Simulated climate change reduced the capacity of lichen-dominated biocrusts to act as carbon sinks in two semi-arid Mediterranean ecosystems

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Abstract The importance of biological soil crusts (biocrusts) for the biogeochemistry of drylands is widely recognized. However, there are significant gaps in our knowledge about how climate change will affect these organisms and the processes depending on them. We conducted a manipulative full factorial experiment in two representative dryland ecosystems from central (Aranjuez) and southeastern (Sorbas) Spain to evaluate how precipitation, temperature and biocrust cover affected the assimilation and net C balance of biocrusts. Chlorophyll fluorescence, net photosynthesis and dark respiration were measured in situ bimonthly during a year. We also conducted daily cycle measurements of net photosynthesis in winter and at the end of spring. In Sorbas, warming reduced the fixation of atmospheric C in biocrust-dominated microsites throughout the year. In Aranjuez, there was an interaction between the three factors evaluated; during winter, net photosynthesis was significantly greater in high biocrust cover plots under natural conditions and in the rainfall exclusion treatment. During the daily surveys, rainfall exclusion and warming reduced C fixation in Sorbas and in Aranjuez respectively. The effects of the treatments evaluated varied with the rainfall and non-rainfall water inputs (NRWIs) registered before

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the measurements. Our results suggest that changes in NRWI regimes as consequence of warming could have a greater impact on the C balance of biocrusts than changes in rainfall amounts. They also indicate that climate change may reduce the photosynthetic ability of lichens, with a consequent reduction of their dominance in biocrust communities at the mid to long term. This could reduce the ability of dryland ecosystems to fix atmospheric C.

Introduction

In drylands, plant interspaces are usually covered by biological soil crusts (hereafter biocrusts), communities composed of bacteria, fungi, algae, lichens, liverworts and mosses (Eldridge and Greene 1994; Belnap 2003; Maestre et al. 2011). The importance of bio-crusts for biogeochemical cycles and hydrogeomorphological processes in drylands is widely recognized (reviewed by Belnap 2003; Belnap and Lange 2003; Belnap 2006). While photosynthetic organisms forming biocrusts have lower net photosynthetic rates than vascular plants, in areas where plants are scarce or physiologically limited, biocrusts are considered a major component of the CO_2 uptake by the whole ecosystem (Lange et al. 1992; Garcia-Pichel and Belnap 1996; Lange 2003). Indeed, and at global scale, a carbon (C) net assimilation of ~ 2.5 Pg a^{-1} by cryptogamic ground covers has been estimated, corresponding to around 4.5 % of net primary production by terrestrial vegetation (Elbert et al. 2012).

Biocrust-forming organisms typically show a fast metabolic response to changes in their microenvironmental conditions, such as water scarcity, high and low temperatures and elevated light exposure (Lange et al. 1997, 1998; Kappen et al. 1998; Kranner et al. 2003; Zheng et al. 2011). Since biocrust constituents occupy the soil surface (usually with higher temperatures than the air during cloudless days), and lack stomatal control, they dry out quickly (Bowling et al. 2011). Hence, they are very sensitive to humidity and temperature pulses, these being the main factors determining their biological activity in drylands (Veste et al. 2001; Grote et al. 2010; Bowling et al. 2011). Most previous studies on the photo-synthetic behaviour of biocrust constituents have been conducted in the laboratory (Lange et al. 2001; Lange 2003; Grote et al. 2010), or have separated them from their underlying soil, with the consequent possibility of having eliminated the major factor influencing their CO_2 exchange (Wilske et al. 2008). There are also important uncertainties about how the metabolic activity of biocrusts will be affected by predicted changes in climate, and how climate change-induced effects on biocrusts will impact the C balance of drylands (Maestre et al. 2013). Therefore, more information about the in situ gas exchange of unaltered biocrusts, as well as a better understanding of the relationship between environmental factors and the photosynthetic activity of biocrusts, is necessary to improve our ability to predict how climate change will impact drylands.

Organisms such as lichens may also be suitable model organisms to detect changes in photosynthetic activity as a result of climate change because of their lack of homeostatic mechanisms to cope with extreme environmental conditions (Lechowicz 1982). This fact is important for the new generation of climate models, which consider the feedbacks between vegetation dynamics and climate change (e.g. Randerson et al. 2009; Thornton et al. 2009;

Friedlingstein and Prentice 2010). To improve our understanding on how climate change will impact the physiological activity of biocrusts, we conducted a full factorial climate manipulative experiment at two field sites in Spain. Based on previous studies that high-lighted the importance of wetting events in the C balance of poikilohydric organisms (e.g. Čabrajić 2009; Reed et al. 2012), and the negative effects that temperature increases have on maintaining soil moisture (e.g. Grote et al. 2010; Su et al. 2012), we hypothesized that predicted changes in climate will have a negative effect on the ability of biocrusts to fix carbon (Maestre et al. 2013), and thus in the capacity of dryland ecosystems to be C sinks. Our objectives were to: (i) explore the main temporal features of the biocrust C fixation ability on daily and seasonal scale, and how they relate to climatic variables; (ii) evaluate how predicted changes in climate (warming of 2–3 °C and ~30 % reduction in rainfall; Escolar et al. 2012) will affect the in situ photosynthetic efficiency and gas exchange of biocrusts; and (iii) verify whether climate change effects on these variables vary with the degree of biocrust development.

Methods

Study sites

The study was conducted at two research sites: Aranjuez (40°02′N–3°32′W; 590 m a.s.l.) and Sorbas (37°05′N–2° 04′W; 397 m a.s.l.), located in central and south-eastern Spain, respectively. Their climate is Mediterranean semi-arid, with a mean annual temperature and rainfall of 15 °C and 349 mm, and 17 °C and 274 mm in Aranjuez and Sorbas respectively. Both sites are Miocene gypsum outcrops, with soils classified as and are classified as Gypsiric Leptosols (IUSS Working Group WRB 2006). The cover of perennial vegetation is below 40 % at both study sites, and is constituted mainly by the tussock grass *Macrochloa tenacissima* (=*Stipa tenacissima*, alpha grass). Some shrubs or dwarf shrubs (e.g. *Retama sphaerocarpa, Gypsophyla struthium, Helianthemun squamatum*), as well as some crass perennial plants (e.g. *Sedum gypsicola, Sedum sediforme*), are also common to both areas. Over half of the plant interspaces are colonized by a well-developed biocrusts dominated by green algae lichens in both sites, being the most abundant *Diploschistes diacapsis, Squamarina lentigera, Cladonia convoluta, Fulgensia spp.* and *Psora decipiens* (see Maestre et al. 2013 for a species checklist).

Experimental design

A full factorial manipulative experiment was setup in July 2008 and May 2010 in Aranjuez and Sorbas, respectively. The factors, all of them with two levels, were: (i) biocrusts cover (Crust; poorly developed biocrusts communities with cover <25 % vs. well developed biocrusts communities with cover >50 %); (ii) warming (WA; natural vs. 2–3 °C tem-perature increase); (ii) and rainfall exclusion (RE; natural vs. ~30 % rainfall exclusion). Throughout the text we refer to the control treatment as the natural temperature and rainfall conditions. The number of replicates was 10 and 8 in Aranjuez and Sorbas, resulting in a total of 80 and 64 experimental plots at these sites, respectively. A minimum separation distance between plots of 1 m was established to minimize the risk of sampling non-independent areas. The plots were 1 m² with a PVC collar of 20 cm in diameter in their centers for biocrust monitoring. The collars were inserted approximately 5–6 cm into the soil, standing out 2–3 cm over it.

The warming treatment aimed to simulate the average of predictions derived from six Atmosphere–Ocean General Circulation Models for the second half of the 21st century (2040–2070) in central and Southeast Spain, which predict increases of 2.1–2.3 °C during winter months, and 3.2–3.5 °C during summer months (De Castro et al. 2005). To achieve a temperature increase within this range, we used open top chambers (OTCs) of hexagonal design with sloping sides of 40 × 50 × 32 cm (see Escolar et al. 2012 for details). These structures were built with methacrylate, and were elevated between 3 and 8 cm from the soil to allow air circulation over the surface of the plots, and thus avoid an excessive overheating.

Predicted changes in rainfall for our study area are subjected to a high degree of uncertainty, but most climate models forecast important reductions—between 10 and 50 %—in the amount of spring and fall rainfall (De Castro et al. 2005). To simulate these conditions, we set up passive rainout shelters (RSs) based upon the design described by Yahdjian and Sala (2002). Each RS has an area of 1.44 m^2 (1.2 × 1.2 m), a mean height of 1 m, and is composed of three methacrylate grooves, which cover approximately 37 % of the surface, connected to plastic bottles that accumulate the excluded water in order to control it. See Escolar et al. (2012) and Maestre et al. (2013) for additional details of the experimental installations and their effects on microclimatic variables.

Microclimate monitoring

The effects of the OTCs and RSs on air temperature and relative humidity (RH) were continuously monitored using automated sensors (HOBO U23 Pro v.2 Temp/RH, Onset Corporation, Bourne, MA, USA), and those on soil surface (0–2 cm) temperature and moisture (0–5 cm depth) were continuously monitored on the two levels of Crust factor using TMC20-HD and EC-5 sensors, respectively (Onset Corp. and Decagon, Inc., Pullman, WA, USA). Soil moisture (0–5 cm depth) was measured discontinuously with time-domain reflectometers (TDR, Topp and Davis 1985). To compare these effects between treatments, air and soil temperatures were calculated as the temperature average during the gas exchange measurement period, and soil moisture measured discontinuously was preferably used.

Two sources of non-rainfall water input (NRWI) were studied: dew and fog. Several studies have found a positive and significant relationship between the duration of these events and the amount of water condensed on the surface (e.g. Zangvil 1996; Beysens et al. 2005; Kidron 2000; Uclés et al. 2013a). But the main advantage of detecting these events lies in providing information on the duration of their occurrence, which could even be more important than their amount regarding biological activity and species distribution (Malek et al. 1999; Kidron and Temina 2013). Hence, dew and fog condensations were studied in terms of their durations, and the NRWI between plots with and without OTC was compared based on this assumption.

Dew occurs when the temperature of the surface where water condenses is equal or lower than the dew point of the surrounding air. Measuring the temperature of the soil surface with the enough accuracy to determinate dew with in situ sensors is difficult, but previous studies have done so using thermocouples buried in the soil (Uclés et al. 2013a, b). Hence, we estimated the duration of dew as the time in which the surface temperatures of the sensors TMC20-HD were below the dew point temperature of the air (this being calculated from the temperature and RH measured by the HOBO U23 sensors).

Fog is produced when the atmospheric water vapour concentration reaches saturation and condensed water droplets remain suspended in the air. In this study, the occurrence of

fog events was considered when relative air humidity was higher than 98.5 %, as the sensors typically have an accuracy error of ±2.5 % (Onset Corporation 2013).

Gas exchange measurements

The CO_2 exchange of the whole soil column, including the biocrusts living on its surface, was measured at six randomly chosen replicates per combination of treatments every 2 months between September 2010 and January 2012. These measurements were conducted at both study sites after dawn, starting when the collars received direct light, and always on cloudless days to avoid the interference of occasional clouds in the response of any treatment, or hour in the daily cycles. This is a representative meteorological situation of the experimental areas as, on average, Aranjuez and Sorbas have 94 and 106 cloudless days per year, respectively; AEMET 2013). Previous studies have found that, in drylands with relevant water supply as dew or fog, such as those we studied, the photosynthetic activity of biocrust constituents peaks during early morning hours in the absence of rain (Kappen 1988; Lange et al. 1992, 2006; Veste et al. 2001). In addition to the absence of clouds, we performed all measurements within a maximum interval of 2 h to maintain homogeneous environmental conditions, so half of the replicates were measured in 1 day, and the other half were measured on the next day.

   We measured net photosynthesis (µmol CO_2 $m^{-2}s^{-1}$) using two infrared gas analyzer (IRGA) systems (LI-6400, Lincoln, NE, USA) connected to a customized methacrylate transparent chamber with a volume of 2,385 cm^3. To ensure the sealing of the chamber on the sample, a toroidal flat disk covered with an air-tight rubberized band was placed between the chamber and the PVC collar. The devices were operated as open dynamic systems, i.e., the chamber air was renewed with a continuous external air flow and the CO_2 flux was calculated as the difference in the [CO_2] between the chamber air (measured by an IRGA referred to as sample) and the external input air (measured by an IRGA referred to as reference). The external input air was taken at two meters above the soil surface by a rod to use a natural atmospheric air without the influence of the biological activity (photosynthesis and respiration of soil and plants) and the operator's breathing on its [CO_2], and a bottle of 6 L was used as a buffer volume in order to use an input air with a stable [CO_2]. The external air circulated through the system with a flow of 800 µmol s^{-1}, and an additional ventilation into the chamber of 0.7 m s^{-1} were used to obtain an adequate air mixing. System flow and IRGA CO_2 zeros were calibrated each day before measurements, and H_2O zeros were calibrated the first of the two consecutive measurement days of each bimonthly data collection. Before each individual measurement we matched the CO_2 readings of the sample and reference IRGAs, as this is very important for the accuracy of the measurements when low ΔCO_2 values are expected (LI-COR 2012). The net photosynthesis value of a plot was recorded when the CO_2 values of the sample and reference IRGAs were stabilized.

   Photosynthetically active radiation (PAR) was measured with a LICOR external quantum sensor (9901-013, LICOR, Lincoln, NE, USA), and with a Field Scout Quantum Light Meter (Spectrum Technologies, Plainfield, IL, USA), both of them placed at the top of the transparent chamber to have a reference value close to the biocrust surface. It was recorded at the same time of the net photosynthetic activity, and was used to consider in the statistical analyzes a potential source of variability in photosynthesis values because of environmental changes unrelated to our treatment. Immediately after these records, dark respiration was measured in the same plots with two soil respirometers (LI-8100, Lincoln, NE, USA). They operated as closed dynamic systems, i.e., there was a continuous

recirculation of air inside the system, but without being renewed with an outside air intake. CO_2 flux was calculated as the change in chamber [CO_2] during the sample enclosure time adjusted to an exponential function. Each respiration measurement lasted 120 s, this being the recommended time when is expected the low flux characteristic of dryland ecosystems (Castillo-Monroy et al. 2011; Rey et al. 2011). A fitting equation between these two systems (LI-6400 and LI-8100) was performed covering the clear chamber attached to LI-6400 with an opaque cloth ($R^2 = 0.96$), and it was applied on the dark respiration records. As both devices measured gas exchange of the whole soil profile, in both cases the respiration of autotrophic and heterotrophic components was present, and gross photo-synthesis could be calculated as the sum of net photosynthesis and soil dark respiration.

Daily cycles of net photosynthesis were also conducted in May 2010 in Aranjuez, and in January 2012 at both study sites. They were performed with the same protocol described above, but the measurements were extended throughout the daylight, and only collars with well-developed biocrusts were measured. During the measurements conducted in May 2010 only net photosynthesis was measured, but in January 2012 net photosynthesis (Li-6400) and dark respiration (LI-8100) were taken, so we could estimate gross photosynthesis.

Chlorophyll fluorescence measurements

Chlorophyll fluorescence was measured by computing the parameter F_v/F_m, an indicator of the status of the photosystem II in photosynthetic organisms (Maxwell and Johnson 2000), with a Handy PEA fluorometer (Hansatech instruments, Kings Lynn, UK). Low values indicate the presence of physiological stress (Maxwell and Johnson 2000). These mea-surements were conducted simultaneously with the bimonthly gas exchange measurements described above, but only in the Sorbas site. F_v/F_m was calculated as the ratio between the variable ($F_v = F_m - F_o$) and the maximum (F_m) fluorescence signal. Prior to measure-ments, lichens were dark adapted using opaque cloths for 30 min. Fluorometer measure-ments of the whole biocrusts community were made in four replicated plots per combination of treatments. Six random measurements per plot were taken in all cases, which were averaged for further analyses.

Data analyses

We evaluated the effects of biocrust cover (Crust), warming (WA), rain exclusion (RE), and their interactions, on the measured variables (net and gross photosynthesis, dark res-piration and F_v/F_m) over time using general linear mixed models (LMMs) by means linear mixed-effects models (lme) procedure from Linear and Nonlinear Mixed Effects Models (nlme) R package (Pinheiro et al. 2013). The generic function of lme fits a linear mixed-effects model in the formulation described in Laird and Ware (1982), but besides allowing for nested random effects (Pinheiro et al. 2013). LMMs expand on the ordinary linear regression model by allowing one to incorporate lack of independence between observa-tions and to model more than a single error term (Cnaan et al. 1997), so temporal correlated errors and variance of the errors can be modeled in order to avoid pseudoreplication and heteroscedasticity problems, respectively.

Four fixed factors were established in the bimonthly survey analyses: measurement date, Crust, WA and RE. All their possible interactions were included in the models. In daily cycle analyses, the Crust factor was not applied, as only high biocrust cover plots (>50 %) were measured. The analyses were implemented in InfoStat software version 2013p (Di

Rienzo et al. 2013), a friendly interface to use R (version 2.15.2). The restricted maximum likelihood (REML) procedure, which takes into account the loss in degrees of freedom resulting from estimating fixed effects (Patterson and Thompson 1971), was used to estimate the variance and covariance components. The best structures for our models were selected with the AIC criterion (Akaike 1973). For the analyses of net and gross photosynthesis, we also evaluated whether the inclusion of PAR as a covariate in the models improved their fit. Fisher's least significant difference (LSD) post hoc test was applied on the most complex interactions of the factors that showed significant differences. The effect of WA on NRWI duration was analyzed for each measurement day using t tests. When the variance was not homogeneous, we used the non parametric Mann–Whitney test instead.

Results

Treatment effects on micrometeorological conditions during measurements

Summer drought was more acute in Sorbas than in Aranjuez (Fig. 1). The distribution of rainfall events was also less equitable in Sorbas site. However, the amount of rainfall registered in the days prior to the measurements was greater in Sorbas, especially in December 2010, September 2011, and November 2011. The winter 2011–2012 was characterized by an unusually low number of rainfall events in Aranjuez. Nighttimes preceeding the measurements were characterized by the formation of dew and fog in Aranjuez and Sorbas, particularly during winter. Dew formation and small events of fog predominated in Sorbas, whereas long duration fog events (more than 4 h) were more common in Aranjuez. Warming reduced the duration of dew and fog at all events, albeit significant differences were only found in short events (two in Sorbas, and another two in Aranjuez; Fig. 1).

During the bimonthly measurements, the WA+RE treatment had consistently the lowest soil moisture values in Sorbas (Fig. S1a, b), whereas in Aranjuez the treatment with such values varied through time and with the degree of biocrust cover (Fig. S1c, d). OTCs caused a soil temperature increase of 1.7 and 3.3 °C on average in Sorbas and Aranjuez respectively (Fig. S2a, b). In Sorbas, this treatment also increased early morning air temperature 2.4 °C in February and 5.6 °C in April (Fig. S2c). In Aranjuez (Fig. S2d), this increase was over 2 °C only in February (2.4 °C), and was lower or did not occur in the rest of dates at both sites, as the temperature differences in plots with and without OTCs were between -1.8 and 1.6 °C. During the January daily cycles (Fig. 2a, b), OTCs caused a maximal increase in air and soil temperatures of 4 and 3.3 °C, respectively, in Sorbas, and of 4.3 and 3.5 °C in Aranjuez. In May (Fig. 2c), the maximal increase in air temperature in Aranjuez was greater (6.8 °C), but increases in soil temperature were similar to those recorded in winter (3.3 °C).

Temporal features of the biocrust gas exchange on seasonal and daily scales

Positive net photosynthesis was only detected during late autumn and winter in both Aranjuez and Sorbas (Fig. 3), coinciding with the peak of gross photosynthesis (Fig. 4). The maximum peaks of gross photosynthesis were observed in the high biocrust cover plots at both study sites (Fig. 4). In Sorbas, dark respiration peaks occurred in late spring in low biocrust cover plots under the RE, WA and RE+WA treatments, and in summer in the rest of the treatments. In Aranjuez, these peaks were detected in spring in low biocrust
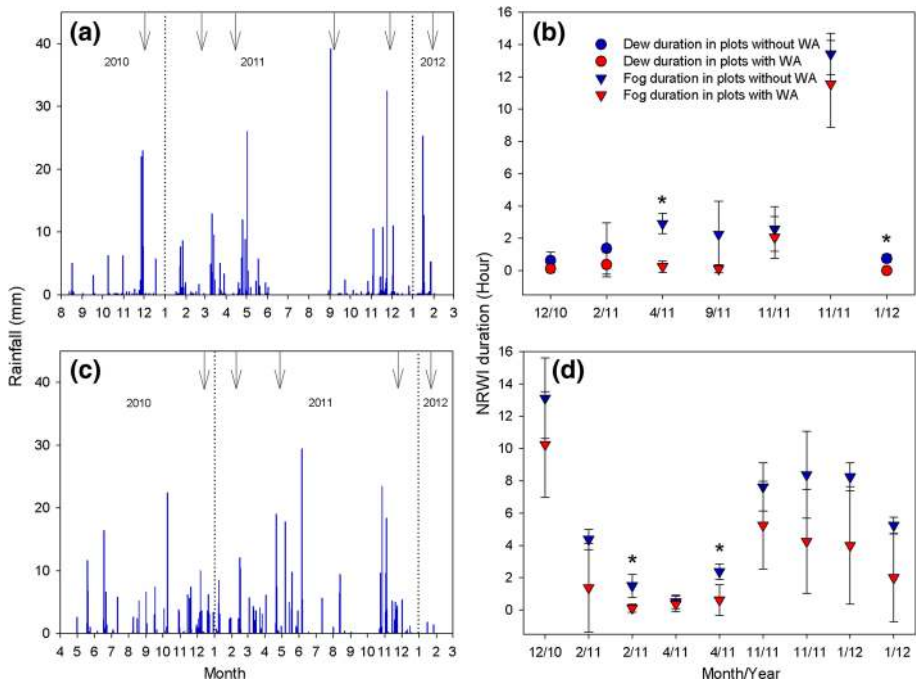
Fig. 1 Rainfall registered during the study period at Sorbas (**a**) and Aranjuez (**c**), and non-rainfall water inputs (NRWI) registered before the gas exchange and chlorophyll fluorescence measurements at Sorbas (**b**) and Aranjuez (**d**). *Asterisks* denote statistically significant reduction of NRWI at $p < 0.05$ in warming treatment (WA) plots. NRWI data are mean $\pm$ SE ($n = 4$)

cover plots under the control, RE and WA treatments, and in the rest of the treatments during late autumn and winter.

Seasonal effects on net photosynthesis were evident in Aranjuez. Antecedent rainfall inputs between December 2010 and April 2011 were similar, and the differences in other environmental variables (e.g., air and soil temperatures, soil moisture) were not relevant during early morning hours at this site (Figs. S1c, d, S2b, d). The most relevant difference between these two months was the NRWI, which was greater in December (Fig. 1), but presumably its effect on photosynthesis was not significant, since precedent rainfalls were abundant. However, important contrasts in the response of the biocrusts were observed, with maximum annual net photosynthesis values in December, and negative values for all treatments in April (Fig. 3c, d); so the biocrust gas exchange response to similar environmental conditions was different depending on the season.

Due to the random nature of rain events in drylands, the photosynthetic activity can also show a high intra-seasonal variability. For example, the effect of the previous winter rainfalls on in situ net photosynthesis over biocrust-forming lichens can be observed comparing December 2010 with February 2011. The C fixation differences between these months were remarkable in both sites because preceding precipitation was much more important in the fist than in the second month (Fig. 1).

The January daily cycles obtained at both sites were very different due to the distinct water availability of the specific measured days (Fig. 1, see antecedent rainfalls). This caused differences in gross photosynthesis; as this variable was around three-fold higher in
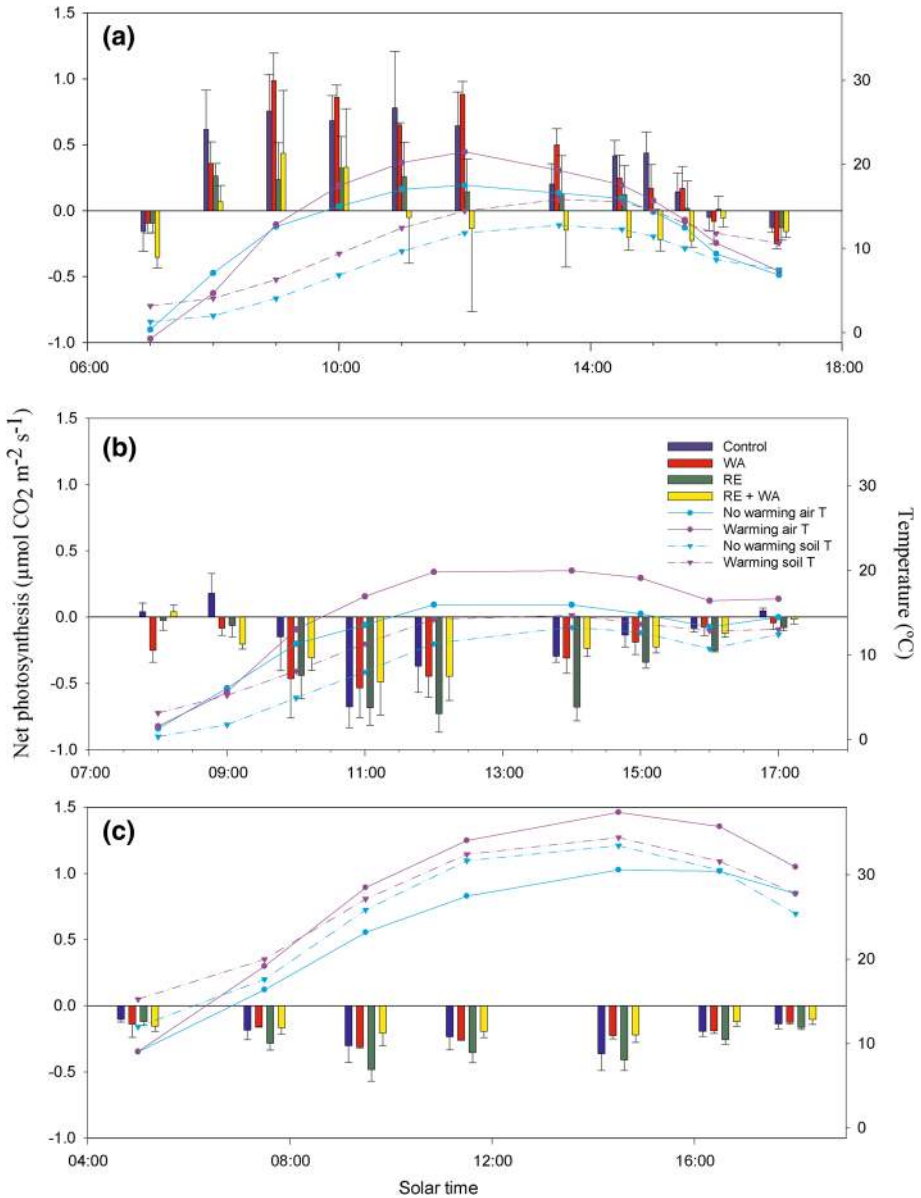
Fig. 2 Daily cycle surveys of net photosynthetic rate in January at Sorbas (**a**) and Aranjuez (**b**), and in May at Aranjuez (**c**). Data are mean ± SE ($n = 6$ in January; $n = 4$ in May). *WA* warming, *RE* rainfall exclusion

Sorbas than in Aranjuez (Fig. 5). At Sorbas (Fig. 2a), net photosynthesis remained positive in all plots (excepting those under the RE+WA treatment) when PAR values were higher than 150 µmol m^{-2} s^{-1}, and a maximum peak was detected at noon. In Aranjuez (Fig. 2b), positive net photosynthesis was only recorded at dawn and dusk in two treatments (control and RE+WA). During the May daily cycle in Aranjuez (Fig. 2c), no positive values of net photosynthesis were observed at any time.
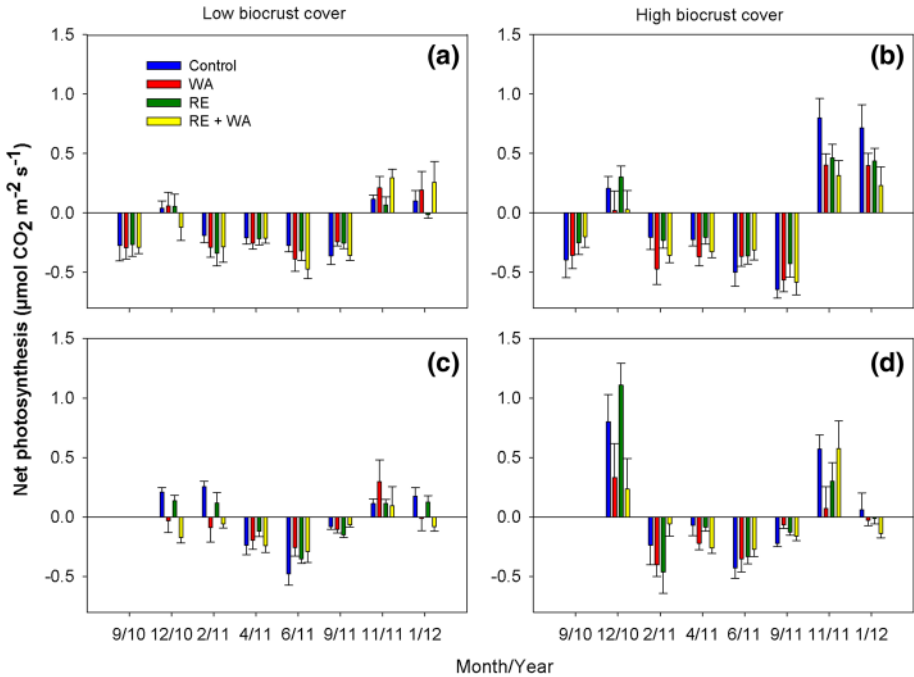
Fig. 3 Temporal variation of net photosynthetic rate at Sorbas (**a**, **b**) and Aranjuez (**c**, **d**) experimental sites. Data are mean ± SE ($n = 6$). *WA* warming, *RE* rainfall exclusion

Impacts of warming and rainfall reduction on the in situ photosynthetic efficiency and gas exchange of the biocrusts

Variation of the effects of climate change as a function of biocrust cover

In the analysis of the bimonthly surveys, where the factor Crust was included, rainfall exclusion and temperature increase showed complex interactions with biocrust cover and the time of measurement, which affected all the variables measured in Sorbas, and the net photosynthesis in Aranjuez. Warming had a greater effect on biocrust performance at Sorbas than at Aranjuez, and reduced C fixation in areas with well-developed biocrusts. Significant interactions found with the statistical models are disclosed below in detail.

A significant Date × Crust × WA interaction was found when analyzing F_v/F_m data from Sorbas (Table S1). An analysis of the Crust × WA interaction for the different surveys revealed that, in December 2010, plots with low biocrust cover and without OTCs had significantly lower F_v/F_m values than those with high biocrust cover plots (regardless of the presence of OTCs). In November 2011, low biocrust cover plots had significantly lower F_v/F_m values than high biocrust cover plots, regardless of the WA levels considered. No significant differences were found in the factor RE (Fig. 6d).

When analyzing net photosynthesis data, a significant Date × Crust × WA interaction was also found at Sorbas (Table S2). When this variable was positive, WA reduced it in high biocrust cover plots (Fig. 6a). But in low biocrust cover plots, net photosynthesis was increased with WA during the last measured winter month. High biocrust cover plots had greater positive C balance than low biocrust cover plots without OTCs, but these
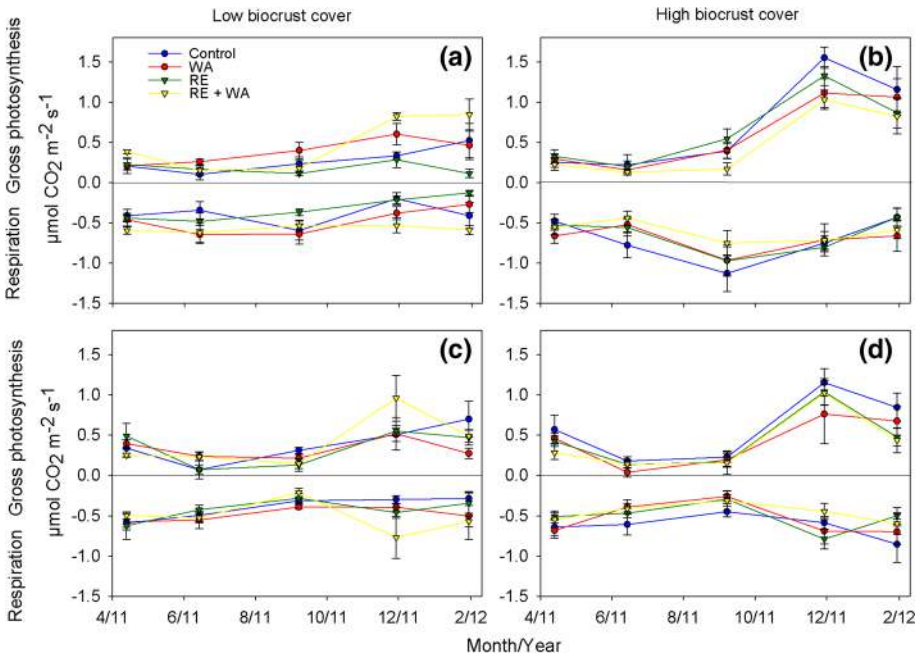
Fig. 4 Temporal variation of gross photosynthetic rate and dark respiration at Sorbas (**a**, **b**) and Aranjuez (**c**, **d**) experimental sites. Data are mean ± SE ($n = 6$). *WA* warming, *RE* rainfall exclusion
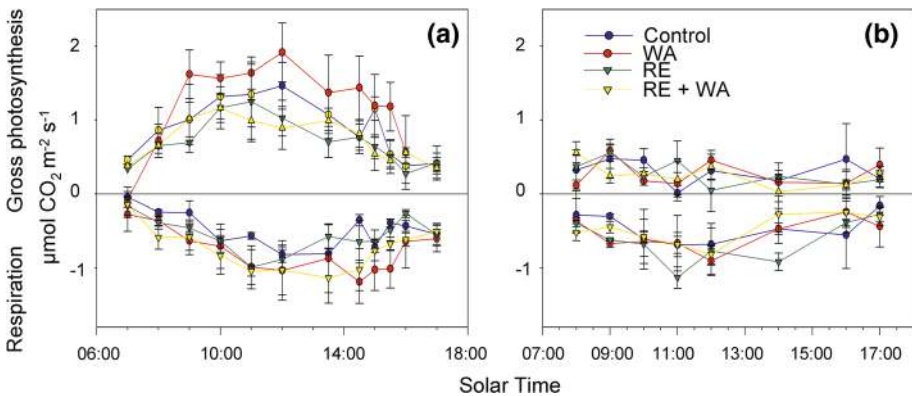

Fig. 5 Daily cycle surveys of gross photosynthetic rate and dark respiration in January at Sorbas (**a**) and Aranjuez (**b**) experimental sites. Data are mean ± SE ($n = 6$). *WA* warming, *RE* rainfall exclusion

differences were not found in the WA treatments. In February and April 2011, when net photosynthesis was negative, WA increased the C emissions in high biocrust cover plots, an effect that was not found in the low biocrust cover plots. No significant effects of RE were found in Sorbas, but in Aranjuez a significant Date × Crust × WA × RE interaction was found (Table S2). In December 2010, control and RE plots with high biocrust cover had a significantly higher net photosynthesis than those from other treatments (Fig. 7a). However, only low biocrust cover plots with control and RE treatments had a positive net
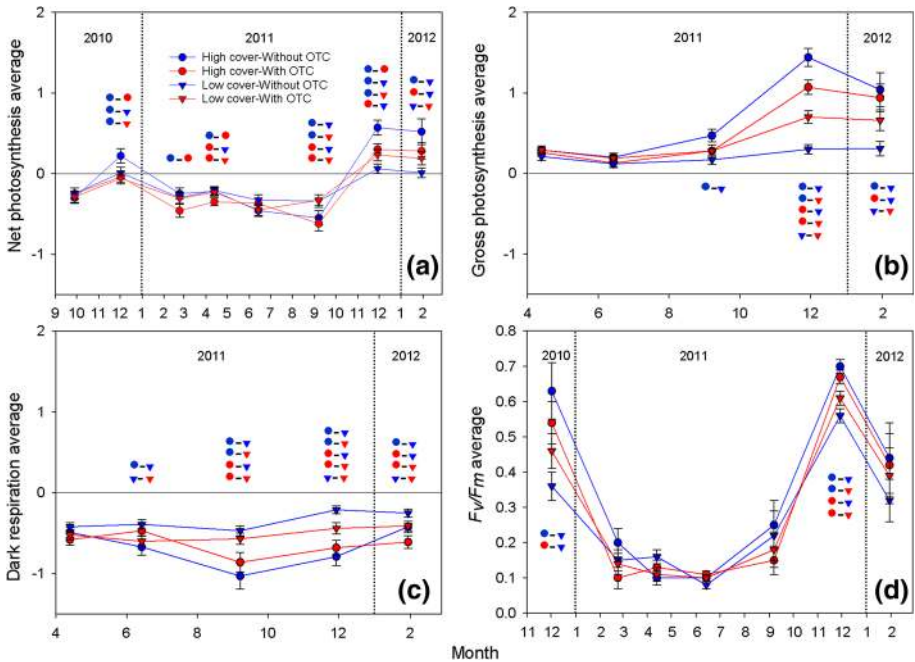
Fig. 6 Fisher's least significant difference (LSD) post hoc results in Sorbas bimonthly surveys: net photosynthetic rate (**a**), gross photosynthetic rate (**b**), dark respiration (**c**) and F_v/F_m (**d**). Treatment *symbols* joined by *dashes* denote statistically different averages at $p < 0.05$ between these treatments within each time. Data are mean $\pm$ SE ($n = 6$). *WA* warming

photosynthesis in February 2011 (Fig. 7b). At this date, the values found in these plots were significantly greater from those found in high biocrust cover plots with either WA or RE, but not with WA+RE treatments.

A significant Date × Crust × WA interaction was found when analyzing gross photosynthesis data from Sorbas (Table S2). Only low biocrust cover plots had significant differences between WA factor levels, as this variable was higher in WA plots during late autumn and winter. In plots without OTCs, gross photosynthesis was significantly higher in high biocrust cover plots than in low biocrust cover plots during September 2011, November 2011 and January 2012 (Fig. 6b). In WA plots, this difference was only found in November 2011. In Aranjuez, a significant Date × Crust interaction was found; high biocrust cover plots had significantly higher values of gross photosynthesis than low biocrust cover plots in late autumn, when maximum photosynthetic rates were reached (Fig. 7c). Rainfall exclusion had not significant effects on gross photosynthesis.

A Date × Crust × WA interaction close to statistical significance was found when analyzing dark respiration in Sorbas (Table S2). As when F values exceed 2 there is a high probability that the results would have been significant with more replicates (Fry et al. 2013), a post hoc analysis for this interaction was performed. Only low biocrust cover plots showed significant differences between WA levels; higher dark respiration was observed in WA plots in late spring (Fig. 6c). Differences between Crust factor levels were also observed: in plots without OTC high biocrust cover showed higher dark respiration than low biocrust cover in four months (June 2011, September 2011, November 2011 and January 2012); this was also found in plots with OTC in September 2011 and January
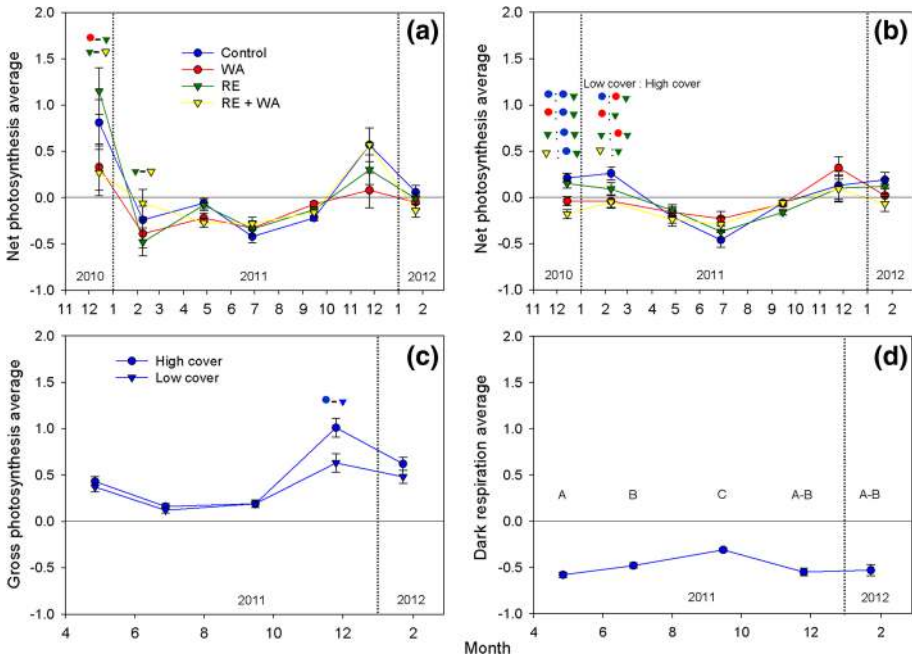
Fig. 7 Fisher's least significant difference (LSD) post hoc results in Aranjuez bimonthly surveys: net photosynthetic rate in high biocrust cover plots (**a**), net photosynthetic rate in low biocrust cover plots (**b**), gross photosynthetic rate (**c**) and dark respiration (**d**). In panels (**a**) and (**c**), the pairs of treatments with statistically different averages within each time are denoted by their legend symbols joined by *dashes*. In panel (**b**), there are no significant differences between the treatments represented within each time. However, significant differences between biocrust cover treatments (i.e. statistical comparison between panels (**a**, **b**)) within each time are shown above the averages. The *first column of symbols* represents the low cover treatments, and after colons, the high cover treatments where significant differences were found. In panel (**d**), significant differences between surveys are shown by *letters*. No *letters* in common denote different averages. All analyses were performed at $p < 0.05$. Data are mean ± SE ($n = 6$). *WA* warming, *RE* rainfall exclusion

2012. In Aranjuez, Date significantly affected dark respiration, with the highest monthly average found in April, (Fig. 7d).

Variation of the effects of climate change as a function of the time scale and water availability

The effects of our treatments also differed with the time scale considered (bimonthly or daily measurements), and with the characteristics of the preceding rainfall and NRWI events. For example, although warming was the most important factor determining responses in Sorbas at early morning hours during bimonthly measurements, rainfall exclusion was the main factor limiting net photosynthesis during the winter daily cycle at this site, as a significant Time × RE interaction was found (Table S3). Plots with rainfall exclusion had significantly lower net photosynthesis than plots without it from 10 A.M. to 2 P.M. (Fig. 8a). So natural precipitation maintained soil moisture at suitable levels allowing photosynthetic activity throughout the day, something that was not achieved when rainfall was experimentally reduced.
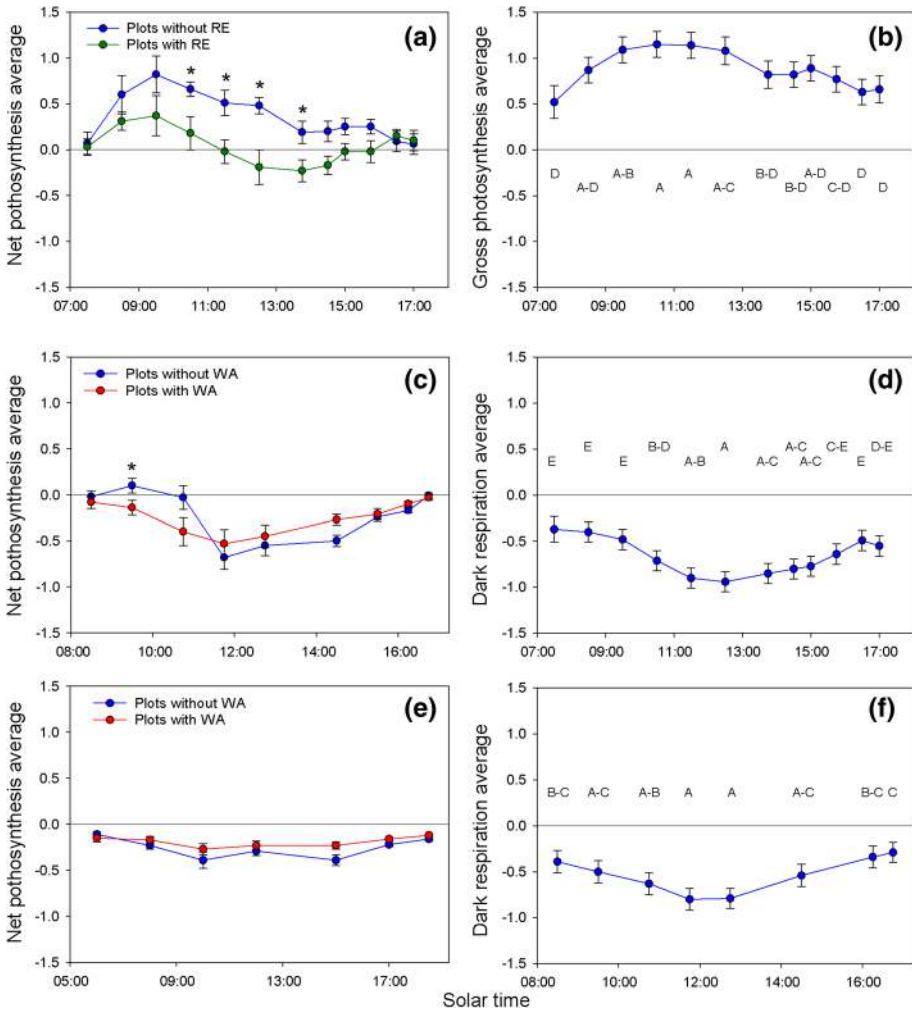
Fig. 8 Fisher's least significant difference (LSD) post hoc results from daily cycle surveys: net photosynthetic rate (**a**), gross photosynthetic rate (**d**) and dark respiration (**e**) in January at Sorbas; net photosynthetic rate (**b**) and dark respiration (**f**) in January at Aranjuez; and net photosynthetic rate (**c**) in May at Aranjuez. In panels (**a–c**), statistical differences between the two treatments within each time are denoted by asterisks. In panels (**d–f**), significant differences between surveys are shown by letter intervals (e.g., a label *A-C* means that a time contains the letters *A*, *B* and *C*). No *letters* in common denote different averages. All analyses were performed at $p < 0.05$. Data are mean ± SE ($n = 6$). *WA* warming, *RE* rainfall exclusion

In Aranjuez, where rainfalls preceding the winter daily cycle measurements were much lower than in Sorbas (Fig. 1), a significant time × WA interaction was found in both January and May (Tables S3 and S4). In January, net assimilation rate was higher and positive in plots without OTC, and negative in plots with OTC, but only from 9 A.M. to 10 A.M (Fig. 8b). In May, the post hoc test did not show significant differences between plots with and without OTC measured in the same hour (Fig. 8c).

Regarding the other gas exchange variables, significantly higher gross photosynthesis values were found in the morning than in the afternoon in Sorbas (Fig. 8d), while none of the factors evaluated affected gross photosynthesis in Aranjuez (Table S3). The dark respiration values found were similar in Aranjuez and Sorbas, and at both sites peaked at midday(Fig. 8e, f; Table S3).

Discussion

The importance of water availability on biocrust activity

In agreement with previous studies (Lange and Green 2003; Wilske et al. 2008), our results show that seasonal variations in the physiological status and the CO_2 exchange of biocrust-dominated microsites are strongly influenced by the hydration state of biocrust constituents. The maximum photochemical efficiency of PSII (F_v/F_m) reflected the typical physiological activity of biocrusts in the Mediterranean, characterized by a strong seasonal oscillation, with a peak of activity in winter, the rainy season of this climate, and a phase of dormancy in summer, the dry season (Wilske et al. 2008; Pintado et al. 2010). The drastic reduction of F_v/F_m observed during spring and summer (Fig. 6d) indicates a photoinhibition situation resulting from damage to PSII reaction centers, or a down-regulation of PSII (Calatayud et al. 1997). We favour the predominance of the second explanation, as when biocrusts returned to better moisture conditions they recovered the maximum F_v/F_m values, and had similar photosynthetic rates to those observed before the dry season. However, biocrust did not reach an optimal photochemical efficiency at our study sites until October, as was shown by Pintado et al. (2010), who monitored in situ chlorophyll fluorescence of biocrust-forming lichens during several years in a site near to Sorbas. This can be seen with the September 2011 measurements in Sorbas, which were conducted after a relevant rain, and with soil temperature values suitable for the activity of biocrusts. In spite of these conditions, respiration was greater than photosynthesis, generating the most negative C balance (C source) found at this site.

Hydration status also had an important role in the metabolic activity of biocrusts over the day. The differences observed in the January daily cycle between Aranjuez and Sorbas can be explained by the unequal rainfall conditions among them. The major water inputs, and consequently higher soil water content found in Sorbas during this month, allowed optimal conditions for C fixation along the day (Fig. 2a), whereas in Aranjuez the lower rainfalls only allowed positive C fixation at early and late hours (Fig. 2b). In May 2010, and while ten days prior to the measurements a rain event of ~ 10 mm took place in Aranjuez, the net photosynthesis was negative throughout the day (Fig. 2c), probably because an important part of the water supply had already evaporated, and also because at that time of the year the photosynthetic capacity of lichens is lower than in winter.

Water pulses and degree of biocrust development as modulators of its responses to climate change

The occurrence, magnitude and timing of the two NRWI sources considered (dew and fog) are key to interpret the results and the differences found between Sorbas and Aranjuez during the bimonthly surveys. The RE treatment reduced the amount of rainfall reaching the plots, but did not affect the water inputs coming from NRWI. Nocturnal and early morning moistening through dew and fog enables photosynthesis immediately after

sunrise, which ceases when biocrusts dry out (Kappen 1988), after ca. 2 h. However, high air temperature accelerates the process of thallus dehydratation, a major environmental stressor in lichens (Hájek et al. 2006). Given all this, the main effects of the warming treatment in our experiment were: (1) the reduction of the early morning wetting time on the thalli, by decreasing the formation of dew on the surface of the biocrusts and intercepting fog; and (2) the reduction of the soil water content because the warming increased evaporation. Therefore the negative effect of WA treatment on biocrust photosynthetic performance was due to its reduction of water availability, also in agreement with Maphangwa et al. (2012). Direct effects of warming on the photosynthetic efficiency of biocrusts can be discarded, as the early morning temperature ranges in plots with and without OTC (Fig. S2) were within the photosynthetic optimal of the dominant lichens from our study sites (Lange et al. 1997, 1998; Lange and Green 2004). Johnson et al. (2012) and Zelikova et al. (2012) also found very limited effects of a 2–3 °C warming alone on biocrust communities dominated by cyanobacteria, cyanolichens and mosses.

Warming had a greater effect on gas exchange variables in Sorbas than in Aranjuez in the bimonthly survey, and this was likely due to the differences in NRWI magnitude observed among the study sites. In Sorbas, dew is the most frequent water input. For example, in a study conducted near this site, dewfall condensation and rain/fog inputs were observed during 78 and 16 % of the nights, respectively (Uclés et al. 2013a). However, fog is the main NRWI source in Aranjuez, as it occurred during 27 % of the nights of this study period, while rainfalls only occurred during 8 % of the nights. In all measured winter months, there was dew formation at Sorbas, and fog events were encountered at Aranjuez (Fig. 1). Since dew is directly related to the temperature of the soil surface, warming reduced dew condensation. Our OTCs were also a barrier to the entry of the fog into the plots, but as they were open at the top and elevated from the soil, only reduced significantly the duration of the small fog events. This effect on small NRWI events probably is critical for early net C balance, since they may be at the limit of providing enough water to compensate and surpass respiration activity. So, as warming had a greater effect on small NRWI events, which were more frequent in Sorbas, this could be the main explanation of why the effects of WA factor were most significant in Sorbas than in Aranjuez when analyzing bimonthly data.

Contrary to what we expected, the rainfall exclusion did not have a detrimental effect at Sorbas in the bimonthly surveys, and even this treatment had higher net photosynthesis than in plots with WA and WA+RE treatments (Fig. 7a) at Aranjuez in December 2010. This fact may also be explained because of the importance of the antecedent NWRIs. During the nighttime previous to the measurements, there were 13 h of fog at Aranjuez, and the rainfall shelters did not reduce the amount of fog as the OTCs did (Fig. 1). Therefore, these results could indicate a more important modulation of the early photosynthesis by NRWI pulses than by rainfalls along an annual cycle. When preceding precipitation was abundant, rainfall exclusion had an effect on the evolution of gas exchange during the whole day, as in the case of Sorbas (Fig. 8a). However, when rainfalls were not large enough to maintain a positive C balance during the whole day, as occurred in the Aranjuez winter daily cycle, temperature became the main factor driving biocrust activity (Fig. 8b). The observed net photosynthesis in control plots during early morning at this site was probably activated by nocturnal fog events, and the WA treatment, that caused an increase of soil temperature of about 3–4 °C (Fig. 2b), increased the dehydration rate of the thalli, and impeded a positive C balance in this treatment when light conditions were more favorable.

Although the data acquisition of our work was not extensive enough to quantify the relative importance of rain and NRWI in the biocrusts gas exchange, their variability,

frequency and timing characteristics suggest that reducing NRWI pulses suitable for carbon fixation could have a greater impact on the biocrust carbon balance at annual scale. For example, other studies performed in the desert of Neveg consider that dew is a more important source of water for biological activity than rain because (1) its lower inter-annual variability, 12 %, compared to 53 % for rainfall (Zangvil 1996); (2) its more frequency, 200 days of dew versus 20 days of rain (Temina and Kidron 2011); (3) and its well distribution over the year, a condition necessary for the formation of biological crust, as this implies that some moisture must be available on a regular basis (Jacobs et al. 1999). The important role of NRWIs in these dryland organisms has also been supported by several studies (e.g. Lange et al. 1994; del Prado and Sancho 2007; Kidron and Temina 2013).

During late autumn and winter, the F_v/F_m values observed in low biocrust cover plots were similar to those observed in high cover plots (Fig. 6d), indicating that the "bare" soil without a well developed and visible biocrust community possessed an abundant colony of free-living cyanobacteria and algae. This was consistent with our gross photosynthetic data (Fig. 6b). Cyanobacteria and algae constitute the early-successional stage during the development of biocrust communities (Garcia-Pichel et al. 2001, Lázaro et al. 2008), and have been described in worldwide dryland regions (Garcia-Pichel et al. 2003; Maestre et al. 2011). The positive effect of warming on the gross photosynthesis of low biocrust cover plots at Sorbas could have been produced because, when hydrated enough, free and lichenized cyanobacteria have a much stronger photosynthesis increase response to temperature than lichen species with green algae as photobiont (Lange et al. 1998; Housman et al. 2006). Dark respiration in low biocrust cover plots at Sorbas was significantly higher with warming in June (Fig. 6c), while this treatment did not affect dark respiration at high cover plots on any season. The respiration response to WA in free cyanobacteria, and the absence of it in green-algal lichens may indicate that the respiration of the first also had a greater sensitivity to temperature increase, or that the latter exhibited higher acclimatization capacity, as their fungal component possesses this ability (Lange and Green 2005).

Cyanobacteria possess a more efficient CO_2 concentrating mechanism (CCM) than green algae (Green et al. 1993; Badger et al. 2006; Price et al. 2008), which counteracts the increase of Rubisco oxygenase activity with temperature, leading to a photorespiration rise (Palmqvist et al. 1994; Smith and Griffiths 1998). Therefore, the CCM mechanism may be more beneficial at high temperatures, where this energy cost is smaller than the energy associated with photorespiration. This difference may also explain why cyanobacterial crusts are often the only biocrust type in arid and hyper-arid ecosystems, and their gross photosynthesis has a resilience to change at temperatures between 20 and 35 °C (Grote et al. 2010). It is also possible that under conditions of less NRWI formation, cyanobacteria have a competitive advantage to avoid desiccation over green algae lichens in terms of water-holding capacity (Lange et al. 1998), production of a protective layer of exopolysaccharides (De Philippis and Vincenzini 1998; Potts 2001), or even migration abilities through soil profile (Garcia-Pichel and Pringault 2001). These characteristics of cyanobacteria could explain why the drying effect of WA did not cause a negative response on the net photosynthesis of low biocrust cover plots (Fig. 6a).

Concluding remarks

Our results illustrate how the timing and magnitude of water pulses drive key ecological processes in dryland ecosystems, in this case, the carbon cycle linked to the metabolic activity of biocrusts. The shifts in these pulses caused by climate change will determine the magnitude of the effects on this biological activity, which will determine responses to

warming of the whole C cycle (Maestre et al. 2013). Our findings also emphasize the importance of NRWIs when understanding biocrust responses to climate change. They indicate that changes in NRWI regimes as consequence of warming could have a greater impact on the C balance of biocrusts than changes in rainfall amounts. Another contribution of this study is the differential response of the biocrusts to the climate change treatments as a function of their development stage. The results suggest that early-successional cyanobacterial biocrust could displace more developed lichen-dominated biocrusts in Mediterranean drylands, as indeed is happening in Aranjuez, the experimental site with more years of climate manipulation (Escolar et al. 2012). These changes induced by climate change have implications for the C cycle in the studied ecosystems, as early-successional biocrust areas have less C fix capacity. Consequently, the importance of dryland ecosystems as a C sink will be reduced if these shifts in the biocrust community take place.

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