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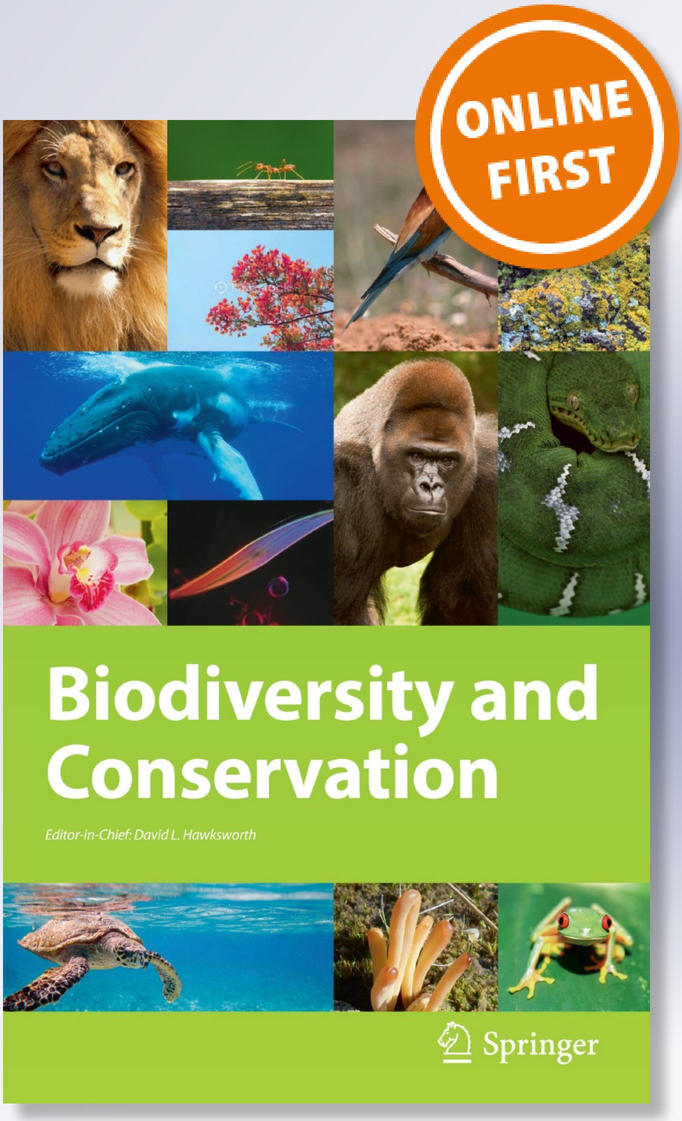

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ORIGINAL PAPER

Continuous chlorophyll fluorescence, gas exchange and microclimate monitoring in a natural soil crust habitat in Tabernas badlands, Almería, Spain: progressing towards a model to understand productivity

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Abstract The Soil Crust International project aims to better understand the functioning of biological soil crust environments (BSC) in Europe in order to understand the importance of these ecosystems. The final objective of this project is to inform and strengthen protection strategies for these types of habitats in the frame of the European Union. To achieve this, four different soil crust regions have been chosen in Europe following latitudinal and altitudinal gradients. The work presented here is based on the simultaneous monitoring of gas exchange, chlorophyll fluorescence and microclimate of the most abundant BSC in one of these four locations, the Tabernas badlands, Almeria, SE Spain, one of the driest regions in Europe. The five BSC types monitored are dominated by the lichen species *Squamarina cartilaginea*, *Diploschistes diacapsis*, *Toninia albilabra* and *Psora decipiens* and by the moss *Didymodon rigidulus*. We aim to understand the conditions in which the BSC are metabolically active in order to get a better knowledge about

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the contribution of the BSC to the carbon budget of the ecosystem. Our first results after nearly 1 year of chlorophyll fluorescence and microclimatic monitoring linked to gas exchange data during typical activity days obtained in the field suggest similar physiological performance between the different BSC types studied. BSC were active under suboptimal conditions, and activity duration was not different whether measured by chlorophyll *a* fluorescence or CO_2 gas exchange, a relationship that will be the basis of a productivity model.

Keywords BSC · Chlorophyll *a* fluorescence · CO_2 gas exchange · Productivity · Arid/semiarid environments · Microclimate

Introduction

Biological soil crusts (BSC) result from an intimate association between soil particles and cyanobacteria, algae, microfungi, lichens and/or bryophytes, which live within, or immediately on top of, the uppermost millimetres of soil (Belnap et al. 2003). They inhabit mainly soil surfaces, are present in regions all over the world and are specially important in arid, semiarid and cold environments (Büdel et al. 2009), where the climatic conditions inhibits the productivity and development of vascular plants. This means that the BSC dominated ecosystems are prevalent in some regions of the world, and that their composition and functioning needs to be understood before assessing key current questions as global nutrient cycles and possible climate change scenarios (Escolar et al. 2012; Maphangwa et al. 2012).

BSC have a recognized role in avoiding soil erosion and protecting against habitat degradation (Belnap et al. 2003; Lázaro et al. 2008). This protection comes from their ability to stabilise the surface of the soil thus protecting against erosion. The hydrology of the soil can also be influenced by the BSC, with a recognized effect on soil infiltration rates (Maestre et al. 2011), which is mainly related with the type of BSC and soil involved in the process. Some studies have shown that the BSC can maintain the soil moisture (Pérez 1997, Cantón et al. 2004) and that they can modify the soil pH (García-Pichel and Belnap 2003). As well as these physico-chemical features, the BSC are relevant in vascular plant succession processes (Escudero et al. 2007) and are essential to understand the functioning and the ecosystem dynamics, mainly in arid and semiarid regions (Grote et al. 2010). If we consider a global scale, Elbert et al. (2009; 2012) proposed that the cryptogamic covers could be responsible for 7 % of the total C input due to terrestrial vegetation and almost 50 % of the total amount of biological N fixation. According to the same authors, this huge amount of N fixation would be responsible for a very high amount of C fixation by vascular plants due to links between photosynthesis and N availability. This clearly emphasises that BSC, which are important components of cryptogamic covers, cannot be ignored when global nutrient cycling models are attempted.

BSC are especially important in arid and semiarid environments and, in general, the lower the water availability, the greater the importance of BSC in the productivity and nutrient cycling of the ecosystem (Lange 2003). The limited productivity of vascular plants within dry environments can make BSC the main contributors for carbon fixing in the whole ecosystem (Lange 2003). BSC are more effective in these environments, because they are composed of cryptogamic organisms that are more resistant to drought than higher plants and, because they are poikilohydric, they are only active when hydrated (Kappen and

Valladares 2007). Ecophysiological studies on the links between the microclimate and the physiological performance of BSC are essential to understand ecosystem functioning. An important question is: when are these BSC active and what is happening physiologically under those conditions? Productivity or nutrients cycling models for BSC which do not consider the microhabitat level run the risk of being unreliable. However, despite this need, there has been little ecophysiological work analyzing the special functional features of BSC ecosystems and also data linking physiology, microclimate, and photosynthetic production are rare, especially from field measurements (Lange 2003). Although the correlation between laboratory and field data in ecophysiological measurements using cryptogams is normally good (Leisner et al. 1997), information obtained in the field is more definitive about the conditions under which physiological activity is occurring. If field data regarding BSC functioning and microclimate are difficult to find, it is even harder to get information regarding long term measurements, which are key to understand the overall physiological behaviour and to develop models on ecosystems productivity (Belnap and Lange 2003). Few research works (Lange et al. 1999; Lange 2000, Lange and Green 2004) have addressed this issue in BSC cryptogams, and the same authors underline the relevance of this type of measurements to reach a more complete understanding of the ecosystem dynamics.

The Soil Crust International (SCIN) project is a multidisciplinary and international research effort to obtain a better understanding of the importance of the BSC dominated ecosystems in Europe (Büdel et al. 2014). In this project, four different regions with typical BSC communities have been chosen across latitudinal and altitudinal gradients: southern Spain, central Germany, southern Sweden and the Austrian Alps. With respect to ecosystem functioning, the project aims to understand the ecophysiological behaviour of the most representative BSC in each of the four regions mentioned before. Chlorophyll fluorescence monitoring is being used to obtain the activity pattern in the four locations together with concurrent microclimate measurements. In addition, field and laboratory measurements are also to be made of CO_2 gas exchange in order to produce a model able to calculate productivity at the different sites. This paper is focused on field results obtained in one of the four SCIN locations, Almería, in SE Spain, a semi-arid region with one of the lowest precipitation rates in Europe and with desert landscapes. As a step on the way to create a model to calculate net carbon gain over selected time periods from microclimate and chlorophyll *a* fluorescence data, our aims are to determine:

1. When, under which microclimatic conditions, and for how long are major types of BSC active.
2. How similar is the ecophysiological behaviour among the different BSC types in the area.
3. How the length of BSC activity, estimated by chlorophyll *a* fluorescence, compares to that determined by simultaneous measurements of CO_2 exchange.
4. What is the relationship between water content, chlorophyll *a* fluorescence and CO_2 exchange for the different BSC under field conditions.

Materials and methods

Site description and species

The Tabernas badlands are located in South East Spain, in the province of Almería. The locality (El Cautivo) has gypsum-calcareous soils and a semi-arid warm Mediterranean climate, with a mean annual precipitation of 230 mm and a mean annual temperature of 18 °C (Lázaro et al. 2008). The location is considered as one of the driest and sunniest in Europe, and has been fully described in several research works (Lázaro et al. 2001, Cantón et al. 2002).

The vegetation of the area is dominated by grasses, dwarf shrubs, annual plants and BSC, the latter normally dominated by lichens and in some cases by cyanobacterial mats and mosses (Lázaro 1995). Lichens are the most important organisms creating BSC in the region, with many typical calcareous terricolous species (Gutiérrez and Casares 1994). For our physiological measurements we chose five BSC types, four of them dominated by lichens and one by a moss, which are representative examples of the BSC vegetation in the area. The four lichen-dominated BSC types contain *Squamarina cartilaginea*, *Diploschistes diacapsis*, *Toninia albilabra* and *Psora decipiens* as dominant crust species. The moss dominated BSC is formed mainly by the species *Didymodon rigidulus*.

Long term chlorophyll *a* fluorescence and microclimate

To obtain accurate information about BSC activity over 1 year we used the Moni-DA (Gademann instruments, Würzburg, Germany; Walz Mess- und Regeltechnik, Effeltrich, Germany), which is a monitoring system developed to obtain concurrent physiological and microclimatic information (see Online Resource 1). The activity data are collected through chlorophyll *a* fluorescence, a widespread technique in plant physiology studies (Green et al 1998; Schroeter et al. 2011). For detailed information on the fluorescence methodology see Schreiber et al. (1994), and Maxwell and Johnson (Maxwell and Jhonson 2000). At a selected time interval of 30 min, the BSC sample is illuminated with a low intensity modulated measuring light and the resulting chlorophyll *a* fluorescence is recorded (Ft). A high intensity, actinic flash of light (about 1 s, 4,000 µmol m^{-2} s^{-1}) is then applied, and the resulting maximal fluorescence is recorded (Fm′, the fluorescence when PSII, photosystem II, is light saturated). The effective quantum use efficiency of PSII (Φ_{PSII}, Yield) can then be calculated in the light as Φ_{PSII} or Yield = (Fm′ − Ft)/Fm′ (the equivalent to Yield after dark adaptation during night measurents is the Fv/Fm, which is the maximum quantum use efficiency of PSII). We have considered all measuring points with Yield values >0 as active and those with Yield values = 0 as inactive. Although the device has an internal filter to remove possible false activity values, we observed that under certain conditions, usually low values of Ft and/or Fm′ some false activity was occasionally indicated. Fortunately, this false activity was clearly recognizable and corrected in the data base. Another relevant parameter obtained form the device is the electron transport rate (ETR, which is the Yield multiplied by incident radiation and correction factors) that is a qualitative indicator of photosynthetic performance.

The central unit of the Moni-DA can record up to 8 measuring channels, each having a probe that records chlorophyll and microclimate parameters, photosynthetic photon flux density (PPFD, µmol m^{-2} s^{-1}) and temperature (T, °C). The allocation of the eight measuring channels was two samples each of *S. cartilaginea*, *D. diacapsis* and *P. decipiens*, and to one sample of *T. albilabra* and the moss (the latter two species were less abundant in the area than the three others). Where two samples of the same BSC were monitored, we have tried to avoid the idea of replication because the exact microclimatic conditions of each sample in the field are likely to be distinct. All the equipment is solar charged and independent of an external power supply, and it also reports data to a web page using either a cellular or satellite modem. This means that data are being continuously saved and the condition of individual probes and the main machine can be continually monitored. In this research work we report data from October 18th 2012 until September 30th 2013. The device is still running and collecting data successfully. In addition to the microclimatic monitoring, a climate station was installed just a few meters from the Moni-DA equipment. This station is battery charged and measures air temperature, air humidity, solar radiation, UV radiation and precipitation every 5 min.

CO_2 gas exchange

Two field campaigns were carried out in the Tabernas Desert from October 18th to 24th 2012 and from February 12th to 23rd 2013. These periods were chosen as they were expected to be periods of reasonable BSC activity (Pintado et al. 2010). During these two periods we obtained 7 days of natural metabolic activity (4 in February and 3 in October) with five clear activity events during them. A tent, installed a few meters from the Moni-DA, was used to house the gas exchange device, which was connected to a nearby generator. For the gas exchange measurements we used the GFS-3000 (Walz Mess- und Regeltechnik, Effeltrich, Germany) which is a portable device to measure CO_2 gas exchange in the field. The device is described in Raggio et al. (2011) and allows accurate and very fast gas exchange measurements in the field.

For CO_2 gas exchange measurements of the BSC we removed complete BSC samples from their original location and placed them inside a wire basket. The majority of the BSC are integral with the soil and, because of this, samples were collected with soil attached. The surplus of soil was then removed, always taking care not to break the surface of the sample. All BSC had soil attached during the measurements except *D. diacapsis*. For most of the time the samples were kept in their wire baskets in their original field locations and were moved to the GFS-3000 for only a couple of minutes to complete a rapid gas exchange measurement, weigh the sample and obtain a yield value using a MiniPAM (Walz Mess- und Regeltechnik, Effeltrich, Germany). After each measurement, the samples within the baskets were placed back into their original habitat. The water content (WC, % dry weight) of the samples was calculated as the difference between sample weight during the measurements and dry weight, measured at the end of the field work after 24 h at 105 °C in an oven. Water contents are expressed as mm of precipitation equivalent (litres per square metre) as this is regarded as being most ecologically relevant for these studies (see Lange et al. 1998 for more details). We worked with ten samples in each gas exchange cycle, made up of two samples of each of the five BSC types chosen for monitoring with the Moni-DA. All samples for gas exchange were from sites with the same orientation as the Moni-DA samples. Gas exchange cycles started normally 1 h before sunrise and were continued until complete desiccation of all samples (i.e. little change in weight, zero CO_2-exchange and zero yield), obtaining net photosynthesis (NP) and dark respiration (DR) data at different ranges of natural WC. Between the gas exchange measurements samples were also exposed to ambient conditions occurring in the field. Gas exchange is reported on a surface area basis and the area of each sample was determined using the program Image J (National Institute of Health, Bethesda, Maryland, USA).

Statistics

As a first step towards a model to predict BSC productivity, links were sought between different metabolic activity indicators as measured by chlorophyll *a* fluorescence data and the gas exchange data. Following this, Fm′, Yield and ETR were plotted against NP, and gross photosynthesis (GP, which was NP+DR). The metabolic indicators obtained from gas exchange and chlorophyll *a* fluorescence were used as dependent and independent variables indistinctly. Different regression equations (polynomial, hyperbolic, exponential rise to maximum and sigmoidal) provided in Sigmaplot 11.0 were used. As a second step for the statistical analyses, the possible significance of the relationship between activity times provided by the two different methodologies was tested using the Wilcoxon signed-rank test with a significance level of $P \leq 0.05$ (www.statpages.org). This test was chosen because the data set did not follow parametric assumptions.

Results

Long term chlorophyll *a* fluorescence

All samples, regardless of BSC type, showed a very similar pattern of activity throughout the year (Fig. 1a). Activity (% of total time active) was high, around 40 % or higher, in autumn from October to December with a clear peak of 60–85 %, depending on sample, in November. A period of low activity, around 20 % or lower, then occurred in January and February followed by a small rise in March (20–30 % activity), and finally a decline to very low levels over summer. No activity was recorded in June, and very low values in July and August after which the activity again increased. This information is amplified in Table 1, which shows mean monthly activity for the eight BSC monitored combined, and allocates % of activity between light and dark periods. The total sum of monthly ETR is also shown.

There was a good fit between % of total activity and total monthly precipitation excluding December data (Fig. 1a, b). The relation for all 8 BSC together between the monthly mean of the % of metabolic activity and monthly mean precipitation was linear and significant ($r^2 = 0.64$, $P = 0.002$, see Online Resource 2). Temperature also showed a very similar pattern for all BSC. Mean T during activity for each month (T_a) were generally below the mean monthly T (T_m, calculated from all data points), with a small number of exceptions during November and some winter months (Fig. 1c). The differences between T_m and T_a were larger in the months with low metabolic activity (summer) than in the more active ones (colder months). The broken line in all Ta values was due to a lack of activity during June for all the samples whilst the lack of T_m and T_a for *T. albilabra* since July was due to a failure in the probe.

CO_2 gas exchange in the field

The two samples of *S. cartilaginea* (named as sample 1 and sample 2) showed the same trends in the daily patterns of CO_2 gas exchange, except for February 21st when sample 1 had higher net photosynthetic values and sample 2 continued to show respiration after desiccation of sample 1 (Fig. 2). Normally, in the early morning, as observed on February 18th, 21st, and 22nd, NP at first increased with rising T and PPFD values, followed by sample desiccation, resulting in a short period of activity. In contrast, the activity was much longer on the 20th due to the samples being wet over the whole day. *D. diacapsis* showed a similar pattern of CO_2 gas exchange to *S. cartilaginea* (Fig. 3). The gas exchange of the remaining three BSC showed the same trends as described above (see Online Resource 3). Data from the October field campaign are not shown, since all general patterns that occurred are also present in the February data.

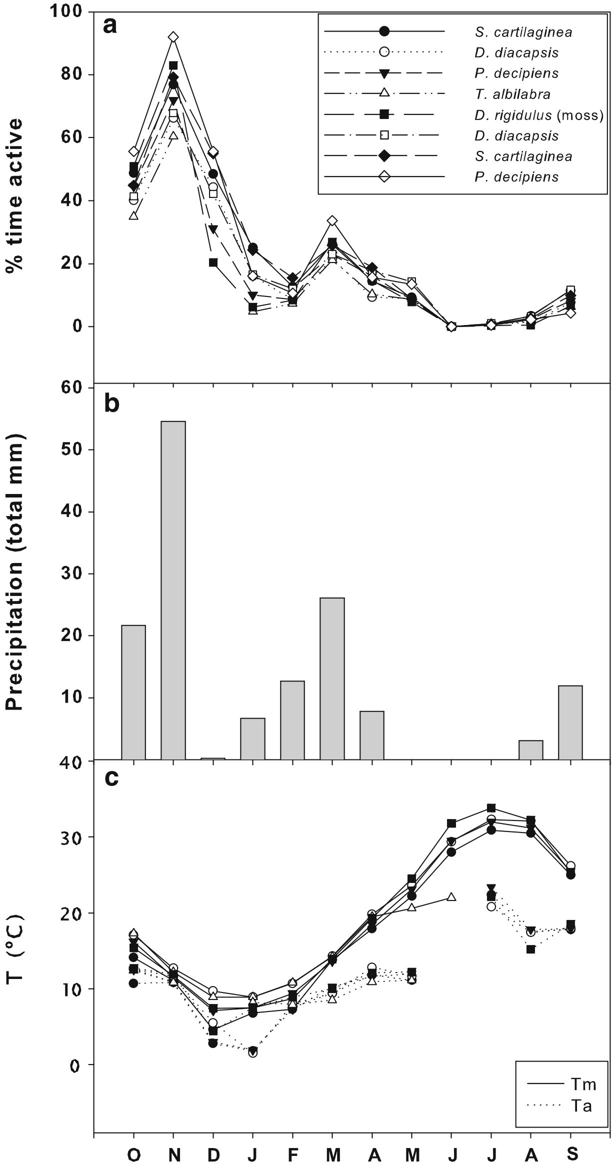

Fig. 1 **a** Metabolic activity in % of time active for the eight biological soil crusts monitored in the Tabernas Desert during the whole measuring period. **b** Monthly total precipitation (mm) during the whole monitoring period in the area. **c** Pattern of the mean monthly temperature at crust level (T_m, *solid line*) and the mean monthly temperature only during metabolic activity at crust level (T_a, *broken line*) for five different BSC types monitored in the Tabernas Desert during the complete monitoring period

Squamarina cartilaginea and *D. diacapsis* had the highest NP whereas *P. decipiens* had the lowest (Table 2). The maximum NP was measured at T around 19 °C for all samples, except for *D. diacapsis*, which had a maximum NP measured at 13 °C. The maximum

Table 1 Monthly means (using the 8 BSC monitored, SD in brackets) for total time monitored samples were active (% of total measurement period), and then divided between activity in the day and in the night; ratio of activity in the day to activity at night light and total monthly electron transport rate (ETR), using the 8 BSC monitored

Month	Time active (% total time)	Active in light (%)	Active in dark (%)	Ratio of active time light/dark	ΣETR
October 2012	45.1 (±6.6)	19.2 (±3.8)	25.9 (±6.8)	0.7	54,768
November 2012	74.7 (±10.1)	30.6 (±6.5)	44.1 (±3.9)	0.7	152,228
December 2012	42.5 (±12.8)	11.8 (±3.9)	30.7 (±9.7)	0.4	23,691 (**230,687**)
January 2013	14.9 (±7.6)	4.1 (±1.8)	10.8 (±6.5)	0.4	11,623
February 2013	10.5 (±2.8)	4.8 (±0.6)	5.7 (±2.2)	0.8	14,126
March 2013	25.2 (±4.0)	10.6 (±2.2)	14.6 (±2.5)	0.7	54,332 (**80,081**)
April 2013	14.6 (±3.3)	8.2 (±2.1)	6.4 (±1.9)	1.3	46,890
May 2013	10.0 (±2.3)	5.4 (±1.5)	4.6 (±0.9)	1.2	34,615
June 2013	0.0	0.0	0.0	–	0 (**81,505**)
July 2013	0.7 (±0.2)	0.4 (±0.1)	0.3 (±0.2)	1.3	2,614
August 2013	2.2 (±1.0)	1.0 (±0.3)	1.2 (±0.7)	0.8	2,806
September 2013	8.2 (±2.6)	3.4 (±1.2)	4.8 (±1.5)	0.7	17,931 (**23,351**)

The accumulated ETR for each three month period is shown in brackets and bold

values of NP were correlated with high values of PPFD in all cases except for *S. cartilaginea* (Table 2). The highest values for DR were measured between 10 and 11 °C.

Comparison between chlorophyll *a* fluorescence, gas exchange and WC in the field during typical activity days

The activity days depicted (Figs. 4, 5, 6) have been selected because they show different climatic conditions which, together, contribute the major proportion of the total activity in the field (see Pintado et al. 2010). On 18/02/13 there was light rain and dew during the night and a clear sky during the day with high PPFD values (Fig. 4). BSC activity was clearly related to the microclimate, ceasing around noon when both T and PPFD reached maximum values (Fig. 4a–c). There was a similar pattern for chlorophyll *a* fluorescence (Yield) and gas exchange measurements indicating a similar time of activity for the in situ and gas exchange samples (Fig. 4d–g). Exceptions were the moss and the *T. alibilabra* BSC which did not show metabolic activity (Yield) on that day whilst samples used for gas exchange did (Fig. 4d, e). Water contents of the samples fell steadily during the entire period of the gas exchange measurements with loss rates increasing with rising PPFD and temperature. (Fig. 4g). *D. diacapsis*, which had the second lowest WC, was the species with the highest NP (Fig. 4e, g). All the other BSC types showed similar rates of DR and NP at different WC. No clear links between WC and Yield were found.

On 20/02/13 there had been some rain during the night. It remained cloudy for the whole day so that T and PPFD only reached maxima of 10 °C and 300 µmol m^{-2} s^{-1}, respectively (Fig. 5b, c). BSC showed metabolic activity over the whole day as measured

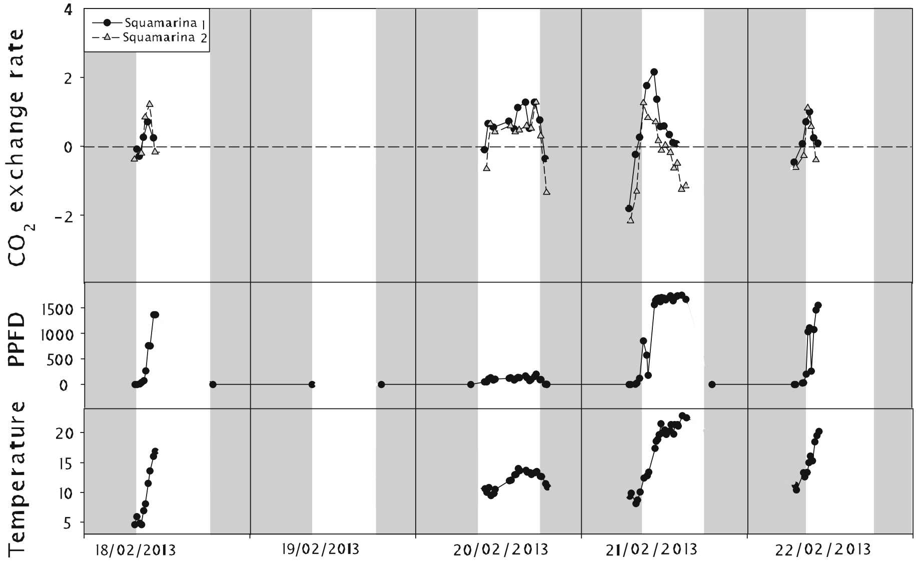

Fig. 2 Daily pattern of CO_2 gas exchange (μmol CO_2 m^{-2} s^{-1}), photosynthetic photon flux density (PPFD, μmol m^{-2} s^{-1}) and temperature (T, °C) in the biological soil crust dominated by *S. cartilaginea* between 18th and 22nd February 2013 in the Tabernas Desert

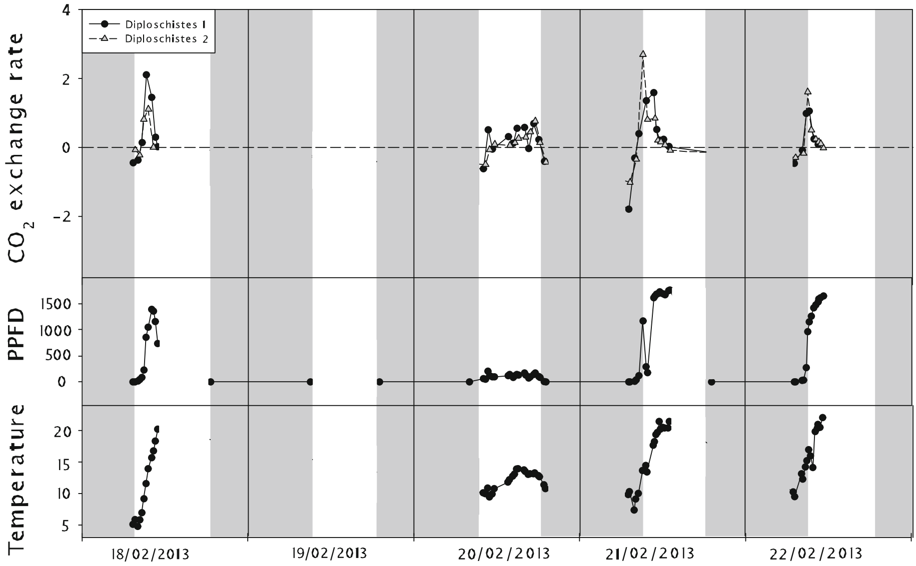

Fig. 3 Daily pattern of CO_2 gas exchange (μmol CO_2 m^{-2} s^{-1}), photosynthetic photon flux density (PPFD, μmol m^{-2} s^{-1}) and temperature (T, °C) in the biological soil crust dominated by *D. diacapsis* between 18th and 22nd February 2013 in the Tabernas Desert

by both chlorophyll *a* fluorescence and gas exchange (Fig. 5a, d, e). The similar pattern between fluorescence and gas exchange can be seen again for all BSC which were active during the measuring period (Fig. 5d, e). The WC was higher for all BSC than on 18/02. *P.*

Table 2 Maximal NP (net photosynthesis) and DR (dark respiration, both in µmol CO_2 m^{-2} s^{-1}), date and time of the measurements and photosynthetic photon flux density (PPFD, µmol m^{-2} s^{-1}) and temperature (T, °C) linked to those values in all the main BSC studied in the Tabernas Desert

	S. cartilaginea	*D. diacapsis*	*P. decipiens*	*T. albilabra*	*D. rigidulus* (moss)
NP max	2.85	2.70	1.95	2.49	2.27
Date	21/10/12	21/02/13	21/02/13	21/02/13	18/02/13
Time	10:55	9:05	12:20	10:44	9:45
DR max	2.17	1.80	2.18	2.10	2.24
Date	21/02/13	21/02/13	21/02/13	21/02/13	21/02/13
Time	7:11	7:01	7:01	7:06	7:09
T NP max	19.55	13.64	19.45	18.66	19.63
T DR max	9.83	9.78	11.18	11.07	11.02
PPFD NPmax	476	1,164	1,658	1,630	1,670

decipiens had the highest WC but the lowest CO_2-exchange rates in contrast to *S. lentigera* with the second highest WC and the highest NP.

The last day (22/02), showed a clear pattern of activation only by dew (Fig. 6). The dew on the surfaces was observed on arrival before dawn. Activation occurred during the night and activity ceased rapidly after sunrise (full sunlight that day) due the low WC and rapid desiccation. The moss was active for a longer than the other BSC (Fig. 6d) but was inactive during later measurements. The WC of the BSC was lower in comparison to the other 2 days, but this did not cause a clear decrease in NP, DR and Yield.

The various attempts made to find links between chlorophyll *a* fluorescence and gas exchange as indicators of metabolic activity were not successful. F_m', Yield and ETR were plotted against NP and GP in several combinations and had very weak correlations even when they were statistically significant ($P < 0.05$). The best correlation found was between NP and YIELD using a hyperbolic fitting ($r^2 = 0.11$, $P < 0.001$) and had very limited physiological relevance.

In relation with the second statistical approach, the lengths of the periods of activity obtained from the gas exchange and the chlorophyll *a* fluorescence measurements over the seven gas exchange days were not statistically different (Wilcoxon signed-rank test, $P = 0.294$). Two main types of activity periods were identified during the field work, long ones (linked to rain and cloudy conditions during the day) and short ones including dew and rain with sunny conditions after sunrise (Fig. 7).

Discussion

The overall aim of this research project is to obtain an estimate for the carbon economy of the various BSC at the four research sites. As a first step towards this aim the nearly 12 months of fluorescence and microclimate monitoring have provided a complete data set in order to better understand under which micro-environmental conditions, and for how long, the main BSC were active. In addition, CO_2 gas exchange measurements were made under field conditions at the same time as chlorophyll fluorescence activity measurements. The similar results provided by the two techniques used to measure the length of activity periods is another important step towards a productivity model related with the different BSC activity in the region.

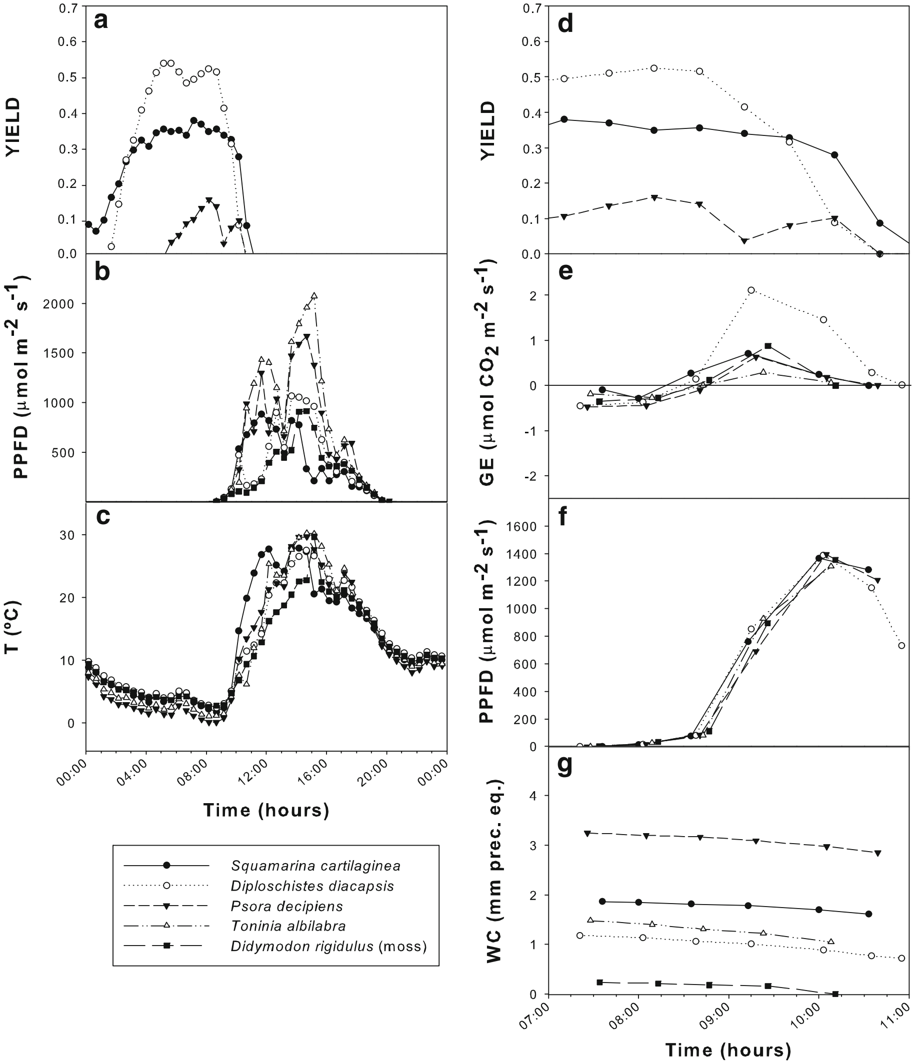

Fig. 4 Metabolic activity and microclimate for five different biological soil crust types for the day 18/02/2013; **a**–**c** effective quantum use efficiency of photosystem II (Yield, **a**), BSC temperature (T °C, **b**), photosynthetic photon flux density (PPFD, μmol m^{-2} s^{-1}, **c**) in the BSC obtained from the Moni-DA over the whole day and **d**–**g** data obtained only during the gas exchange period (7:00–11:00), Yield (**d**), GE (μmol CO_2 m^{-2} s^{-1}, **e**), PPFD (μmol m^{-2} s^{-1}, **f**) and water content of the gas exchange samples (WC, mm precipitation equivalent, **g**)

The first of our aims has been achieved by the continuous monitoring of BSC activity for 1 year (Fig. 1a; Table 1). The results obtained over the summer showed a clear reduction in the BSC metabolic activity lasting for a long period during the year, which underlines the extreme conditions for plant life in the Tabernas Desert. The activity was highest during the autumn months (October to December), followed by winter (January–March) and spring (April–June). The accumulated ETR is an indicator of photosynthetic

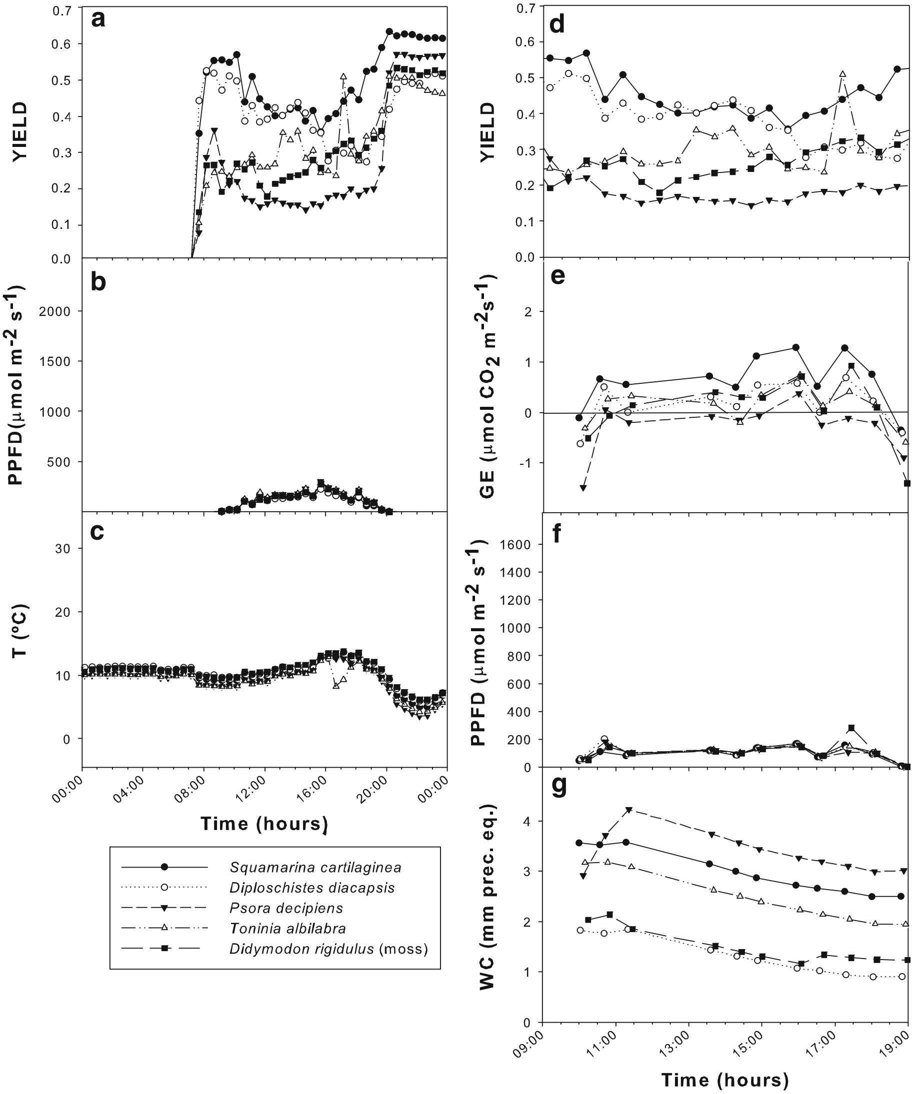

Fig. 5 Metabolic activity and microclimate for five different biological soil crust types for the day 20/02/2013; **a**–**c** effective quantum use efficiency of photosystem II (Yield, **a**), BSC temperature (T °C, **b**), photosynthetic photon flux density (PPFD, μmol m^{-2} s^{-1} **c**) in the BSC obtained from the Moni-DA over the whole day and **d**–**g** data obtained only during the gas exchange period (9:00–19:00), Yield (**d**), gas exchange(GE μmol CO_2 m^{-2} s^{-1}, **e**), PPFD (μmol m^{-2} s^{-1}, **f**) and water content of the gas exchange samples (WC, mm precipitation equivalent, **g**)

performance, and the results show how, again, the autumn months were much better for C fixation in Tabernas during the year monitored, with an accumulated ETR between 2 and 3 times higher than winter and spring. The latter two seasons had similar values and show how the longer periods of activity in the light in spring compensate for the longer activity period (twice as long) during the winter. The activity of the BSC samples in the Tabernas

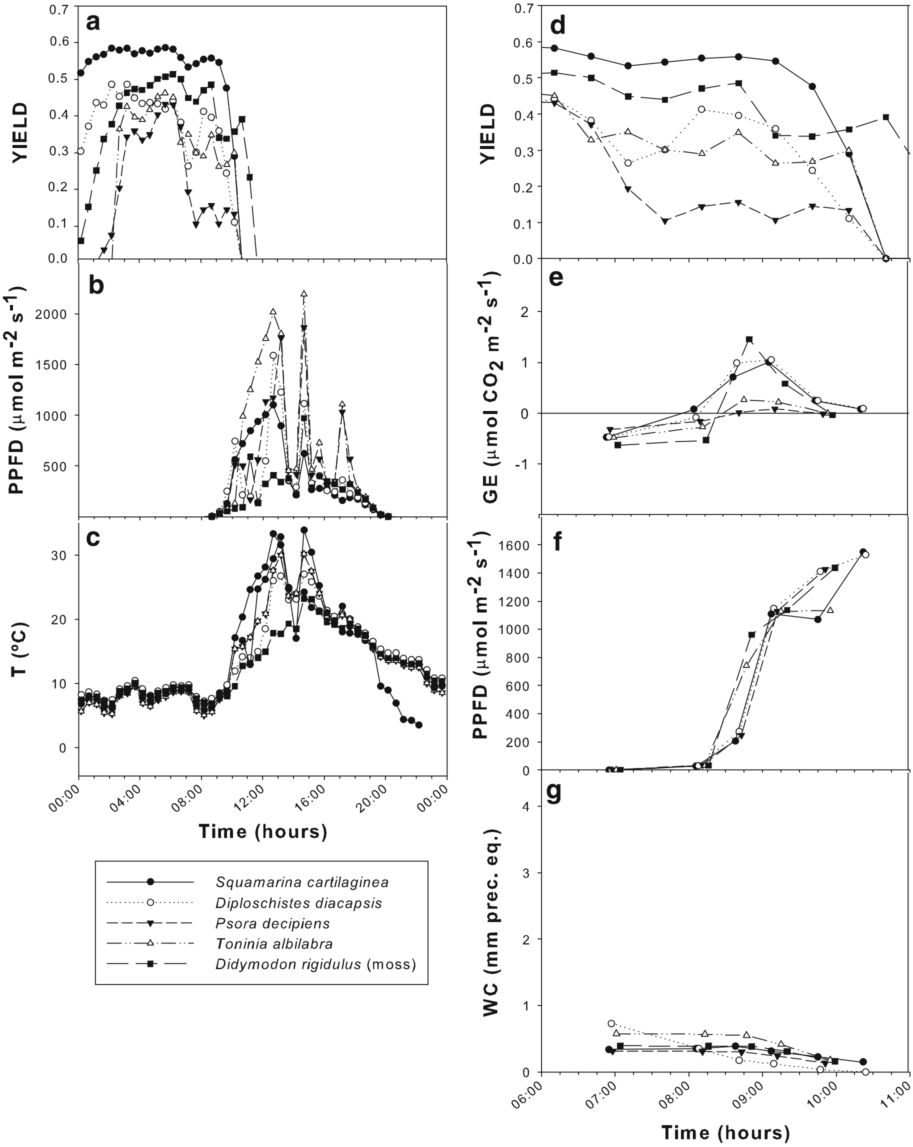

Fig. 6 Metabolic activity and microclimate for five different biological soil crust types for the day 22/02/2013; **a**–**c** effective quantum use efficiency of photosystem II (Yield, **a**), BSC temperature (T °C, **b**), photosynthetic photon flux density (PPFD, µmol m^{-2} s^{-1} **c**) in the BSC obtained from the Moni-DA over the whole day and **d**–**g** data obtained only during the gas exchange period (6:00–11:00), Yield (**d**) gas exchange (GE, µmol CO_2 m^{-2} s^{-1}, **e**), PPFD (µmol m^{-2} s^{-1}, **f**) and water content of the gas exchange samples (WC, mm precipitation equivalent, **g**)

Desert over the whole measuring period was 20.7 % ± 3.6 of the total time (mean of the eight BSC monitored during the whole year). This value fits well with the 20 % of activity reported by Pintado et al. (2010) for *D. diacapsis* measured for 2 years at a nearby site in Tabernas. This percentage of activity lies between the values found by Lange et al. (1999)

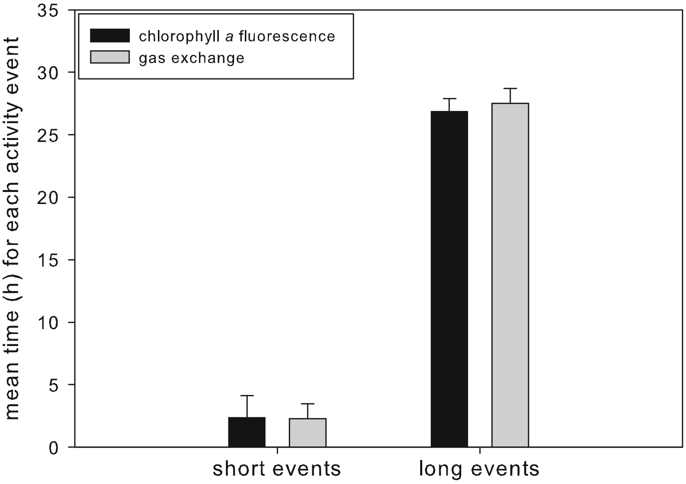

Fig. 7 Mean time with standard deviation for length of the activity periods (h) compared in short and long activity events measured with two different techniques (chlorophyll fluorescence and gas exchange) in the field. Total $n = 38$ (24 for short events and 14 for long events in each methodology), all different BSC types used are included

under temperate conditions in Central Germany (53.5 %), and the values from arid regions than can be below 10 % (Lange 2003). The total time of activity reported here, therefore, aligns well with the semiarid environment where measurements were made and the pattern of activity also opens interesting lines of investigation linking macro- and microenvironmental climatic conditions with metabolic activity of the BSC.

Although each sample monitored showed a different monthly percentage of activity the annual pattern of metabolic activity was almost identical for all types of BSC (Fig. 1a) which points to consistent physiological behaviour of the BSC components. One possibility is that there is little difference among the species dominating the BSC for the parameters measured here, but to decide this needs further detailed physiological studies. The most likely factor driving metabolic activity is hydration as all BSC component species are poikilohydric. BSC can be activated by three sources of water. The first is rain and a preliminary analysis of the data shows this to be very important, with a good link between precipitation and activity (Fig. 1, see also Online Resource 2). The second is dew, and heavy dew is particularly likely in this area due to the clear skies and consequential low surface temperatures at night. Our preliminary analysis shows that dew activation occurs (i.e. activation not aligned with rainfall, see data in December Fig. 1a, b and also Fig. 6) and that it is linked to relative air humidities between 85 and 90 %, at least in the period selected (see Online Resource 2). The importance of dew and rain in this area was also reported by Del Prado and Sancho (2007) and Pintado et al. (2010). Apart from rain and dew, a third possible factor for metabolic activity in BSC is hydration by water vapour alone (Lange et al. 1997). Activation by water vapour is known to be much more common in green algal lichens than in bryophytes. So, the similar activity pattern for the moss BSC (that only become active with liquid water, Rundel and Lange 1980; Green et al. 2011) and the lichen-dominated BSC suggest that water vapour is less important than rain and dew. Our work allows us to extend the exhaustive physiological studies done with *D. diacapsis* in the same locality (Pintado et al. 2005, 2010) to all the relevant BSC in the area, providing a larger data set and allowing comparisons between BSC types.

In addition to the permanent activity monitoring, the amounts of CO_2 fixed or lost by each of the BSC types during each day was simultaneously measured when activity occurred in two field campaigns (Figs. 2, 3 and Online Resource 3). Although actual rates and duration of CO_2 gas exchange were determined by the actual climatic conditions on each day as well as hydration status, the different BSC types reacted very similarly not only in the length of the period of activity but also in the maximal CO_2 gas exchange rates observed. The mean maximal rates of NP and DR calculated for all samples together gave 2.45 ± 0.35 and 2.08 ± 0.17 µmol CO_2 m^{-2} s^{-1}, respectively, and the similarity of the mean values for the individual species (Table 2) suggests common trends in C fixation by the main BSC in the field. Our values are within the ranges reported by different authors (Lange 2003; Büdel et al. 2013).

As well as knowing when and under which conditions are the BSC active, and the amount of CO_2 exchange under those conditions, it is also important to have a good correlation between fluorescence and CO_2 gas exchange if a predictive model is to be developed using these parameters. The lengths of active periods measured by long term chlorophyll fluorescence during gas exchange measurements (Fig. 7) were not statistically different, and this is a valuable finding.

Our next step will be to calculate the net C gain for the BSC. This is not straight forward as there are complex interactions between mode and degree of activation, actual environmental conditions and, although overall activity patterns are almost identical, the actual rates of CO_2 exchange can be species-specific (Lange et al. 1995). Several approaches will be used. One is to establish criteria to identify typical days (i.e. with identical activity patterns, such as dew activation) in our Moni-DA data set and to quantify these as a base for long term modelling. Figures 4, 5, 6 show three representative days of activity in the field. The days 18/02 and 22/02 are typical in Tabernas because of the strong irradiation, but the BSC samples were hydrated by different water sources. During the first day there was a light rain during the night and dew, whereas on 22/02 there was a clear activation only by dew. This caused higher water contents during the first day, but not necessarily higher gas exchange or yield values in all BSC, mainly because of the changing conditions of PAR, T and thallus WC in the field. The third day (20/02) revealed a completely different behaviour because of the unusual cloudy conditions. There was some rain during the morning, which created the highest WC in the BSC as observed during the whole period. These weather conditions caused a long-lasting activity period. This allowed net C gain during the whole day and showed that conditions of low light and T causing long activity periods are the more profitable for the BSC studied.

Model development is made more difficult by some complexities in species photosynthesis. The first is thallus WC because highest WC is not necessarily linked to highest gas exchange values (see *P. decipiens* in Figs 5e, g). Depression of photosynthesis at high thallus WC considerably lowers net carbon gain in several lichen species, as e.g. shown by Lange (2003) for *S. lentigera*. At present we do not know the importance of this behaviour as it is not only species-specific but it will not occur during activation by dew or light rainfall. This effect will be analysed during CO_2 gas exchange measurements in the lab, which will be reported at a later stage. Yields were also maximal at moderate to low thallus WC and do not indicate the degree of any depression at high WC. The Yield and ETR are also not necessarily related with C fixation in many higher plants and this is also true for lichens and bryophytes (Leisner et al 1997; Green et al. 1998). No good links between F_m', ETR, Yield and CO_2 exchange have been found in a preliminary analysis of our long term data set and in the results presented here. The weak correlations found between the supposedly better related parameters (Yield and NP, $r^2 = 0.11$) points to a general lack of links between the metabolic parameters provided by both techniques. Despite of this, the activity times measured by the two techniques were equivalent, and this is a valuable result in order to link the long term and short term metabolic measurements obtained by chlorophyll *a* fluorescence and gas exchange respectively.

Another complication is the known behaviour that lichens are mainly active under suboptimal conditions in the field (Green et al. 2007; Green 2009; Schroeter et al. 2011). We find the same effect here. Figure 1c shows the relationship of mean temperature for the entire measuring period (T_m) and mean temperature when active (T_a) for all the BSC. The mean T_m of the 8 BSC studied was 19 °C, whereas T_a was 9.4 °C. Pintado et al. (2010) reported exactly the same T_m after 2 years in *D. diacapsis*, but with a lower Ta of 8.8 °C, which could indicate that most activity was during the winter months. The differences between T_a and T_m are largest during the periods of highest temperatures and lower metabolic activity. A complete analysis of all the Moni-DA data comparing microclimate and metabolic activity reinforces this idea, with greatest activity under conditions of light and T that were very different to optimal values for photosynthesis (data not shown). BSC are, therefore, mainly active under conditions of lower T and PPFD, and are inactive under the extreme conditions typical of arid/semiarid environments. Extrapolations from photosynthetic matrices obtained in the laboratory are not really possible without taking into account the actual conditions when BSC are active.

A further potential complication are CO_2 fluxes occurring in soils not linked to biological activity, especially in arid and semiarid environments with basic soils and under dry conditions, which could be important in C cycles worldwide (Xie et al. 2009; Ma et al. 2013; Rey et al. 2013). To overcome this problem, we used a second fluorometer (MiniPAM,) in order to check the metabolic activity of all BSC studied. When the BSC became inactive as indicated by chlorophyll fluorescence (which means that the organisms responsible of C fixation were dry), we detected gas exchange showing NP values between 10 and 25 % (in isolated cases close to 50 %) of the maximum values observed, probably due to the abiotic fluxes mentioned. Although these values, assumed to be relevant under the driest conditions, can be identified and were removed from our data set, our results reinforce the relevance of knowing the importance of these CO_2 emissions in arid/semiarid ecosystems.

The relevance of data sets related with productivity is not only important for C fluxes models. The BSC environments worldwide have shown links between multifunctionality (where productivity is included) and species richness (Maestre et al. 2012a). This emphasizes the relevance of studies showing data of different BSC CO_2 gas exchange rates. According to Lange (2003), the BSC from arid and semiarid regions can have higher chlorophyll contents and as much productivity in a surface basis as vascular plants from the same habitats. With arid and semiarid regions of the world being threatened by possible rises in T and different water availability (Maestre et al. 2012b), the understanding of the relevance of BSC on a global scale is crucial to develop protection strategies for these formerly overlooked habitats.

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