

The CO₂ exchange of biological soil crusts in a semiarid grass-shrubland at the northern transition zone of the Negev desert, Israel

B. Wilske^{1,2,*}, J. Burgheimer³, A. Karnieli³, E. Zaady^{4,**}, M. O. Andreae², D. Yakir¹, and J. Kesselmeier²

¹Department Environmental Science and Energy Research, Weizmann Institute of Sciences, Rehovot 76100, Israel

²Max Planck Institute for Chemistry, Biogeochemistry Department, P.O. Box 3060, 55020, Mainz, Germany

³The Remote Sensing Laboratory, Jacob Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, Sde Boker Campus, 84990, Israel

⁴The Desertification and Restoration Ecology Research Center, Jacob Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, Sde Boker Campus, 84990, Israel

* now at: Department of Environmental Sciences, The University of Toledo, Toledo, Ohio 43606-3390, USA

** now at: Department of Natural Resources, Agriculture Research Organization, Gilat Research Center, Ministry of Agriculture, Mobil Post Negev 85280, Israel

Received: 12 March 2008 – Published in Biogeosciences Discuss.: 9 May 2008

Revised: 19 August 2008 – Accepted: 29 August 2008 – Published: 21 October 2008

Abstract. Biological soil crusts (BSC) contribute significantly to the soil surface cover in many dryland ecosystems. A mixed type of BSC, which consists of cyanobacteria, mosses and cyanolichens, constitutes more than 60% of ground cover in the semiarid grass-shrub steppe at Sayeret Shaked in the northern Negev Desert, Israel. This study aimed at parameterizing the carbon sink capacity of well-developed BSC in undisturbed steppe systems. Mobile enclosures on permanent soil borne collars were used to investigate BSC-related CO₂ fluxes in situ and with natural moisture supply during 10 two-day field campaigns within seven months from fall 2001 to summer 2002. Highest BSC-related CO₂ deposition between -11.31 and -17.56 mmol m⁻² per 15 h was found with BSC activated from rain and dew during the peak of the winter rain season. Net CO₂ deposition by BSC was calculated to compensate 120%, -26% , and less than 3% of the concurrent soil CO₂ efflux from November–January, February–May and November–May, respectively. Thus, BSC effectively compensated soil CO₂ effluxes when CO₂ uptake by vascular vegetation was probably at its low point. Nighttime respiratory emission reduced daily BSC-related CO₂ deposition within the period November–January

by 11–123% and on average by 27%. The analysis of CO₂ fluxes and water inputs from the various sources showed that the bulk of BSC-related CO₂ deposition occurs during periods with frequent rain events and subsequent condensation from water accumulated in the upper soil layers. Significant BSC activity on days without detectable atmospheric water supply emphasized the importance of high soil moisture contents as additional water source for soil-dwelling BSC, whereas activity upon dew formation at low soil water contents was not of major importance for BSC-related CO₂ deposition. However, dew may still be important in attaining a pre-activated status during the transition from a long “summer” anabiosis towards the first winter rain.

1 Introduction

Vast areas throughout the semiarid and arid areas of the world are covered by so called biological soil crusts (BSC), which consist of communities of cyanobacteria, green algae, lichens, mosses, microfungi and bacteria in various proportions (Belnap et al., 2001; Karnieli et al., 2001; West, 1990). BSC-forming organisms are well adapted to environments with unreliable water supply by their capability to survive under changing tissue water contents, a feature which is called poikilohydry. Equipped with the poikilohydric feature that



Correspondence to: B. Wilske
(brkwils@yahoo.com)

allows perpetual cycles of desiccation and hydration of cells without damage to biological functions (Belnap et al., 2001), BSC successfully complement the sparse cover of vascular vegetation in many dryland ecosystems. Remote sensing studies confirmed the large contribution of photosynthetically active BSC surfaces in semiarid areas (Karnieli and Tsoar, 1995; Karnieli et al., 1996, 1999). Recently, remote sensing studies were also successful in following the phenological cycle of BSC as well as probing differences in the seasonal changes of their CO₂ assimilation (Burgheimer et al., 2006a, b).

Numerous laboratory studies have provided benchmark data of photosynthesis and respiration in relation to biomass or chlorophyll content of BSC organisms (e.g., Lange et al., 1970, 1998; Palmer and Friedmann, 1990; San José and Bravo, 1991). With respect to their large surface cover, BSC have been discussed as being an important additional sink for atmospheric carbon in semiarid and arid areas (Cable and Huxman, 2004; Beymer and Klopatek, 1991; Lange et al., 1992; Zaady et al., 2000). The compilation of area-based net photosynthesis in different BSC types showed a wide range of maximum CO₂ uptake rates equivalent with deposition fluxes between -0.11 and $-11.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Lange, 2001). However, previous field studies investigating the gas exchange of BSC used mostly samples either on naturally loose and inert substrate, such as gravel, or separate samples in Petri-dishes (e.g., Lange et al., 1994; Levi et al., 1981; Kappen et al., 1980; Zaady et al., 2000). Separation of soil-dwelling BSC from the underlying soil compartment may eliminate a major factor influencing their CO₂ exchange. In a recent study by Housman et al. (2006), soil-dwelling BSC were investigated in situ but the protocol included laboratory-like rewetting of the samples prior to the measurements.

With respect to their poikilohydric feature, the relevance of potential water resources such as rain, fog, and dew, is crucial for the understanding of BSC-related CO₂ fluxes in an area. For instance, a rainfall gradient of 200–250 mm exists from the coastal region to the arid core of the Negev Desert, Israel. Dew precipitation accounts on average for 33 mm or 25–30% of the annual precipitation in the gravel desert of the Negev highlands (Evenari, 1981), and it was concluded that dew and fog play a particular role for BSC activity (e.g., Lange et al., 1994; Veste et al., 2001). However, significant differences exist in the amount of dew on a medium spatial scale (Kidron, 2000), so that dew and fog increase by 0.03 mm per 100 m increase in elevation from the coastal lowlands to the highlands of the Negev (Kidron, 1999). Thus, fog and dew may not play a major role for BSC activity in the lowland plains of the Negev (Kidron et al., 2002).

The objectives of the present study were (1) to investigate seasonal CO₂ fluxes with BSC in a typical semiarid grass-shrub ecosystem with special regard to the environmental conditions for soil-dwelling BSC, which can be assumed being partly determined by the underlying soil. (2) To compare BSC-related fluxes with CO₂ efflux from bare soil in order

to allow estimates on changes in CO₂ flux following disturbance that can essentially deplete BSC growth in semiarid areas. We used a specially designed twin-cuvette system to investigate BSC in situ and to account for both, the strong gradients of heat- and water holding capacity within the BSC-soil continuum and the influence of previously accumulated soil water on BSC hydration and related CO₂ fluxes.

2 Materials and methods

2.1 Study area

The study was conducted within the International Long Term Research site Sayeret Shaked (LTER-SSK) in the northern Negev Desert, Israel (31°17'N 34°37'E, 160–190 m a.s.l., <http://lter.bgu.ac.il/sites/ssd.aspx>). Loess soil covers the Eocene chalk bedrock in the area with a layer up to 1.1 m thick. The loess soil contains 14% clay, 27% silt, and 59% sand (Zaady et al., 2000). The sandy loam to loam soil texture (Birkeland, 1999) provided a solid surface for BSC growth under semiarid conditions. Several small watersheds cut the terrain and drain the runoff into a wadi. Located on the 200 mm isohyet, LTER-SSK is representative for the transition from the semiarid to the arid desert in Israel with the typical grass-shrub vegetation of the transition zone. LTER-SSK was fenced in 1987 and allows studies of natural ecosystem dynamics without the influence of livestock grazing. Growth of grasses (e.g., *Stipa capensis* Thunb.) complemented by a variety of annual forbs dominated the area from February to early summer, but throughout the year the area is mainly characterized by scattered patches of shrubs (*Noaea mucronata* (Forssk.) Asch. and Schweinf., *Atractylis serratulooides* Cass., *Thymelea hirsuta* L.) and the extensive growth of BSC (Shachak et al., 1998; Zaady et al., 2000).

2.2 Biological soil crusts

The composition and distribution of BSC within LTER-SSK was previously surveyed by Zaady et al. (1998, 2000). The BSC in the area consist of the three main components (1) cyanobacteria (*Nostoc punctiforme* L., *Microcoleus vaginatus* (Vauch.) Gomont), (2) “dark” crustose cyano-lichens (*Collema spec.*), and (3) mosses (*Crossidium crassinerve* De Not., *Aloina bifrons* De Not.). At the time of the measurements, BSC covered about 60% of the ground surface (Burgheimer et al., 2006a). Contributions of the three main components alternated on the large scale and on the micro-scale following micro topography and microclimate. Conversely, and despite changing contributions on a square meter scale, all the three components were present in most places. Hence, a mixed composition of BSC was found to be most representative for the BSC-related CO₂ fluxes in the area. Accordingly, mini plots with mixed BSC were enclosed and sampled, which comprised cyanobacteria, lichens, and mosses in 1:1:1 proportion.

2.3 Experimental set-up and protocols

The CO₂ exchange of BSC was investigated during 10 three-day field campaigns from 21 November 2001 to 7 May 2002. Campaigns were scheduled based on the weather forecast and conducted when precipitation was expected.

2.3.1 Prep of sample plots

One month prior to the experiments, permanent soil borne collars (acrylic glass, ID 143 mm) enclosing 0.016 m² of native BSC growth were inserted into the soil (55 mm below and 5 mm above the soil level) on a slightly NNE declining slope. Edge-disturbances caused by the collar embedment were smaller than 5 mm. Additional collars were installed for reference plots, which enclosed soil without BSC growth. The top 10 mm in the reference collars were removed, refilled with soil, and then once flooded with distilled water to recover the settled structure of the soil. To prevent BSC growth, the same procedure was repeated with the upper 5 mm every second month at the end of a field campaign. Thereby, the reference plots were kept as much as possible comparable with disturbed areas where soils still contain populations of soil bacteria and micro fungi but no natural BSC development.

2.3.2 The enclosure system

Two cuvette frames (acrylic glass, ID 143 mm, H 40 mm) were equipped with Teflon bags inside and on top (Fig. 1). The cuvette tops included one inlet (ID 12.7 mm) and three outlet ports (ID 6.4 mm), a Teflon fan, a thermocouple (Type E, Campbell, Loughborough, UK) for air temperature, and a thermo-hygrometer (HM122, Vaisalla, Helsinki, FI). A flow rate of 1 dm³ 60 s⁻¹ (L min⁻¹) per cuvette was maintained by a radial fan (U64, Micronel, Tagelswangen, CH) upstream and flow controlled pumps downstream of the enclosures. Ambient air was flushed via Teflon tubes (ID 25.4 mm) from a 3-m distance. The downstream open-ended air pass was coupled to the cuvettes with 0.12 m Teflon tubes (ID 12.7 mm). The inlet ports of the cuvettes were flexibly half-blocked with overlapping stripes of Teflon tape. Resistances within the tubes were empirically adapted to provide a pulse-free flushing under ambient pressure conditions. Cuvette tops were either attached to the sample- (i.e., enclosing BSC), the reference, or to blank-collars. Blank-collars were mobile and top-covered with Teflon foil. A cuvette top on a blank-collar formed an empty all-Teflon coated enclosure to measure CO₂ mixing ratio in ambient air (C_a) without exchange at active surfaces.

2.3.3 CO₂ exchange measurements

The CO₂ exchange was measured using an infrared gas analyser (IRGA, LI-7000, LICOR, Lincoln, USA) in differential mode. Soil CO₂ efflux was measured as the difference be-

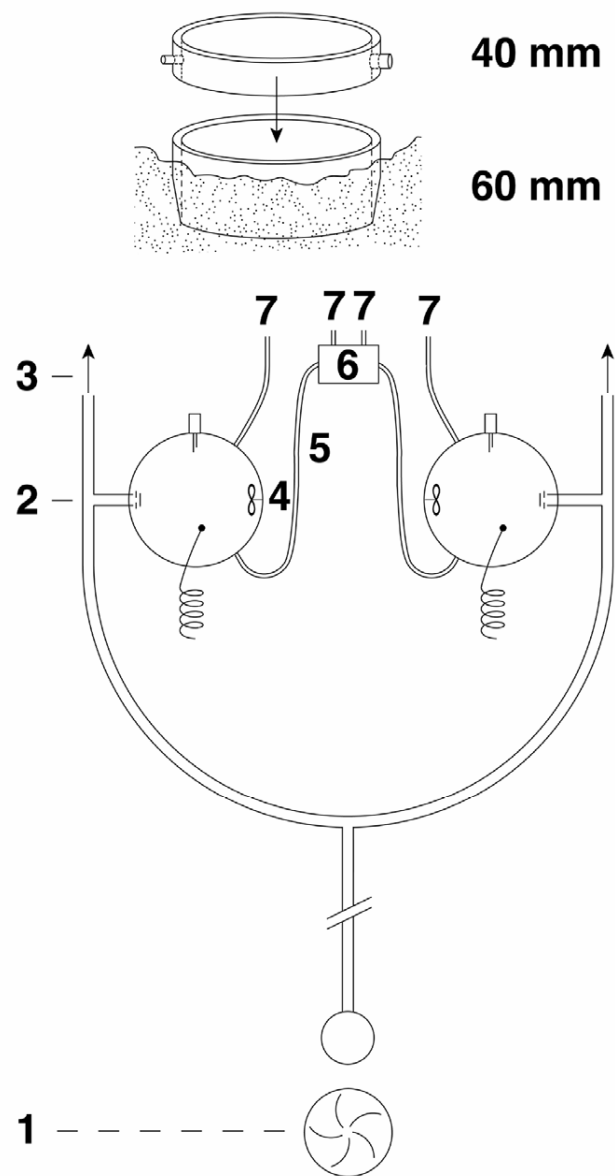


Fig. 1. Twin-cuvette system to measure BSC-related net CO₂ flux: (1) radial fan on 25.4-mm Teflon tubing, (2) 25.4-mm to 12.7-mm Teflon connection to cuvette, (3) 25.4-mm open end tubes, (4) cuvette fan, (5) 6.4-mm connection, (6) infrared gas analyzer, (7) flow control and pumps. Cuvette top height 40 mm, collar height 60 mm, both ID 143 mm; transparent Teflon cuvette window on top 0.016 m².

tween a soil sample and a blank collar (C_a). BSC-related CO₂ fluxes were obtained by measuring one BSC sample versus one soil sample. Hence, soil CO₂ efflux was subtracted instantaneously. The measurement system and this type of differential measurement were tested in the laboratory and under field conditions in Sayeret Shaked and two other sites in the Negev Desert. We compared three types of measuring BSC-related CO₂ flux: (1) Single BSC and

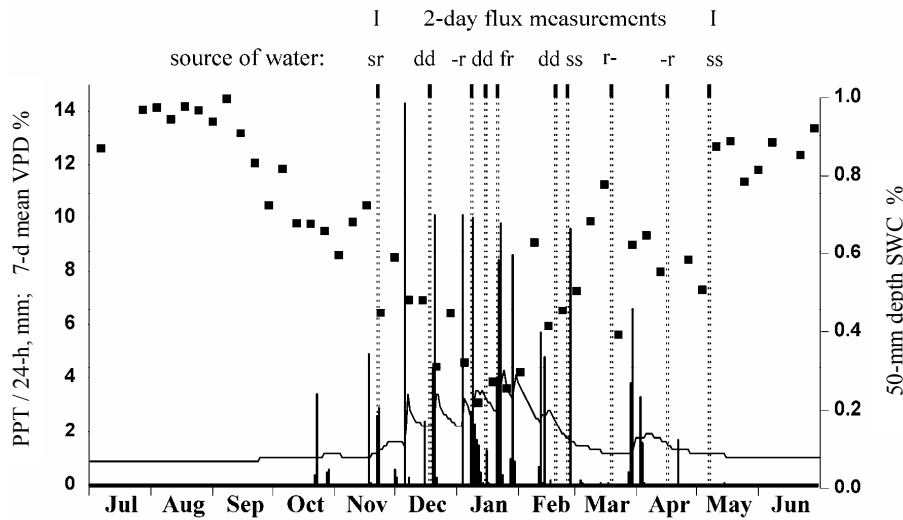


Fig. 2. Moisture parameters and periods of flux measurements during the hydrological year 2001-2002 in SSK-LTER. Bottom X-axis: month from 1 June 2001–30 May 2002; top X-axis: periods of measurements (vertical dot line); left Y-axis: 7-d averages of vapour pressure deficit, % (■, cut-off at 15%), and total precipitation per 24 h, mm (vertical bars); right Y-axis: soil moisture at 50-mm, % (thin line). Climate data from TEMS.

soil samples were measured separately in the absolute mode by enclosing one sample type at a time, while the reference channel of the IRGA was flushed with CO₂-H₂O-purged atmosphere air. (2) Similarly, single BSC and soil samples were measured while the IRGA reference channel was flushed with air from a blank cuvette (C_a). (3) BSC-related fluxes were measured in the differential mode by enclosing simultaneously one BSC and one soil sample and flushing the IRGA sample and reference channel with air from the BSC- and the soil enclosure, respectively. Small offsets between the absolute modes (1) and (2) were corrected by subtracting the blank cuvettes offset (C_a versus C_a). BSC-related CO₂ fluxes from single sample measurements were calculated as the difference between the results of individual BSC and soil samples. Based on 10-min averages of consecutive measurements of dry and wet samples during nights and over-casted days, a difference of 0.1 $\mu\text{mol mol}^{-1}$ was not significant between results of both types of calculated BSC-related fluxes and as obtained from the differential mode. Therefore, the differential mode allowed a more rapid measurement of BSC-related fluxes except for periods when precipitation changed the moisture conditions significantly. To obtain maximum sensitivity and precision in this low flux system, measurements in differential mode were routinely checked against ambient air from a blank cuvette. Enclosures were alternated between three to four BSC- and two soil samples. The general enclosure time of a sample was 15 min, but protocols were also adapted to fluctuations of light, temperature, and moisture, looking for the best trade-off between data acquisition and keeping samples open for natural exchange of heat and moisture.

Positive and negative fluxes represented CO₂ emission and deposition, respectively. However, the terms “emission” and “deposition” are not meant to distinguish between biotic and abiotic sources and sinks. Emission was derived from BSC respiration and/or soil CO₂ efflux but may also include, e.g., CO₂ displacement by infiltration of rain. CO₂ deposition referred to CO₂ uptake by BSC photosynthesis but may also include, e.g., CO₂ wet deposition to wet BSC surfaces. Finally, BSC-related fluxes represent fluxes due to BSC activity plus potential effects of BSC growth on the soil.

2.3.4 Quality control and data processing

Flow controllers were regularly checked with a calibrated unit in the lab. IRGA calibrations followed standard procedures and showed a deviation of $\leq 0.05 \mu\text{mol mol}^{-1}$ CO₂ over 2–4 weeks. The operation in differential mode substantially improves measurement precision. To improve the accuracy of the measurements, CO₂ raw data were corrected for drifts due to IRGA temperature and water content of sample air using linear regressions from blank cuvettes records (C_a vs. C_a). Data with high uncertainty due to excessive variance of blank values were eliminated. Presented data of CO₂ exchange relied on 10-min blank averages with standard deviations $< 0.01 \mu\text{mol m}^{-2} \text{s}^{-1}$. A difference of 0.05 $\mu\text{mol m}^{-2} \text{s}^{-1}$ was resolved in most of the records; exchange rates below this threshold are not discussed. To calculate 15-h fluxes, data gaps were filled using stepwise regression.

2.3.5 Environmental conditions

Three to five 30-mm soil cores were sampled for gravimetric soil water content (SWC) at the beginning and end of a day, and after single precipitation events. Standard probes close to the sample plots recorded the following microclimate conditions in one-minute intervals: Photosynthetic active radiation (PAR, LI-190SZ, LICOR), short wave radiation (CM11, Kipp&Zonen, Delft, NL), precipitation events (two Wetness Sensing Grids, Campbell), temperature and air humidity 0.2 and 0.5 m above soil surface (Handylog 503-2MB, Driesen&Kern, Hamburg, FRG; Rotronic, Walz, Efeltrich, FRG), temperatures of soil surface and air 10 mm above soil surface (covered Type E thermocouples, Campbell). Annual courses of climate parameters in 15-min time resolution were also obtained from the meteorological station of the Terrestrial Ecosystem Monitoring network (TEMS, http://www.fao.org/gtos/tems/tsite_show.jsp?TSITE_ID=1609, now at <http://www.slu.cmc-amman.gov.jo/data.phtml?site=sayeret/sayeret.html>), which was located at a distance of 300 m from the sample plots.

3 Results

3.1 Annual pattern of BSC-related CO₂ flux

Reported CO₂ fluxes represent net exchange by soil-dwelling BSC (i.e., BSC-related flux with negative values representing deposition), except where soil CO₂ efflux is indicated. BSC-related CO₂ fluxes were investigated from the onset of the winter rain season to the following dry season (21 November 2001–7 May 2002). The period included 93% of the annual precipitation (PPT), and the periods of increased soil water content (SWC) and lower vapour pressure deficit (VPD) (Fig. 2). Only 10.0 mm and 0.1 mm of rain fell before and after the measurements, respectively. Total PPT at LTER-SSK was 150.8 mm and 25% below average within the one year from dry to dry season (1 June 2001–30 May 2002). TEMS records showed 42% of annual PPT occurred in conjunction with the lowest monthly mean temperature in January.

The seasonal pattern of BSC-related CO₂ fluxes showed an increase in net deposition from November 2001 towards the peak of the rain season in January 2002 (Fig. 3a–e), and a subsequent change to emission due to dominance of respiration (Fig. 3f–k). One-minute records of BSC-related CO₂ deposition peaked in January with $-2.15 \mu\text{mol m}^{-2} \text{s}^{-1}$. Maximum 10-min mean CO₂ deposition was -0.17 , -1.71 , and $-0.11 \mu\text{mol m}^{-2} \text{s}^{-1}$ in November, January, and April, respectively (Fig. 3a, e, i). Based on gap filled data, mean CO₂ net deposition with active BSC during daytimes were $0.38 \text{ mmol m}^{-2} \text{ h}^{-1}$ and $3.82 \text{ mmol m}^{-2} \text{ h}^{-1}$ in December and January, respectively (Table 1, 15 h/length of time (L.o.t.)).

Only emission fluxes were measured after January (Table 1). BSC-related CO₂ emission during daytime reached $0.13 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in November and $0.27 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in January, higher emission rates of 1.01, 0.39, and $0.64 \mu\text{mol m}^{-2} \text{ s}^{-1}$ from BSC were observed following low moisture supply under increasing temperatures in February, March and April, respectively (Fig. 3f, h, i). From February to May, the photoautotrophic surfaces of the BSC (mosses, lichens, cyanobacteria) were mostly dry. Periods with low emission from superficially dry BSC indicated increased sub-surface microbial respiration within the BSC samples as compared to the soil plots.

Night CO₂ emission from well-hydrated BSC in January was 0.05 – $0.2 \mu\text{mol m}^{-2} \text{ s}^{-1}$ at air temperatures inside the enclosure (T_{sa}) $< 5^\circ\text{C}$ (Fig. 3c, d), it reached up to $0.45 \mu\text{mol m}^{-2} \text{ s}^{-1}$ when T_{sa} was $> 5^\circ\text{C}$ (Fig. 3e). T_{sa} below 5°C corresponded to soil surface temperatures (T_{soil}) between -0.5 and -3.4°C . Mean emission due to dark respiration of BSC was $0.09 \text{ mmol m}^{-2} \text{ h}^{-1}$, $0.35 \text{ mmol m}^{-2} \text{ h}^{-1}$, and $0.21 \text{ mmol m}^{-2} \text{ h}^{-1}$ in December, January, and February, respectively (Table 1, 15 h/length of time). Night respiratory emissions were equal to 11–123% of the daily BSC-related net CO₂ deposition (November–January). Both the total day and the night time emission fluxes decreased after the measurements in March.

Day- and night time emission fluxes reduced the total BSC-related CO₂ deposition of $-82.3 \text{ mmol m}^{-2}$ by 44% and 25%, respectively, which resulted in a net deposition of $-26.1 \text{ mmol m}^{-2}$ per 300 h or a net flux of $-0.09 \text{ mmol m}^{-2} \text{ h}^{-1}$ (Table 1). In our approach to gap fill the most consistent data set, three hours of lower daytime fluxes were not reflected. Night respiratory emission reduced BSC-related deposition fluxes by 50%, if the same emission was assumed for the preceding six hours of the nights (18:00–24:00). These corrections and the 60% BSC cover reduced the net deposition by BSC for the 20 days of measurements to -3.3 mmol m^{-2} .

3.2 Light and temperature control on fluxes

CO₂ fluxes with hydrated BSC were controlled by light and temperature. The CO₂ exchange of activated BSC reached the light compensation at PAR values of 35 – $40 \mu\text{mol m}^{-2} \text{ s}^{-1}$ at T_{sa} 1 – 5°C , and 55 – $60 \mu\text{mol m}^{-2} \text{ s}^{-1}$ at T_{sa} 10 – 15°C . Minor changes in light intensity were only effective under low temperature conditions, whereas larger changes in light intensity were required to significantly change the BSC-related CO₂ fluxes under higher temperatures conditions, which usually started prevailing after mid morning hours. Average CO₂ deposition fluxes per $100 \mu\text{mol m}^{-2} \text{ s}^{-1}$ PAR were calculated to be $-0.20 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ($r^2=0.95$) and $-0.24 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ($r^2=0.9$) for T_{sa} of 1 – 5°C and 10 – 15°C , respectively. Temperature-related maximum CO₂ deposition was derived from regressions including at least four of the highest

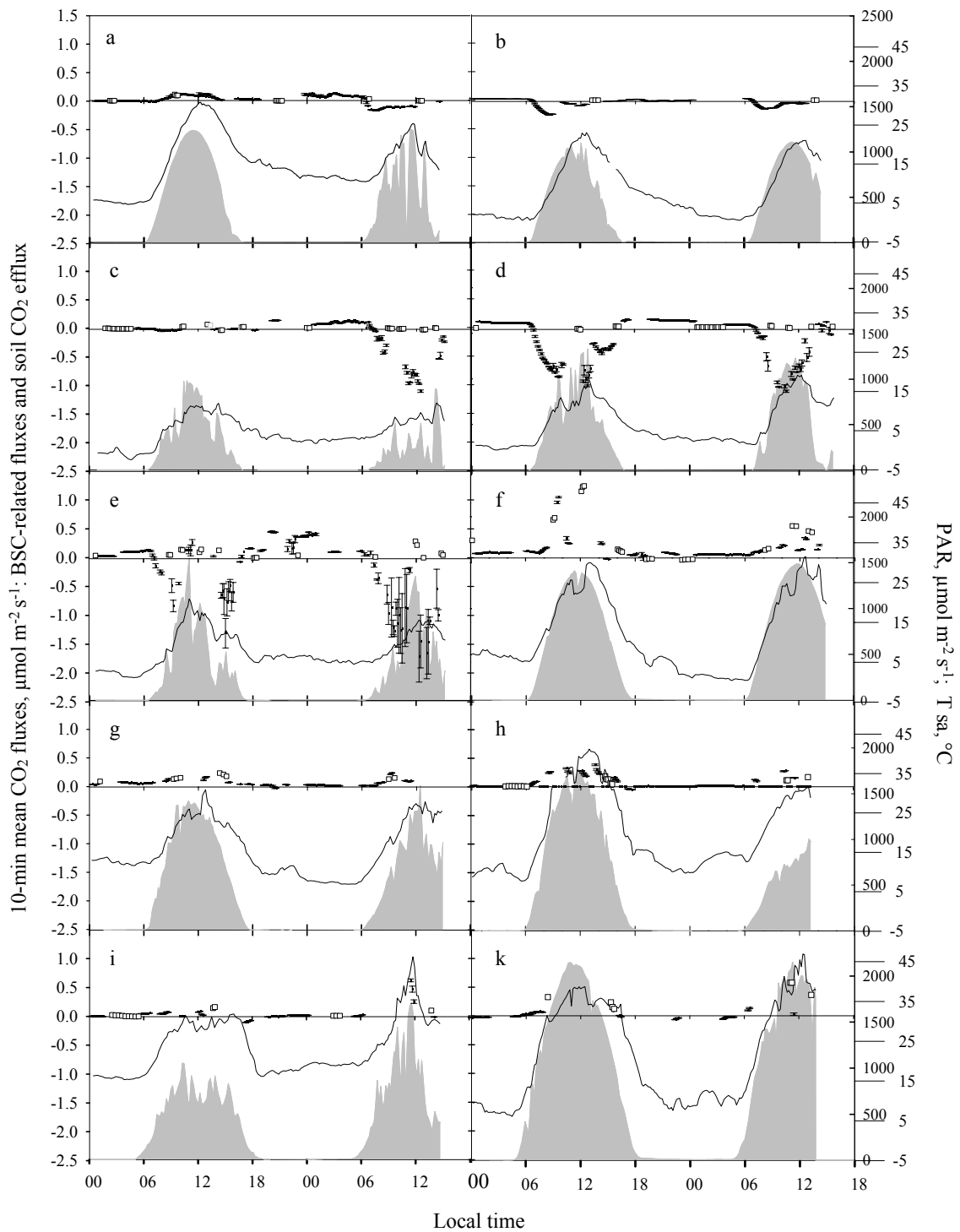


Fig. 3. a-k BSC-related net CO₂ flux ($\mu\text{mol m}^{-2} \text{s}^{-1}$, 10-min mean bars +90 confidence, emission positive), soil CO₂ efflux (\square , 10-min mean), photosynthetically active radiation (PAR, grey) and air temperature in the enclosure (T_{sa} , thin line) during 10 field campaigns including two consecutive days from beginning to end of the wet season 2001/2002 at LTER-SSK: (a) 21–22 November, (b) 17–18 December, (c) 7–8 January, (d) 14–15 January, (e) 20–21 January, (f) 18–19 February, (g) 24–25 February, (h) 18–19 March, (i) 15–16 April, (k) 6–7 May.

Table 1. BSC-related CO₂ fluxes, soil CO₂ efflux, and concurrent moisture and temperature conditions during 20 days from November 2001 to May 2002.

Date d/m/y	Conditions			Mean T_{soil}		BSC L.o.t. ¹			BSC Flux 15 h ⁻¹			total mmol m ⁻²	Gap fill %	Soil 15 h ⁻¹ total mmol m ⁻²	BSC ⁶⁰ 24 h ⁻¹ mmol m ⁻²	Soil 24 h ⁻¹ mmol m ⁻²
	Water Source type	PPT mm	SWC mg g ⁻¹	● °C	☉ °C	☉↓ h	☉↑ h	●↑ h	☉↓ mmol m ⁻²	☉↑ mmol m ⁻²	●↑ mmol m ⁻²					
21/11/01	sm	–	nd	0.6	15.1	3.0	6.2	4.2	–0.04	2.18	0.06	2.20	11	3.0	1.39	4.8
22/11/01	r	2.6	nd	7.9	11.7	5.2	–	5.8	–1.83	–	2.26	0.43	15	0.5	1.71	0.8
17/12/01	d (grass)	nd	nd	–3.3	7.7	6.2	–	5.7	–2.78	–	0.53	–2.25	22	1.1	–1.00	1.76
18/12/01	d (grass)	nd	nd	–3.3	6.5	6.8	–	nd	–2.20	–	0.53	–1.67	49	1.0	–0.68	1.60
7/01/02	sm	–	58	–2.4	4.4	2.8	–	–	–0.33	–	0.00	–0.33	60	1.1	–0.20	1.76
8/01/02	r drizzle	2.7	nd	–0.5	4.5	7.0	–	6.2	–16.06	–	2.24	–13.82	30	0.4	–7.03	0.64
14/01/02	d	0.5	102	–3.4	4.3	7.0	–	6.8	–18.17	–	2.01	–16.16	19	0.6	–8.77	0.96
15/01/02	d	0.5	98	–0.8	6.7	5.3	–	6.0	–12.92	–	1.61	–11.31	37	0.6	–5.82	0.96
20/01/02	f	nd	64	–2.6	0.5	2.6	↓	6.5	–3.44	↓	1.74	↓	↓	↓	–0.14	–
20/01/02	r	nd	nd	↑	6.4	1.0	2.8	↑	–3.56	1.87	↑	–3.38	33	3.5	–1.01	5.28
21/01/02	r	4	141	0.7	5.4	6.8	–	6.2	–20.97	–	3.41	–17.56	17	4.6	–8.62	6.60
Nov–Jan									–82.3	4.1	14.4	–63.9		16.4	–30.2	25.2
18/02/02	d	nd	61	3.5	13.7	–	5.7	5.8	–	7.75	1.97	9.72	42	23.5	7.10	29.28
19/02/02	d	nd	40	–1.8	14.4	–	8.2	5.3	–	5.01	1.18	6.19	37	10.5	4.61	13.68
24/02/02	sm	–	26	8.9	18.5	–	7.5	5.7	–	3.18	1.13	4.31	39	5.2	3.34	7.32
25/02/02	sm	–	28	4.6	17.5	–	7.8	5.2	–	1.70	0.43	2.13	33	5.0	1.62	7.08
18/03/02	r	0.1	24	9.8	28.9	–	8.0	5.5	–	7.10	0.47	7.57	63	2.7	4.88	4.32
19/03/02	–	–	19	12.4	23.7	–	7.2	4.8	–	4.71	0.44	5.15	60	4.1	3.49	6.00
15/04/02	–	–	14	9.0	18.6	–	8.0	5.2	–	1.31	0.25	1.56	63	2.9	1.13	4.56
16/04/02	(r)	<0.1	15	9.9	25.5	–	0.5	5.5	–	0.51	0.02	0.53	72	4.2	0.33	6.12
6/05/02	sm	–	12	5.8	34.3	–	2.0	4.7	–	0.38	0.02	0.41	66	8.1	0.26	10.8
7/05/02	–	–	nd	8.6	33.7	–	0.5	–	–	0.18	0.00	0.18	79	9.7	0.11	12.72
Feb–May									0	31.8	5.9	37.8		75.9	26.9	101.9
Total flux	300 h, based on 15 h per day								–82.3	35.9	20.3	–26.1		92.3	–3.3	127.1

Fluxes gap-filled 00:00–15:00 h; and calculated to 24 h⁻¹; ¹L.o.t. length of time (h) including >90% of the flux; ●/☉ day/night; ↓/↑ deposition/emission; BSC⁶⁰ calculated to 60% cover; SWC upper 3 cm at 08:30–09:00 h; d f r sm dew fog rain soil moisture; d (grass) dew formed on grass; n.d. not determined.

deposition rates with optimally hydrated BSC, such as given immediately after precipitation and between decreased CO₂ uptake owing to water suprasaturation and due to dry out (e.g., 17 December 2001, 8 and 20 January 2002). Maximum CO₂ deposition at T_{sa} 5°C, 10°C, and 18°C (each ±0.5°C) were –0.67, –0.26, and –0.08 μmol m⁻² s⁻¹ per 100 μmol m⁻² s⁻¹ PAR, respectively (Fig. 4). From non-gap-filled data, more than 90% of the BSC-related CO₂ deposition occurred at air temperatures below 15°C, where it reached the maximum. The data at 15°C showed an unrealistic correlation with light as they derived from a period (21 January 2002) when the gas exchange was hampered by fluctuating light conditions and partial water suprasaturation. Light conditions changed up to 920 μmol m⁻² s⁻¹ PAR per 10 min and frequent rains led repeatedly to water films on BSC surfaces, which caused large changes in CO₂ fluxes within the averaging periods (Fig. 3e).

On the other hand, changing cloud cover and the associated light fluctuation resulted in lower temperatures and delayed desiccation of BSC during days without repeated moisture supply. Under such conditions, BSC maintained photosynthesis for seven hours, although they were only activated by dew in the morning (Fig. 3d: 14 January 2002, Table 1).

Overall, BSC-related CO₂ fluxes correlated better with light than with temperature if they resulted from higher amounts of PPT (0.5, 1, 2 mm); it was vice versa for fluxes that resulted from the lowest moisture supply (PPT=0.1 mm) (Fig. 5a, b). Correlation with PPT=1 mm was weak due to two periods when BSC were probably subjected to stronger desiccation and related fluxes would have fit better in the PPT category 0.5-mm.

3.3 CO₂ flux pattern relative to moisture supply

The CO₂ flux from BSC samples and soil plots was the same under dry conditions (10-min mean difference ≤0.01 μmol m⁻² s⁻¹), which indicated that BSC were inactive and did not contribute to the flux (e.g., Fig. 3c, 7 January 2002). Net CO₂ fluxes with BSC were measured upon water supply from rain (six days), dew (six days), soil moisture (five days), and fog (20 January 2002, fog in the morning and rain after noon). Potential effects of the type of moisture supply on the magnitude of daily BSC-related CO₂ deposition were evaluated using gap filled fluxes for the period 00:00 to 15:00 h, which encompassed the daily hours consistently including the maximum share of measured data (Table 1). We found that rain and dew can result in similar time periods of BSC activity maintaining significant CO₂

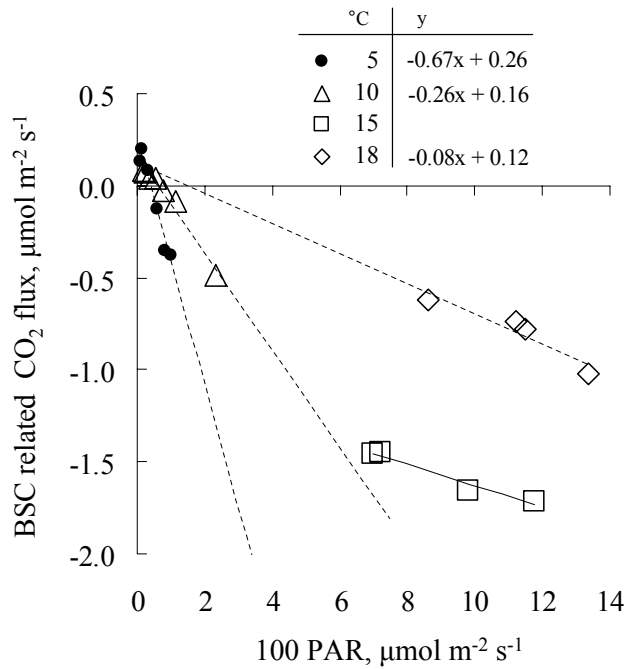


Fig. 4. Temperature-related maximum CO₂ deposition with BSC. Regressions based on at least the four highest deposition rates (10-min mean) to well hydrated BSC, i.e., after precipitation and between decreased uptake owing to water supersaturation and due to desiccation. Regression for 15°C was omitted as the data showed an unrealistic correlation with light (explanation see text).

deposition. BSC-related CO₂ flux yielded the largest and third largest 15-h total with recurrent rain events (21 January 2002: $-17.56 \text{ mmol m}^{-2}$) and frequently recurring drizzle (8 January 2002: $-13.82 \text{ mmol m}^{-2}$) respectively. Similarly, the second ($-16.16 \text{ mmol m}^{-2}$) and fourth largest ($-11.31 \text{ mmol m}^{-2}$) 15-h total CO₂ deposition were obtained from days where BSC activity was supplied only by massive dew in the morning (14 and 15 January 2002).

CO₂ deposition after 2.6 mm PPT was low in the beginning (22 November 2001) as compared with daily deposition rates following on less precipitation at later times of the rainy season. Erratic rain with PPT < 0.1 mm at the end of the rainy season resulted even in a 30-min emission burst, although it affected only minor parts of the sample (Fig. 3i, 16 April 2002).

While the type of moisture supply per se was less indicative for the magnitude of BSC-related CO₂ deposition, formation of massive dew was only observed subsequent to repeated rain events when soil moisture was high and VPD was low. For example, despite similar low mean T_{soil} of -3.4 and -2.4 °C during the preceding nights, massive dew formed on 14 January 2002 with daily recurring precipitation during the six preceding days (total PPT 16 mm), but not on 7 January 2002 with no precipitation during the preceding three days, respectively. Increased SWC (Fig. 2) also delayed the

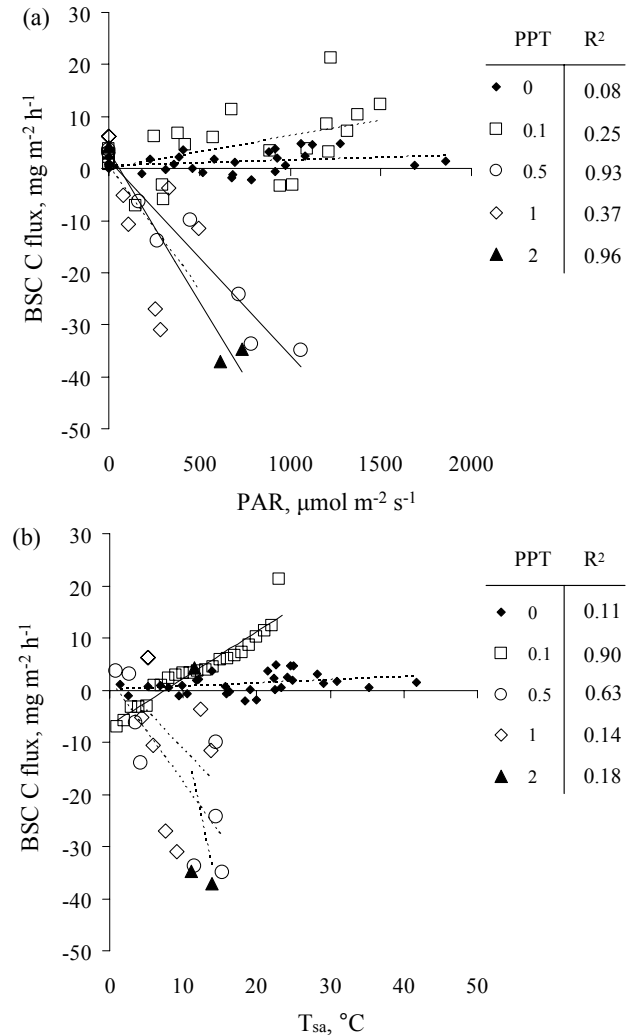


Fig. 5. Correlation of BSC-related CO₂ fluxes with (a) light and (b) temperature separated into categories of PPT received (mm).

desiccation of BSC (Fig. 3d, Table 1: 14–15 January 2002), but low SWC as single water source resulted only in CO₂ emission (Fig. 3g, 24–25 February 2002).

Before the peak of the rain season, when soil moisture was still low (December 2001), we observed dew formation on dry grass blades from the last vegetation season, on outcropping stones, and in two of the sample collars. Droplets trickled down from grass blades and wetted surrounding BSC, while large patches of BSC surfaces without standing grass matter were visually dry. BSC-related CO₂ deposition during the two days 17–18 December 2001 reached 10–13% of the highest 15-h flux total, but less than an estimated 25% of the BSC surfaces were affected by this type of moisture supply.

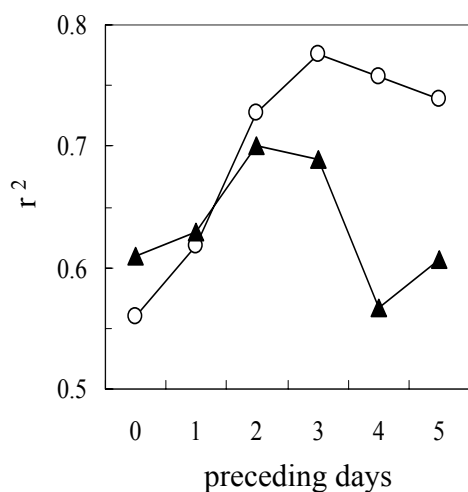


Fig. 6. Correlation coefficients between daily BSC-related CO₂ deposition (15 h) and amount (Δ)/frequency (O) of PPT for the same day (0) and the preceding 5 days.

We tested a potential effect of soil moisture on the photosynthetic uptake of BSC and found a significant influence of the short-term history of moisture on BSC-related CO₂ fluxes. CO₂ fluxes were correlated with both the amount of PPT and its frequency based on PPT records in 15-min intervals (Fig. 6). Maximum correlation between daily BSC-related CO₂ fluxes and PPT frequency was found for the period, which reflected the preceding three days ($r^2=0.78$). The correlation with the amount of PPT was similar reflecting the last two ($r^2=0.70$) and three days ($r^2=0.69$).

We also tested the predictability of BSC-related CO₂ deposition based on moisture-related parameters that were provided from the nearby LTER weather station. Three 3-hour day periods of CO₂ fluxes (07:00–10:00, 10:00–13:00, 13:00–16:00) were correlated with concurrent amounts of PPT, averages of relative air humidity (rh), VPD and soil moisture at 50 mm. CO₂ deposition did not correlate well with distinct amounts of PPT. VPD lower than 10% encompassed 90% of the CO₂ deposition and 70% of the mean emission fluxes were associated with VPD higher than 10% (Fig. 7a). About 75% of the significant CO₂ deposition with BSC was associated with SWC higher than 0.18% (Fig. 7b).

3.4 Soil CO₂ efflux

Soil CO₂ emissions were mostly lower than $0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ or insignificant from November to January. Ten-minute mean soil CO₂ efflux reached up to 0.12, 0.28, 1.24, and $0.58 \mu\text{mol m}^{-2} \text{s}^{-1}$ in November, January, February and May, respectively. Night time efflux from the soil was to >95% below $0.05 \mu\text{mol m}^{-2} \text{s}^{-1}$ and within the noise level of the measurements. Soil CO₂ efflux increased with SWC and temperature if we compared

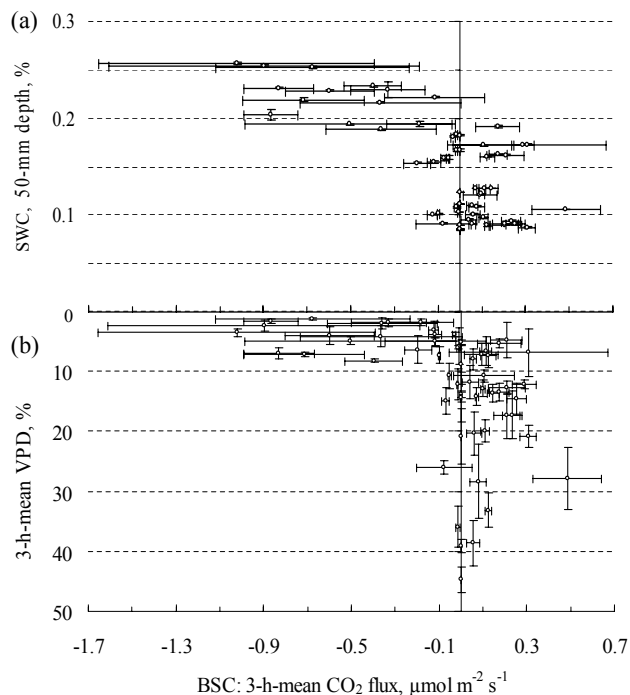


Fig. 7. BSC-related net CO₂ fluxes ($\mu\text{mol m}^{-2} \text{s}^{-1}$) versus VPD (%) and SWC at the 50-mm level (%). Values represent 3-h means \pm SD of three daytime periods (07:00–10:00, 10:00–13:00, 13:00–16:00) for fluxes, VPD, and SWC. VPD <10% and >10%, was related with 90% of net deposition and 70% of net emission, respectively. Almost 75% of net deposition was related with SWC >0.18%.

individual days before and after the peak of the rain season. For instance, the difference in daytime mean T_{soil} was only 1.4°C (Table 1) but SWC was significantly higher and maximum soil CO₂ efflux was $1.12 \mu\text{mol m}^{-2} \text{s}^{-1}$ higher on 21 November 2001 than on 18 February 2002 (Figs. 2 and 3a, f). Vice versa, soil moisture had returned to the same low level in May as it was in November, but daytime mean T_{soil} was 19.2°C higher and maximum soil CO₂ efflux was $0.46 \mu\text{mol m}^{-2} \text{s}^{-1}$ higher on 6 May 2002 (Fig. 3k). Soil CO₂ efflux increased continually with temperature at lowest SWC but did not follow temperature at SWC $60\text{--}120 \text{ mg g}^{-1}$, and the emission decreased with increasing temperature at the highest SWC (Fig. 8). The irregular pattern at higher SWC can be explained by changing moisture gradients and different parts of the soil column contributing to the fluxes. Individual flux data could have also been influenced by gas dilution in or gas displacement by infiltrating water. Note that data were not available and values set to zero for T-SWC pairs 0:120, 20:90, 20:120, and 40:150.

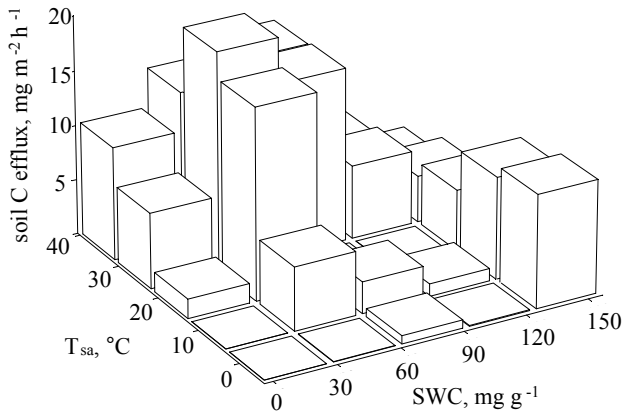


Fig. 8. Soil CO₂ effluxes (in mg C) based on air temperature in the sample enclosure (T_{sa}) and gravimetric soil water contents (SWC) from soil samples at the site.

Total CO₂ efflux from the soil was calculated to 92.3 mmol m⁻² for 300 h of measurement (Table 1). Based on 60% BSC cover, about 38% of the emission from the soil was compensated by the surplus of BSC-related net deposition. However, compensation of soil CO₂ efflux changed significantly, if we include estimates of the remaining BSC night respiration (see above) as well as 24-h soil efflux (November–January: mean flux h⁻¹* 24 h; February–May: mean flux h⁻¹* 18 h plus 6 h base emission of 0.05 μmol m⁻² s⁻¹). While BSC compensated 120%, they added 26% and compensated only 2.6% of/to the soil efflux within the periods November–January, February–May, and November–May, respectively.

4 Discussion

4.1 BSC-related CO₂ fluxes and soil efflux

We studied the in situ CO₂ exchange of soil-dwelling mixed BSC and compared it with CO₂ fluxes from the soil in a typical semiarid grass-shrubland. BSC-related net deposition compensated only 2.6% of the concurrent soil CO₂ efflux during the sum of measurement periods. However, the soil-dwelling BSC represented a significant CO₂ sink during the period of increased precipitation frequency (here December–January), which typically includes the annual low for the growth of vascular vegetation in the region. Thus, the peak of BSC-related CO₂ flux underlined the complementary character of BSC growth in grass- and shrub dominated ecosystems.

BSC-related CO₂ deposition rates were comparable to values reported in a previous laboratory study. BSC of similar composition from LTER Sayeret Shaked yielded a maximum CO₂ deposition of $-1.6 \mu\text{mol m}^{-2} \text{s}^{-1}$ after three days of regular water supply (samples “North up”, PAR 500 μmol m⁻² s⁻¹, T_{sa} 22°C) (Zaady et al., 2000). We mea-

sured $-1.44 \mu\text{mol m}^{-2} \text{s}^{-1}$ (10-min mean) under similar light but lower temperature conditions two hours after 0.2 mm PPT during the peak of the rain season (20 January 2002, T_{sa} 13°C, PAR 540 μmol m⁻² s⁻¹). The difference of 9°C under which the fluxes were measured indicated a lower temperature adaptation of BSC in the field than in the laboratory. A lower temperature optimum is plausible with respect to the minor relevance of CO₂ uptake at $T_{sa} > 15^\circ\text{C}$, which contributed <10% to the BSC-related deposition in the field.

A seasonal temperature adaptation of dark respiration, as observed with soil crust lichens under temperate conditions (Lange and Green, 2005) is probably of less importance for BSC under semiarid climates. BSC showed the highest rates of nocturnal respiration from January until mid-February under the regime of low temperatures but sufficient to moderate moisture supply. Lower emissions during other months and warmer nights occurred under much lower moisture conditions.

Similarly, it seems difficult to extrapolate CO₂ deposition of mixed BSC based on their components, particularly if such calculations refer to concurrent optima of light, temperature and hydration, which cannot play a significant role for BSC-related CO₂ deposition in the field. For instance, maximum net CO₂ deposition to BSC dominated by *Collema tenax* and *Microcoleus sp.* were -5.3 and $-0.187 \mu\text{mol m}^{-2} \text{s}^{-1}$ under laboratory conditions, respectively (Jeffries et al., 1993; Lange et al., 1998). In this study, BSC consisted of cyanobacteria (*Microcoleus*), lichens (*Collema*), and mosses in similar contributions, and the highest 10-min mean CO₂ deposition was $-1.71 \mu\text{mol m}^{-2} \text{s}^{-1}$ with individual values during the same interval reaching up to $2.15 \mu\text{mol m}^{-2} \text{s}^{-1}$. Thus, the maximum CO₂ deposition fluxes were lower as expected from a lichen-cyanobacteria composition, and even higher deposition fluxes were expected regarding the moss contribution in the samples.

Consistent with a study of Maestre and Cortina (2003), we found significant emissions from the semiarid soil under regimes of low moisture supply coupled with higher soil temperatures. In spite of different temperature amplitudes, the bulk of CO₂ effluxes were similar between the soil in SE Spain (ca. $<0.0\text{--}0.58 \mu\text{mol m}^{-2} \text{s}^{-1}$, including mean +SE) (Maestre and Cortina, 2003) and in Sayeret Shaked ($0.15\text{--}0.58 \mu\text{mol m}^{-2} \text{s}^{-1}$). Similarly consistent, soil CO₂ effluxes showed a clipping of the upper half of the previous flux range ($0.33\text{--}0.43 \mu\text{mol m}^{-2} \text{s}^{-1}$) in a Mediterranean savanna ecosystem in California during the dry season (Tang et al., 2003). The slightly broader range of soil CO₂ efflux in the present study is explained by larger changes in conditions from the cold and wet to the hot and dry season.

4.2 Water availability

The measurements were successful to record BSC-related CO₂ fluxes in relation to different frequencies, quantities and types of moisture supply (rain, dew, fog), which play a major

role for soil-dwelling BSC in semiarid areas (Lange, 2001; Kappen et al., 1980). BSC-related CO₂ deposition showed better correlation with total PPT including the preceding two and three days than with the amount of PPT per day or individual precipitation event. We interpret this result as an effect of SWC on BSC hydration, which implies principal differences to strictly pulse-dependent systems (Cable and Huxman, 2004). Wet soil obviously delayed BSC desiccation and facilitated increased dew formation. Higher SWC from frequent rain events may provide also conditions for another type of water recycling (from soil upward) to support BSC photosynthesis. Yamanaka and Yonetani (1999) demonstrated that water vapour transport and condensation occurs in sandy loams depending on temperature gradients between soil layers. It seems most plausible that during nights condensation also occurs at soil-attached BSC. A control of evaporation by BSC intercepting water vapour is supported by the recent finding that BSC have retarding effects on evaporation under a low rainfall regime (Zhang et al., 2008).

A better correlation of BSC-related CO₂ deposition with frequency of PPT than with individual amounts ensues also from the upper limit of PPT that can be reclaimed for BSC-activity. For instance, 9.4 of 10 mm recorded for the period 18 February–14 March fall within 30 min (26 February 2002). The benefits for vascular plants and BSC must be low from such rains as extremely high PPT results in a larger runoff fraction (Zaady et al., 2001).

Short-term respiratory CO₂ emission from BSC can be expected on rewetting after long dry periods (Lange et al., 1992), and BSC are particularly vulnerable to higher PPT frequency during hot and dry periods due to the lack of protective pigment production (Belnap et al., 2004). We observed one emission burst in April 2002. The emitted CO₂ quantum was low but so was the inducing amount of PPT, which was not recorded by the nearby weather station. However, the frequency and overall importance of such events is most probably low under the present climate.

The first observed rewetting by rainfall in November did not initiate an emission burst but BSC switched over to CO₂ uptake immediately. Adaptation of BSC owing to a pre-activation phase that results in a gradual recovery from “summer dormancy” may reduce losses due to respiratory bursts. This hypothesis of a “hold position” is supported by the seasonal development of the BSC’s spectral reflectance properties (Burgheimer et al., 2006a). While there were only two major rain events prior to the experiments, earlier reports point to abundant events of dew preceding the rainy season in the northern Negev desert (Zangvil, 1996). New techniques revealed that only vapour adsorption by soil surfaces is a common phenomenon, whereas actual formation of dew on the soil is rare in the plains of the northern Negev (Agam and Berliner, 2003). Dew formation occurred more often on plant matter. We observed that dew runoff from grass matter standing beyond the life cycle may represent an

alternative water source for soil-dwelling BSC in semiarid grasslands in the early winter season prior to an increased frequency of rain.

Finally, as continuous measurements of BSC are difficult (Lange et al., 1997), it would be helpful to model the bulk of BSC related CO₂ deposition by standard climate parameters. Among four parameters tested (PPT, rh, SWC, VPD) VPD was the most promising single parameter, which might serve as a surrogate of the BSC activity-/temperature relation to roughly assess BSC-related CO₂ fluxes.

4.3 Uncertainties and representativeness

Enclosure measurements may overestimate poikilohydric activity due to conservation of moisture. Minimizing the enclosure period can reduce such effects (Lange et al., 1997). Enclosure rotation was limited by manual operations and requirements to obtain statistically valid means. With sufficient water to keep surrounding BSC moist until late morning or noon, measurements overestimated periods of net CO₂ deposition by up to 20 min.

Only 7% of the annual PPT occurred outside of the campaign period. As BSC require water to activate their gas exchange (Lange, 2001), their contributions to CO₂ fluxes can be assumed to be low or insignificant for most of the time of the dry season (in this study May–September) (Belnap et al., 2004). As a result of scheduling field campaigns according to weather forecast, the frequency of rain events was slightly overrepresented in our measurements (0.30) as compared with the campaign season (0.23). More measurements in January were retrospectively justified because the month received 42% of the annual PPT. The conjunction of rain frequency and conditions delaying BSC desiccation (e.g., low solar radiation and VPD) suggest that CO₂ deposition occurred during two third of the days in January. At the same time, the area was still free from grasses, and BSC were not deprived of light even at low elevation of the sun. Thus, the observed peak of CO₂ deposition due to BSC photosynthesis was consistent with environmental conditions, and we have reason to assume that our results reflect a representative profile of seasonal BSC-related CO₂ fluxes.

5 Conclusions

While BSC yield net CO₂ deposition upon any type of moisture supply, low moisture supply resulting in short periods of low uptake rates can hardly compensate for respiratory CO₂ emission. Higher frequencies of rains during the winter displayed important synergisms for CO₂ deposition fluxes and the growth of the widespread type of mixed BSC in semiarid grass-shrub steppe ecosystems. It is proposed that water/soil interactions can account for most of the positive effects following increased precipitation during the cold season. These effects include increased dew formation, delayed

desiccation, and potentially immediate condensation of evaporative water at BSC. These features, related to the soil's capacity for water redistribution, further corroborate that fewer precipitation events of higher intensity, as expected from climate change, would be not of advantage for the growth of mixed BSC. With respect to instantaneous CO₂ fluxes, the loess soil in the semiarid environment represents a source for CO₂, which is triggered by moisture and its rate influenced by temperature. Disturbances in semiarid ecosystems that inhibit BSC growth will increase the net CO₂ efflux particularly during the low periods of vascular plant growth. Finally, a reliable assessment of BSC-related annual CO₂ deposition seems only possible if based on a comprehensive consideration of the different water sources, including their frequency and amounts, for several years.

Acknowledgements. This study was supported by a fellowship of the Minerva Society to B. W. We gratefully acknowledge the financial support by the Max Planck Society. We are much obliged to the Mitrani Department of Desert Ecology, Ben-Gurion University of the Negev, Sde Boker Campus, for providing an excellent base for all aspects of the extensive fieldwork. We thank Kadmiel Maseyk for his permanent readiness for discussions.

Edited by: T. Laurila



The publication of this article is financed by the Max Planck Society.

MAX-PLANCK-GESellschaft

References

- Agam, N. and Berliner, P. R.: Diurnal water content changes in the bare soil of a coastal desert, *J. Hydrometeorol. Am. Met. Soc.*, 5, 933–933, 2004.
- Belnap, J., Phillips, S. L., and Miller, M. E.: Response of desert biological soil crusts to alterations in precipitation frequency, *Oecologia*, 141, 306–316, 2004.
- Belnap, J., Buedel, B., and Lange, O. L.: *Biological Soil Crusts: Characteristics and Distribution*, in: *Biological Soil Crusts: Structure, Function, and Management*, edited by: Belnap, J. and Lange, O. L., 3–30, Springer, New York, 2001.
- Beymer, R. J. and Klopatek, J. M.: Potential contribution of carbon by microphytic crusts in pinyon-juniper woodlands, *Arid Soil Res Rehabil.*, 5, 187–198, 1991.
- Birkeland, P. W.: *Soils and Geomorphology*, 3rd edition, Oxford University Press, New York, 430 pp., 1999.
- Burgheimer, J., Wilske, B., Maseyk, K., Karnieli, A., Zaady, E., Yakir, D., and Kesselmeier, J.: Ground and space spectral measurements for assessing semi-arid ecosystem phenology related to CO₂ fluxes of biological soil crusts, *Rem. Sens. Environ.*, 101, 1–12, 2006a.
- Burgheimer, J., Wilske, B., Maseyk, K., Karnieli, A., Zaady, E., Yakir, D., and Kesselmeier, J.: Relationships between Normalized Difference Vegetation Index (NDVI) and carbon fluxes of biological soil crusts assessed by ground measurements, *J. Arid Environ.*, 64, 651–669, 2006b.
- Cable, J. M. and Huxman, T. E.: Precipitation pulse size effects on Sonoran Desert soil microbial crusts, *Oecologia*, 141, 317–324, 2004.
- Evenari, M.: Ecology of the Negev Desert, a critical review of our knowledge, in: *Developments in Arid Zone Ecology and Environmental Quality*, edited by: Shuval, H., 1–33, Balaban, Philadelphia, 1981.
- Housman, D. C., Powers, H. H., Collins, A. D., and Belnap, J.: Carbon and nitrogen fixation differ between successional stages of biological soil crusts in the Colorado Plateau and Chihuahuan Desert, *J. Arid Environ.*, 66, 620–634, 2006.
- Jeffries, D. L., Link, S. O., and Klopatek, J. M.: CO₂ fluxes of cryptogamic crusts, I. Response to resaturation, *New Phytol.*, 125, 163–173, 1993.
- Kappen, L., Lange, O. L., Schulze, E. D., Buschbom, U., and Evenari, M.: Ecophysiological investigations on lichens of the Negev Desert, VII, The influence of habitat exposure on dew imbibition and photosynthetic productivity, *Flora*, 169, 216–229, 1980.
- Karnieli, A., Kokaly, R. F., West, N. E., and Clark, R. N.: Remote sensing of biological soil crusts, in: *Biological Soil Crusts: Structure, Function, and Management*, edited by: Belnap, J. and Lange, O. L., 431–455, Springer, New York, 2001.
- Karnieli, A., Kidron, G. J., Glaesser, C., and Ben-Dor, E.: Spectral characteristics of Cyanobacteria soil crust in semiarid environment, *Rem. Sens. Environ.*, 69, 67–75, 1999.
- Karnieli, A., Shachak, M., and Tsoar, H.: The effect of microphytes on the spectral reflectance of vegetation in semiarid regions, *Rem. Sens. Environ.*, 57, 88–96, 1996.
- Karnieli, A. and Tsoar, H.: Spectral reflectance of biogenic crust developed on desert dune sand along the Israel-Egypt border, *Int. J. Rem. Sens.*, 16, 369–374, 1995.
- Kidron, J. G.: Analysis of dew precipitation in three habitats within a small arid drainage basin, Negev Highlands, Israel. *Atmos. Res.*, 55, 257–270, 2000.
- Kidron, J. G.: Altitude dependent dew and fog in the Negev Desert, Israel, *Agric. For. Meteorol.*, 96, 1–8, 1999.
- Kidron, J. G., Herrnstadt, I., and Barzilay, E.: The role of dew as a moisture source for sand microbiotic crusts in the Negev Desert, Israel. *J. Arid Environ.*, 52, 517–533, 2002.
- Lange, O. L. and Green, T. G. A.: Lichens show that fungi can acclimate their respiration to seasonal changes in temperature, *Oecologia*, 142, 11–19, 2005.
- Lange, O. L.: Photosynthesis of soil-crust biota as dependent on environmental factors, in: *Biological Soil Crusts: Structure, Function, and Management*, edited by: Belnap, J. and Lange, O. L., 217–241, Springer, New York, 2001.
- Lange, O. L., Belnap, J., and Reichenberger, H.: Photosynthesis of the cyanobacterial soil-crust lichen *Collema tenax* from arid lands in southern Utah, USA: role of water content on light and temperature responses of CO₂ exchange, *Funct. Ecol.*, 12, 195–202, 1998.
- Lange, O. L., Reichenberger, H., and Walz, H.: Continuous monitoring of CO₂ exchange of lichens in the field: Short-term enclosure with an automatically operating cuvette, *Lichenologist*, 29, 259–274, 1997.
- Lange, O. L., Meyer, A., Zellner, H., and Heber, U.: Photosynthesis and water relations of lichen soil crust: field measurements in the

- coastal fog zone of the Namib desert, *Funct. Ecol.*, 8, 253–264, 1994.
- Lange, O. L., Kidron, G. J., Büdel, B., Meyer, A., Kilian, E., and Abeliovich, A.: Taxonomic composition and photosynthetic characteristics of the “biological soil crusts” covering the sand dunes in the western Negev Desert, *Funct. Ecol.*, 6, 519–527, 1992.
- Lange, O. L., Schulze, E. D., and Koch, W.: Ecophysiological investigations on lichens of the Negev desert, III. CO₂ gas exchange and water relations of crustose and foliose lichens in their natural habitat during the summer dry period, *Flora*, 159, 525–528, 1970.
- Levi, Y., Berner, T., and Cohen, Y.: CO₂ exchange of loess soil crust algae in the Negev desert of Israel, in: *Developments in Arid Zone Ecology and Environmental Quality*, edited by: Shuval, H., 43–48, Balaban, Philadelphia, 1981.
- Maestre, F. T. and Cortina, J.: Small-scale spatial variation in soil CO₂ efflux in a Mediterranean semiarid steppe, *Appl. Soil Ecol.*, 23, 199–209, 2003.
- Palmer, Jr. R. J. and Friedmann, E. I.: Water relations, thallus structure and photosynthesis in Negev desert lichens, *New Phytol.*, 116, 597–603, 1990.
- San José, J. J. and Bravo, C. R.: CO₂ exchange in soil algal crusts occurring in the *Trachypogon* savannas of the Orinoco Llanos, Venezuela, *Plant Soil*, 135, 233–244, 1991.
- Shachak, M., Sachs, M., and Moshe, I.: Ecosystem management of desertified shrublands in Israel, *Ecosystems*, 1, 475–483, 1998.
- Tang, J., Baldocchi, D. D., Qi, Y., and Xu, L.: Assessing soil CO₂ efflux using continuous measurements of CO₂ profiles in soils with small solid-state sensors, *Agric. For. Meteorol.*, 118, 207–220, 2003.
- TEMS (Terrestrial Ecosystem Monitoring Sites), in: *Global Terrestrial Observing System (GTMOs)*, www.fao.org/gtos/tems, last access: 15 October 2008.
- Veste, M., Littmann, T., Friedrich, H., and Breckle, S. W.: Microclimatic boundary conditions for activity of soil lichen crusts in sand dunes of the north-western Negev desert, Israel, *Flora*, 196, 465–474, 2001.
- West, N. E.: Structure and function of microphytic soil crust in wildland ecosystems of arid and semiarid regions, *Advance. Ecol. Res.*, 20, 179–223, 1990.
- Yamanaka, T. and Yonetani, T.: Dynamics of the evaporation zone in dry sandy soils, *J. Hydrol.*, 217, 135–148, 1999.
- Zaady, E., Shachak, M., and Moshe, Y.: Ecological Approach for Afforestation in Arid Regions of the Northern Negev Desert, Israel, in: *Deforestation, Environment and Sustainable Development, A Comparative Analysis*, edited by: Vajpeyi, D., 219–238, Greenwood Publishing, USA, 2001.
- Zaady, E., Kuhn, U., Wilske, B., Sandoval-Soto, L., and Kesselmeier, J.: Patterns of CO₂ exchange in biological soil crusts of successional age, *Soil Biol. Biochem.*, 32, 959–966, 2000.
- Zaady, E., Groffman, P., and Shachak, M.: Nitrogen fixation in macro- and microphytic patches in the Negev desert, *Soil Biol. Biochem.*, 30, 449–454, 1998.
- Zangvil, A.: Six years of dew observations in the Negev Desert, Israel. *J. Arid Environ.*, 32, 361–371, 1996.
- Zhang, Z. S., Liu, L. C., Li, X. R., Zhang, J. G., He, M. Z., and Tan, H. J.: Evaporation properties of a revegetated area of the Tengger Desert, North China. *J. Arid Environ.*, 72, 964–973, 2008.