

Published in final edited form as:

Soil Biol Biochem. 2015 January 1; 80: 9–17. doi:10.1016/j.soilbio.2014.09.019.

Biocrusts modulate warming and rainfall exclusion effects on soil respiration in a semi-arid grassland

Cristina Escolar¹, Fernando T. Maestre^{1,*}, and Ana Rey²

¹Área de Biodiversidad y Conservación, Departamento de Biología y Geología, Física y Química Inorgánica, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, E-28933 Móstoles, Spain

²Department of Biogeography and Global Change, Museo de Ciencias Naturales, C.S.I.C., Serrano 115, 28006 Madrid, Spain

Abstract

Soil surface communities composed of cyanobacteria, algae, mosses, liverworts, fungi, bacteria and lichens (biocrusts) largely affect soil respiration in dryland ecosystems. Climate change is expected to have large effects on biocrusts and associated ecosystem processes. However, few studies so far have experimentally assessed how expected changes in temperature and rainfall will affect soil respiration in biocrust-dominated ecosystems. We evaluated the impacts of biocrust development, increased air temperature and decreased precipitation on soil respiration dynamics during dry (2009) and wet (2010) years, and investigated the relative importance of soil temperature and moisture as environmental drivers of soil respiration, in a semiarid grassland from central Spain. Soil respiration rates were significantly lower in the dry than during the wet year, regardless of biocrust cover. Warming increased soil respiration rates, but this response was only significant in biocrust-dominated areas (> 50% biocrust cover). Warming also increased the temperature sensitivity (Q_{10} values) of soil respiration in biocrust-dominated areas, particularly during the wet year. The combination of warming and rainfall exclusion had similar effects in low biocrust cover areas. Our results highlight the importance of biocrusts as a modulator of soil respiration responses to both warming and rainfall exclusion, and indicate that they must be explicitly considered when evaluating soil respiration responses to climate change in drylands.

Keywords

biological soil crusts; lichen; soil respiration; climate change; drylands; Q_{10}

INTRODUCTION

Arid, semi-arid and dry-subhumid ecosystems (drylands hereafter) constitute the largest terrestrial biome on Earth, covering ~41% of the total land surface (Safriel and Adeel, 2005). Drylands are of paramount importance for the Earth's carbon (C) cycle, as their soils store more than 25% of the belowground global C pool (Safriel and Adeel, 2005), and are a

*Corresponding author: Phone: +34914888511; Fax: +34916647490; fernando.maestre@urjc.es.

potential sink for the stabilization of the atmospheric CO₂ concentration (Lal, 2004). Their importance will increase in the future, as recent studies indicate that the extension of global drylands will increase by 10% at the end of this century as a consequence of ongoing climate change (Feng and Fu, 2013). Despite the extent and importance of drylands, and the fact that soil respiration is a major process of soil C loss in these areas (Conant et al., 2000; Castillo-Monroy et al., 2011a; Thomas, 2012), soil respiration has been less studied there than in other ecosystems (Bond-Lamberty and Thomson, 2010).

Soil respiration is known to vary significantly among major vegetation types (Raich and Tufekcioglu, 2000). Plants, however, are not the only organisms modulating soil C cycling in drylands. Biological soil crusts (biocrusts), communities composed of cyanobacteria, algae, mosses, liverworts, fungi, bacteria and lichens living in the uppermost millimeters of the soil surface in drylands worldwide (Belnap and Lange, 2003), play a major role in C cycling in these environments. They fix atmospheric CO₂ (over 2.6 Pg of C per year globally; Elbert et al., 2012), regulate the temporal dynamics of net CO₂ uptake (Wilske et al., 2008, 2009), and influence the abundance and activity of soil enzymes such as β -glucosidase (Bowker et al., 2011; Miralles et al., 2013). Biological soil crusts are also important when assessing soil respiration in drylands. Castillo-Monroy et al. (2011a) found that biocrust communities dominated by lichens were responsible for more than 40% of the total C released annually via soil respiration in a semi-arid grassland from Central Spain. These authors also found that soil respiration was more sensitive to increased soil temperature when biocrusts were present. Feng et al. (2013) noted how the disturbance of biocrusts dominated by algae, mosses and lichens increased soil respiration fluxes in the Mu Us desert (northwest China). Other authors have found that biocrusts contribute considerably to soil respiration patterns in the Kalahari Sands, which are strongly linked to the activity of cyanobacteria (Thomas et al., 2008; Thomas and Hoon, 2010; Thomas, 2012). These results highlight the need to consider biocrusts explicitly when studying soil respiration in drylands.

Given the sensitivity of soil respiration in drylands to changes in both soil temperature and moisture (e.g., Almagro et al., 2009; Conant et al., 2000; Thomas and Hoon, 2010; Castillo-Monroy et al., 2011a; Rey et al., 2011; Lane et al., 2013), it is imperative to improve our understanding on how soil respiration will be affected by climate change in these areas. Climate change is expected to have large effects on the composition of biocrust communities (Escolar et al., 2012; Zelikova et al., 2012; Yeager et al., 2012), and on associated C and nitrogen cycling (Reed et al., 2012; Maestre et al., 2013). However, few studies so far have experimentally assessed in the field how expected changes in temperature and rainfall with climate change will affect soil respiration dynamics in biocrust-dominated ecosystems (Maestre et al., 2010, 2013). These studies would be highly valuable for improving our ability to predict future C losses via soil respiration, and to improve our understanding about the C cycle in drylands under different climate change scenarios.

In July 2008, we set up a manipulative experiment in a typical semiarid grassland dominated by biocrusts in central Spain to evaluate the impacts of increased air temperature ($\sim 2.7^\circ\text{C}$ of average increase) and decreased precipitation ($\sim 37\%$ reduction) on biocrust communities and associated ecosystem processes (Maestre et al., 2010, 2013; Escolar et al., 2012; Ladrón

de Guevara et al., 2014). In this study, we investigate the impact of these climate manipulations and the degree of biocrust development on soil respiration in two years with distinct precipitation inputs and patterns. Our objectives were to: i) investigate the relative importance of soil temperature and soil moisture as environmental drivers of soil respiration, and ii) evaluate how biocrusts affect the sensitivity of soil respiration to warming and rainfall reduction under different climate change scenarios.

MATERIALS AND METHODS

Study area

This research was conducted in the Aranjuez Experimental Station, in the center of the Iberian Peninsula (40°02' N–3°32' W; 590 m a.s.l.). The climate is Mediterranean semi-arid, with average annual temperature and rainfall of 15°C and 349 mm, respectively. The soil is derived from gypsum, has pH values ~7, and is classified as Gypsic Leptosol (IUSS Working Group WRB, 2006). Perennial vegetation is patchily distributed and dominated by the tussock grass *Stipa tenacissima* and the N-fixing shrub *Retama sphaerocarpa*. The open areas between perennial plant patches contain a well-developed biocrust community dominated by lichens such as *Diploschistes diacapsis*, *Squamaria lentigera*, *Fulgensia subbracteata*, *Toninia sedifolia*, and *Psora decipiens* (see Maestre et al., 2013 for a species checklist).

Experimental design

We established a factorial experimental design with three factors, each with two levels (see Escolar et al., 2012 for details): biocrust cover (poorly developed biocrust communities with cover < 25% vs. well-developed communities with cover > 75%), warming (control vs. a temperature increase) and rainfall exclusion (control vs. rainfall reduction). We established ten replicated plots (1.25 × 1.25 m) per combination of treatments, resulting in a total of 80 experimental plots. To minimize the risk of sampling non-independent areas all the plots were separated at least by 1 m.

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 Spain (de Castro et al., 2005). These models predict an increment of annual temperature ranging from 2.6°C (B2 IPCC scenario) to 2.8°C (A2 IPCC scenario). To achieve a temperature increase within this range, we used open top chambers (OTCs) of hexagonal design with sloping sides of 40 cm × 50 cm × 32 cm (Appendix A). Forecasted changes in rainfall for our study area are subject to a high degree of uncertainty, but all models predict a significant reduction of the days with significant (> 1 mm) rainfall during spring and fall (between 10 and 50%; de Castro et al., 2005). To achieve a rainfall reduction in the range of that forecasted, we used passive rainfall shelters (RS) of 1.44 m² composed by three gutters of methacrylate covering ~37% of this surface (Appendix A), based upon the design of Yahdjian and Sala (2002). Open top chambers and rainfall shelters were set up in July and November 2008, respectively. We continuously monitored the effects of treatments on soil temperature (0–2 cm depth) and soil moisture (0–5 cm depth) using automated sensors (HOBO Pro v2 Temp/RH and H8 Data Loggers, Onset Corporation,

Bourne, USA and ECH2O humidity sensors, Decagon Devices Inc., Pullman, USA). See Escolar et al. (2012) and Maestre et al. (2013) for additional details on the experimental design and the microclimatic effects of both OTCs and RS.

Soil respiration measurements

Within each plot, we inserted a PVC collar (20 cm diameter, 8 cm height) 5 cm into the soil for measuring soil respiration. These measurements were made *in situ* with a portable LI-8100 Automated Soil CO₂ Flux System (LICOR, Lincoln, Nebraska, USA) between November 2008 and January 2011 at intervals ranging from one to four months. We measured soil respiration between 10.00 and 14.00 h (local time, GTM+1), a period typically used in previous studies conducted in similar semi-arid ecosystems (Maestre and Cortina, 2003; Jia et al., 2006; Castillo-Monroy et al., 2011a; Rey et al., 2011). During each of the 21 surveys conducted (Fig. 1b, 1c), half of the plots were randomly measured in a day and the other half in the next day. Regularly we removed small plants, litter and grasses inside the PVC collars. At the time of soil respiration measurements, we monitored soil temperature at 0-2 cm depth with protected diodes, and volumetric soil moisture at 0-5 cm depth by time domain reflectometry (TDR; Topp and Davis, 1984).

Environmental controls on soil respiration

We modelled the dependency of soil respiration on temperature (T) and moisture (SWC) according to the following relationships:

$$R_s = f(T) * f(SWC) \quad (1)$$

and

$$f(T) = R_{\text{basal}} e^{\beta T} \quad (2)$$

where R_s is the measured soil respiration rate ($\mu\text{mol m}^{-2}\text{s}^{-1}$), R_{basal} is the basal soil respiration rate ($\mu\text{mol m}^{-2}\text{s}^{-1}$), and T is the soil temperature (in °C) measured at 0-2 cm, SWC is the volumetric soil water content measured at 0-5 cm (in %), R_{basal} and β are estimated parameters. This relationship was fitted separately to all treatments. The Q_{10} , defined as the increment in soil respiration when T increases by 10°C, was calculated as (Luo and Zhou, 2006):

$$Q_{10} = e^{10\beta} \quad (3)$$

The relationship between R_s and SWC was determined by fitting a linear relationship:

$$f(SWC) = Y_o + a\text{SWC} \quad (4)$$

where Y_o and a are fitted parameters.

Between November 2008 and November 2009 only 214 mm of rainfall were registered (Figure 1d), so we consider this period as a “dry” year. In contrast, the period between January 2010 and January 2011 received 553 mm of rainfall (Figure 1d), so we consider this

period as a “wet” year. The equations described above were applied to these years separately.

To reduce the noise in the soil respiration data set, we first sorted all the data according to soil temperature and then were rounded off to the nearest degree. Then we determined the thresholds on which soil respiration was controlled by soil temperature and moisture. When soil moisture was on average above 11% in the different treatments and years, soil respiration rate was controlled only by soil temperature (Appendix B). Below this threshold (mostly in the summer), soil respiration was primarily controlled by soil moisture.

Statistical analyses

Preliminary analyses of soil respiration measurements showed that significant biocrust \times rainfall reduction and biocrust \times warming interactions were found. Thus, we conducted separate analyses of for low and high biocrust cover plots. Differences in soil respiration rates between treatments were tested with a three-way (warming, rainfall exclusion and time) ANOVA, with repeated measures of one of the factors (time). Prior to these analyses, data were tested for ANOVA assumptions and were log-transformed when necessary. Regression analyses were used to evaluate the relationships between soil respiration and both soil temperature and soil moisture. To compare the Q_{10} values between the different treatments in the two years considered, we determined the standard error of the β parameter and its confidence interval (provided by the regression analyses). We assumed that differences between Q_{10} values were significant when 95% confidence intervals did not overlap (Zar, 1999). The same procedure was followed for comparing the slope values of the relationship between soil moisture and respiration in the two years considered. All the statistical analyses were conducted using SPSS 15.0 statistical software (SPSS Inc., Chicago, Illinois, USA).

RESULTS

Treatment effects on environmental variables

Soil temperature and moisture showed marked seasonal variation. Soil temperature increased steadily until mid-summer (August), reaching maximum values of 38°C in June 2009 and 36°C in June 2010 in the control plots (Appendix C). Throughout the experimental period, air and soil temperatures were on average 2.7 °C and 2.4 °C higher in the warming treatment than in the control treatment (Figure 1a, Appendix C), respectively. Soil volumetric water content was higher in the wet than in the dry year (Figs. 1e, f). Maximum and minimum values of this variable were registered during spring/winter (30% for March 2009 and 32 % for January 2010) and summer (2 % for September 2009 and 1% for August 2010), respectively. Rainfall shelters did not substantially modify air and soil temperatures, as differences between RE and control plots were, on average, below 0.4 °C (Figure 1a, Appendix C). These shelters excluded on average 33% of incoming precipitation and reduced volumetric water content by 3% on average, albeit they promoted important reductions in this variable after main rainfall events (Figure 1e, f).

Treatment effects on soil respiration

Soil respiration rates showed marked seasonal variation, following changes in soil temperature during winter and spring, and in soil moisture the rest of the year (Figs. 1b, c). The temporal trend was similar in both years regardless of the initial biocrust cover, with maximum and minimum soil respiration rates measured in spring and summer, respectively (Figure 1). In both cases, higher soil respiration rates were measured in the wet than in the dry year. Soil respiration rates were significantly higher in the high than in the low biocrust cover plots (Figure 1). In the dry year, a significant warming (WA) \times rainfall exclusion (RE) interaction was observed when analyzing this variable in the high biocrust cover areas (Between-subjects tests: $F_{1,36} = 5.75$, $P = 0.022$). In these plots, WA significantly increased soil respiration over the whole year (Between-subjects tests: $F_{1,18} = 13.24$, $P = 0.002$), an effect that was not evident when both WA and RE were considered (Between-subjects tests: $F_{1,18} = 0.14$, $P = 0.715$). No significant main effects or interactions were found in the low biocrust cover areas (Between-subjects tests: $F_{1,36} < 0.14$, $P > 0.70$ in all cases). In the wet year, WA significantly increased soil respiration in biocrust-dominated areas (Between-subjects tests: $F_{1,36} = 3.89$, $P = 0.056$), but not in low biocrust cover areas (Between-subjects tests: $F_{1,36} = 1.78$, $P = 0.190$). During this year, no significant WA \times RE interaction was observed, regardless of biocrust cover (Between-subjects tests: $F_{1,36} = 2.47$, $P = 0.125$ and $F_{1,36} < 0.01$, $P = 0.947$ for the high and low biocrust cover areas, respectively). The effect of RE was not significant either, regardless of biocrust cover (Between-subjects tests: $F_{1,36} = 1.21$, $P = 0.278$ and $F_{1,36} = 0.03$, $P = 0.875$ for the high and low biocrust cover areas, respectively).

Environmental controls on soil respiration

Soil temperature accounted for a substantial part of the seasonal variation in soil respiration (more than 50% and 60% in low and high biocrust cover plots, respectively, during both years, Appendix D). In the dry year, and in the low biocrust cover plots, soil respiration was exponentially related to soil temperature when soil moisture was above 15%, 10% and 7% in the RE, WA and RE + WA treatments, respectively (Appendix B). In the high biocrust cover plots, these thresholds were 7%, 16% and 10% for the RE, WA and RE + WA treatments, respectively. In the wet year, and in the low biocrust cover plots, soil respiration was exponentially related to soil temperature when soil moisture was above 13%, 7% and 8% in the RE, WA and RE + WA treatments, respectively. In the high biocrust cover plots, these thresholds were 7%, 14% and 14% for the RE, WA and RE + WA treatments, respectively. These soil moisture values occurred between December and June of the wet year and until May of the dry year, and occasionally after rainfall events. Below these soil moisture values, soil respiration was driven by variations in soil moisture alone according to a linear relationship (Appendices B and D). Overall, empirical models combining both soil temperature and moisture used successfully predicted soil respiration rates in both years in all the treatments (Figures 2 and 3). They explained up to 92% of the observed temporal variation in soil respiration, with the exception of the control plots in the wet year, when the fitted model explained only 43% of this variation.

Estimated Q_{10} values across all treatments ranged from 1.5 to 2.2 in the dry year, and from 1.6 to 3.3 in the wet year (Figure 4a). There were no significant differences between

treatments in the Q_{10} values in the dry year, regardless of biocrust cover. In the wet year, the Q_{10} values were significantly higher in the WA and WA + RE treatments than in the other treatments in the low and high biocrust cover plots, respectively. The slope values of the linear regression between volumetric soil water content and soil respiration ranged from 0.03 to 0.17 in the dry year, and from 0.08 to 0.25 in the wet year (Figure 4b). In the dry year, slope values were significantly higher in the WA than in the control treatment regardless of initial biocrust cover. In the high biocrust cover plots, the highest slope was found in the RE + WA treatment. In the wet year, the slope of the linear relationship with soil moisture was only significantly higher in the RE + WA treatment than in the control treatment in high biocrust cover plots (Figure 4b). No significant differences among the treatments evaluated were found in the low biocrust cover plots.

DISCUSSION

Biocrust and climate manipulation effects on soil respiration

Observed soil respiration rates were comparable to those reported in other arid and semiarid ecosystems (Maestre and Cortina, 2003; Rey et al., 2011; Thomas et al., 2011; Wang et al., 2014), and followed similar temporal patterns. As we did not measure soil respiration under the plant canopies, and the dominant plant species (*S. tenacissima*) does not extend its roots beyond its canopy (Puigdefábregas et al., 1999), we expect root respiration not to be a substantial contributor to the measured respiration rates. Although the temporal trends were similar in low and high biocrust cover plots, soil respiration rates were almost doubled in the later, indicating that visible components of biocrust communities (mosses and lichens) contributed considerably to soil respiration. While our experimental design and measurements do not allow us to separate the contributions of visible (mosses and lichens) vs. non-visible (e.g. bacteria and fungi) biocrust components, we can assume that differences in soil respiration between low (where they are mainly the outcome of microbial respiration) vs. high biocrust cover areas are mainly due to the biological activity of the mosses and lichens themselves (either directly or indirectly via their effects on soil microbial communities and fertility; Castillo-Monroy et al., 2011b; Steven et al., 2014; Maier et al., 2014). There is evidence for this from previous research evaluating the effects of visible biocrust components on soil respiration, both at our study area (e.g. Castillo-Monroy et al. 2011a) and elsewhere (e.g., Maestre and Cortina, 2003; Castillo-Monroy et al., 2011a; Thomas et al., 2008; Rey et al., 2011; Feng et al., 2013). In all these studies, soil respiration rates are typically higher in areas with well-developed and visible biocrusts than in those without them. Similarly, Feng et al. (2014) also found that soil respiration increased in a gradient going from algae- to moss- to lichen-dominated biocrusts in a desert ecosystem from northwest China.

Soil respiration rates were substantially lower in the dry than the wet year, regardless of biocrust cover. This result suggests that soil moisture limitation reduced the activity of both soil microorganisms and biocrust-forming lichens in the dry year (Luo et al., 2008; Shen et al., 2009; Rey et al., 2011; Peng et al., 2013; Wang et al., 2014). Apart from differences in rainfall inputs during both years, the duration of suitable conditions for the formation of dew in our study area (i.e., periods where air relative humidity is 100%) was reduced by 5% in

the dry compared to the wet year (Appendices E and F). The photosynthetic activity of biocrust-forming lichens, and thus their C inputs to the soil, in our study area is highly dependent on nocturnal moistening provided by dew inputs (Ladrón de Guevara et al., 2014), a response observed in drylands elsewhere (e.g. Lange et al., 1994; Veste et al., 2001; del Prado and Sancho, 2007). Rey et al. (2011) suggested that microbes located on or just beneath the soil surface are hydrated not only by rainfall events, but also by dew generated in the early morning, which may likely exert enough control to stimulate microbial activity and soil respiration in semi-arid environments. A laboratory study using biocrusts from our study area found that dew-like water inputs stimulated both the respiration of their constituent lichens and the activity of soil microbes associated to them (Delgado-Baquerizo et al., 2013). Thus, additional inputs of water for microbial and biocrust activity coming from dew may explain why soil moisture was not a major driver of soil respiration even when it was below 10%. Differences with other studies showing that soil respiration was more dependent on soil moisture (e.g. Rey et al., 2011) may be explained because root respiration, which strongly depends on soil moisture, was not likely a major contributor to soil respiration in our study whereas biocrusts, which can respond to air humidity and thus are less dependent on soil water inputs, were an important component of the total soil respiration rates measured. This fact may also help to explain why our rainfall exclusion treatment did not have strong effects on soil respiration, as a 33% reduction in precipitation only reduced soil moisture by 3% on average. We must note that rainfall exclusion did not decrease the duration of periods when air relative humidity is 100% (Appendices E and F), and hence dew could be formed equally well in this treatment.

Soil respiration significantly increased with warming, particularly in high biocrust cover plots during the wet year. Our results agree with those reported for warming experiments, where significant increases in soil respiration with warming have been reported during the first years after the experimental set up (e.g. Rustad et al., 2001; Luo et al., 2001; Niinistö et al., 2004; but see Lellei-Kovács et al., 2008; de Dato et al., 2010). The increase in the magnitude of soil respiration with warming was modulated by biocrusts, as it was only significant in the high biocrust cover areas. Differences in the magnitude of warming effects with biocrust development can be driven by several mechanisms. These include the respiration of the lichens and mosses themselves, which accounts for a substantial amount of total soil respiration occurring after small rainfall events (Cable and Huxman, 2003), and can be triggered by dew events in the study area (Delgado-Baquerizo et al., 2013; Ladrón de Guevara et al., 2014). In this direction, research conducted in the Kalahari Sands (Botswana) has shown how rainfall events as small as 1.6 mm can hydrate the biocrust layer and promote peaks in soil respiration (Thomas and Hoon, 2010). Differences in soil fertility between low and high biocrust cover areas can also contribute to this effect, as soil respiration is also controlled by the amount of available soil organic C (Sponseller, 2007; Moyano et al., 2012). Similarly to what it has been found in other biocrust-dominated areas (Thomas, 2012; Feng et al., 2013), surface soil organic C contents (0-1 cm depth) are a 77% higher in high than in low biocrust cover areas in our study site (Maestre et al., 2013). The effects of warming on soil respiration in high biocrust cover areas could be further reinforced by the changes in the cover and performance of the biocrust community promoted by this treatment. Indeed, we have previously reported how warming caused a reduction in

biocrust cover and net CO₂ uptake of high biocrust cover areas in our experiment (Maestre et al., 2013). How the reduced C inputs to the soil created by the reduced cover and activity of biocrusts affect the long-term dynamics of soil respiration with warming is a topic that must be elucidated by future studies.

Soil respiration responses to the combined effects of warming and rainfall exclusion differed both between years and with the degree of biocrust development. The lack of significant warming effects in biocrust-dominated areas when rainfall was also excluded in the dry year may have been caused by the overall reduction in soil moisture promoted by this treatment (Fig. 1e), which likely limited microbial activity and soil respiration (Castillo-Monroy et al., 2011a).

Effects of climate change treatments on Q_{10} and modeled soil respiration rates

In our study area, temperature was the best predictor of soil respiration only when soil moisture was not a limiting factor (mainly during winter and parts of spring and autumn). In contrast, soil respiration is controlled by soil moisture during the warmest periods of the year (mainly during the summer). According to this, exponential relationships between soil temperature and soil respiration were used during the winter, spring and autumn and linear relationships between soil moisture and respiration during summer. Using these relationships, we explained up to 92% of the temporal variation observed in soil respiration. Similar relationships have been successfully used by previous studies (Castillo-Monroy et al., 2011a; Rey et al., 2011; Thomas, 2012; Wang et al., 2014; Feng et al., 2014), highlighting the importance of jointly considering both soil temperature and soil moisture when modeling soil respiration in drylands.

The temperature sensitivity of soil respiration observed in our study (Q_{10}) is within the range reported for other dryland ecosystems (Rey et al., 2011; Nie et al., 2012; Wang et al., 2014). Many previous studies have reported how Q_{10} changes depend on both soil moisture and temperature (e.g., Reichstein et al., 2003; Nie et al., 2012; Jia et al., 2013; Zhou et al., 2014). Significant increments in the average Q_{10} values in the warming and warming + rainfall exclusion treatments compared to values in the control treatment were observed in the wet year in the high and low biocrust cover areas, respectively. These results indicate that, under dry conditions, temperature is not the main environmental factor controlling soil respiration. As described by Zhou et al. (2009), soil water content influences temperature sensitivity because at low water content diffusivity of oxygen is low, and soil microbial respiration is limited. Whereas other studies investigating soil respiration in other semiarid soils have found a negative relationship between incubation temperature and Q_{10} response (Conant et al., 2004), warming increased Q_{10} in our experiment. Other studies conducted in drylands reported higher values of Q_{10} in high biocrust cover than in low biocrust cover areas (Castillo-Monroy et al., 2011a; Feng et al., 2013), a response that we did not observe. In general, the increment in Q_{10} observed in the warming and warming + rainfall exclusion treatments during the wet year in high and low biocrust cover areas suggests that expected climatic changes will increase the temperature sensitivity of soil respiration in semiarid ecosystems. This increment may result in a further increase in soil respiration, which would

increment soil C losses (Fig. 3), and reduce the ability of biocrusts to act as a sink of atmospheric CO₂ (Maestre et al., 2013; Ladrón de Guevara et al., 2014).

The control of soil moisture over soil respiration was particularly important when soil water content was limiting (dry year) and in biocrust-dominated areas. Soil moisture may limit soil respiration in two ways, either by limiting soil aeration under high moisture conditions or by stressing microorganisms when it is limiting (Rey et al., 2002). The relationship between soil moisture and respiration at our study site is linear, with the maximum respiration rates occurring in the wettest year, which were higher under well-developed biocrust communities. The significant effect of the warming + rainfall exclusion treatment in relation to the control plots on the slope of the moisture-respiration relationship indicates that the soil water content achieved under these conditions may promote the O₂ diffusion into the soil, thereby increasing the soil respiration rate (Chen et al., 2011).

Concluding remarks

We found that a 2–3°C warming increased soil respiration rate and Q₁₀ values in biocrust-dominated areas, particularly during the wet year. The combination of warming and rainfall exclusion had similar effects in low biocrust cover areas. These climate change effects will reduce the ability of biocrusts to act as CO₂ sink, reducing soil fertility in the long term. They can also have negative and cascading effects on both the soil biota and soil processes that depend on biocrust cover and activity (Castillo-Monroy et al., 2011b; Elbert et al., 2012; Maestre et al., 2011). Overall, our data highlight the importance of biocrusts as a modulator of soil respiration responses to both warming and rainfall exclusion in a Mediterranean semiarid grassland, and indicate that these organisms must be explicitly considered when evaluating soil respiration responses to climate change in drylands.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

ACKNOWLEDGEMENTS

We thank P. Alonso, A. P. Castillo-Monroy, S. Soliveres, P. Garcia-Palacios, M. Bowker, R. Mou, V. Ochoa and B. Gozalo for their help with the field measurements. We would also like to thank an anonymous reviewer and David Elliot for useful comments on the manuscript. C. E. was supported by a graduate fellowship from the British Ecological Society (Studentship 231/1975). This research was funded by the European Research Council under the European Community's Seventh Framework Programme (FP7/2007-2013)/ERC Grant agreement 242658 (BIOCOM). We would like to thank IMIDRA and Comunidad de Madrid for granting us access to the Aranjuez Experimental Station.

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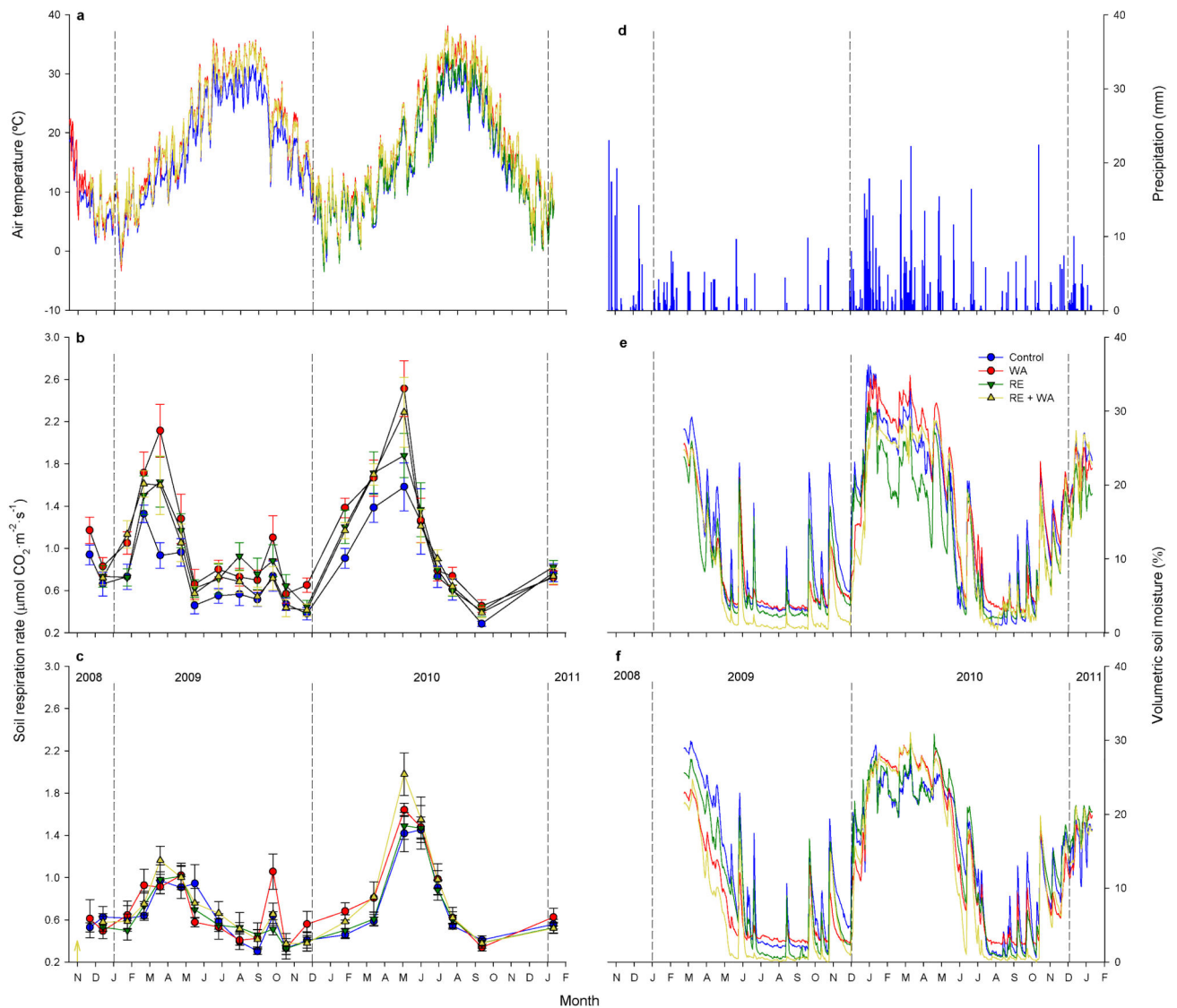


Figure 1.

Temporal variation in measured values of air temperature (a), soil respiration (b, c) precipitation (d), and of soil moisture (e, f) at the study site between November 2008 and January 2011 in high (b, e) and low (c, f) biocrust cover plots. Temperature and moisture data represent daily means; the standard errors of air temperature and soil moisture data are omitted for clarity. $n = 5, 10$ and 3 for air temperature, soil respiration and soil moisture, respectively. WA = warming, RE = rainfall exclusion.

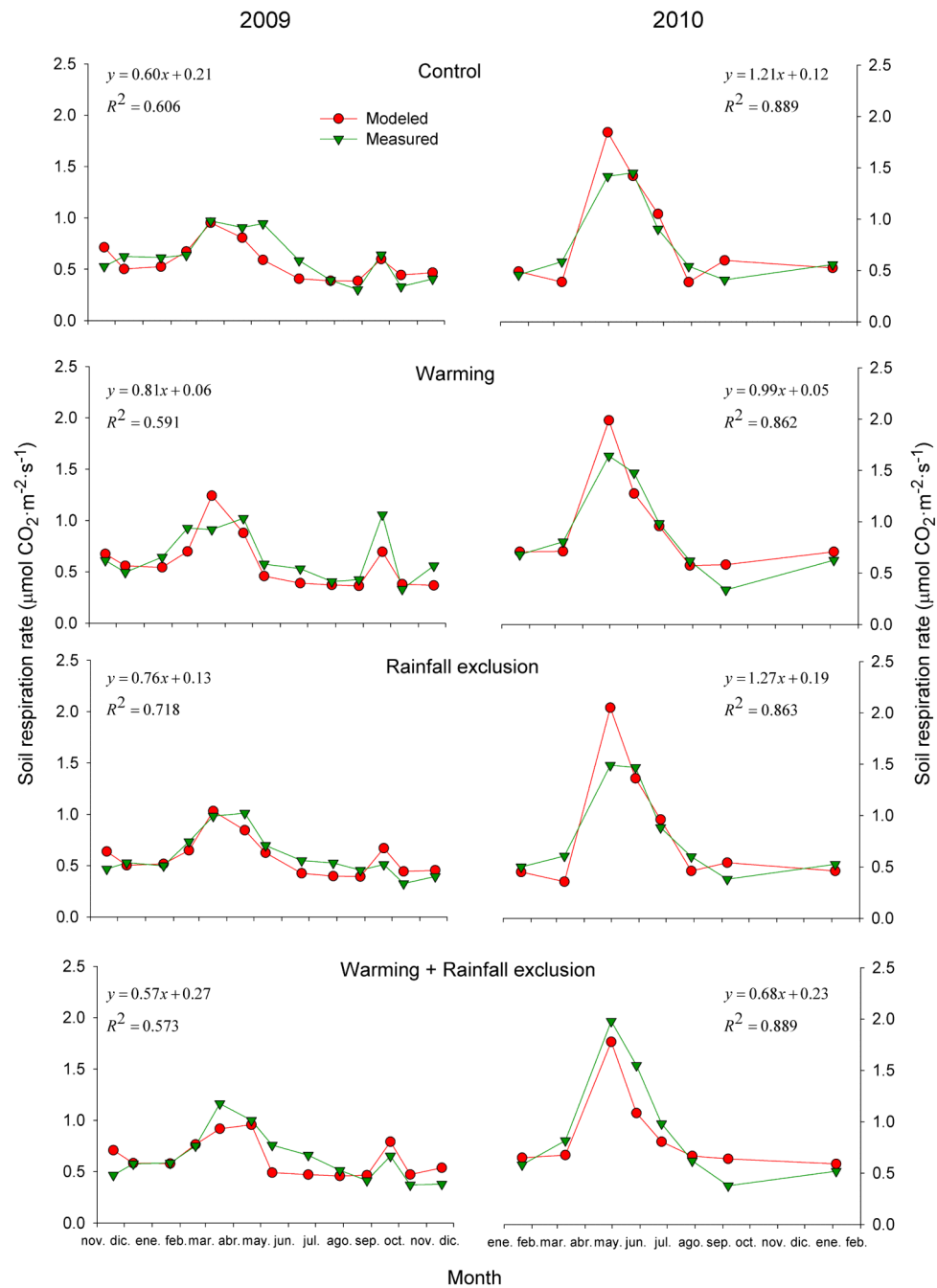


Figure 2. Measured and modeled soil respiration between November 2008 and January 2011 in the low biocrust cover plots. Results of the regression fitted to the data are shown in each panel.

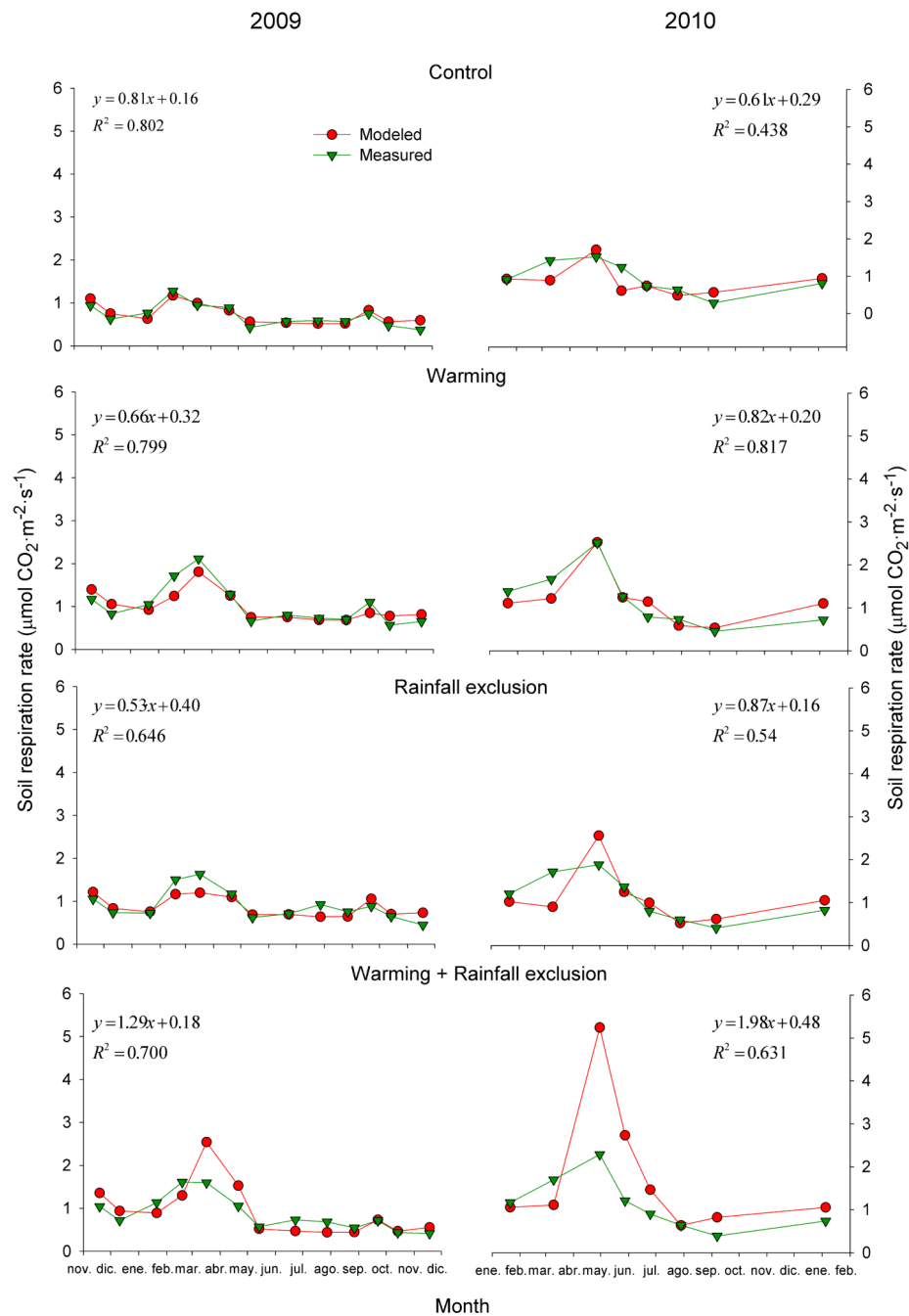


Figure 3. Measured and modeled soil respiration between November 2008 and January 2011 in the high biocrust cover plots. Results of the regression fitted to the data are shown in each panel.

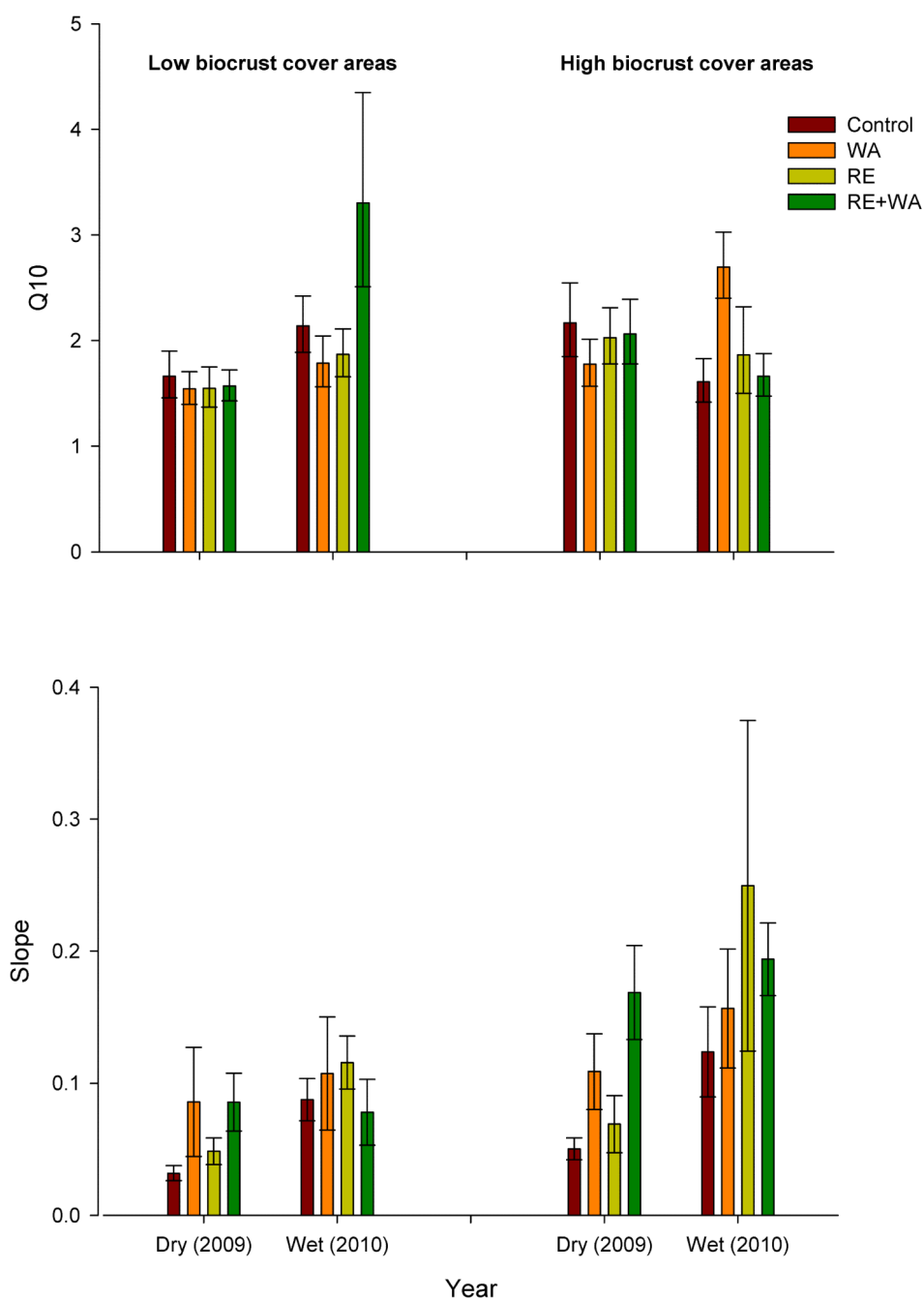


Figure 4.

Q_{10} values estimated for the different treatments in the dry and wet years. Error bars denote 95% confidence intervals. WA = warming, and RE = rainfall exclusion.