PPI_{max} . In each period, different lowercase letters indicate significant differences among species. In each species, different subscripts letters indicate significant differences between reduction and recovery periods. In *Helichrysum microphyllum*, different capital letters indicate significant differences between control and rainfall reduction treatments.

	Exponential constant decay, k (PPI % ⁻¹)		Water potential threshold, ψ^*_{pd} (MPa)	
	Reduction period	Recovery period	Reduction period	Recovery period
<i>C.</i> <i>monspeliensis</i>	0.38 a		-2.48 a	
<i>D.</i> <i>pentaphyllum</i>	0.46 a _a	0.21 a _b	-2.38 a	-2.61 a
<i>H.</i> <i>microphyllum</i>	control	0.85 Ab _a	-1.55 Ab _a	
	drought	0.62 Ba _b	-2.15 Ba _a	-0.43 b _b

Table 2 Reduced Plant level Photosynthetic Index (PPI_{red}) and parameters used in PPI_{red} computation in *Cistus monspeliensis*, *Dorycnium pentaphyllum* and *Helichrysum microphyllum* in control and rainfall reduction treatment. Values are mean \pm SE; $n = 3$.

		Maximum Plant level Photosynthetic Index (PPI _{max}) ($\mu\text{molCO}_2 \text{ m}^{-2}\text{s}^{-1}$)	Period with low photosynthetic rates, (Dur _{ep}) (% of the year)	Reduced Plant level Photosynthetic Index, (PPI _{red}) ($\mu\text{molCO}_2 \text{ m}^{-2}\text{s}^{-1}$)
control	<i>C. monspeliensis</i>	37.9 \pm 3.3	25 \pm 2	1.52 \pm 0.24
	<i>D. pentaphyllum</i>	13.7 \pm 2.1	11 \pm 2	1.36 \pm 0.46
	<i>H. microphyllum</i>	42.6 \pm 5.8	54 \pm 5	0.81 \pm 0.18
drought	<i>C. monspeliensis</i>	32.0 \pm 5.6	27 \pm 1	1.18 \pm 0.17
	<i>D. pentaphyllum</i>	15.4 \pm 3.6	11 \pm 1	1.46 \pm 0.49
	<i>H. microphyllum</i>	29.3 \pm 2.8	51 \pm 1	0.57 \pm 0.05