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► **To cite this version:**

B. Wilske, J. Burgheimer, A. Karnieli, E. Zaady, M. O. Andreae, et al.. The CO₂ exchange of biological soil crusts in a semiarid grass-shrubland at the northern transition zone of the Negev desert, Israel. Biogeosciences Discussions, 2008, 5 (3), pp.1969-2001. hal-00298003

HAL Id: hal-00298003

<https://hal.science/hal-00298003>

Submitted on 18 Jun 2008

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**BSC-related CO₂
fluxes in a semiarid
grass-shrub steppe**

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

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Received: 12 March 2008 – Accepted: 20 March 2008 – Published: 9 May 2008

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Abstract

Biological soil crusts (BSC) contribute significantly to the soil surface cover in many dry-land 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.

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1 Introduction

Biological soil crusts cover vast areas throughout the semiarid and arid areas of the world (Belnap et al., 2001; Karnieli et al., 2001). BSC consist of communities of cyanobacteria, green algae, lichens, mosses, microfungi and bacteria in various proportions (Belnap et al., 2001; West, 1990). BSC-forming organisms are well adapted to environments with unreliable water supply as they share the poikilohydric feature of cell-hydration, which allows perpetual cycles of desiccation and hydration without damage to biological functions (Belnap et al., 2001). Equipped with the poikilohydric feature, 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

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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–

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190 m a.s.l., <http://www.ilternet.edu/networks/ILTER-ISRAEL.htm>). 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). 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. Grasses are dominant (e.g., *Stipa capensis* Thunb.) during the main growing season from February to April, but throughout the year the area is mainly characterized by scattered patches of shrubs (*Noaea mucronata* (Forssk.) Asch. & Schweinf., *Atractylis serratuloides* 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.

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2.3 Experimental set-up and protocols

(1) 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) Preparation 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.

(3) The enclosure system (Fig. 1): Two cuvette frames (acrylic glass, ID 143 mm, H 40 mm) were equipped with Teflon bags inside and on top. 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

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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. Differential measurements between two empty cuvettes represented the blank-cuvette offset (C_a versus C_a).

(4) CO₂ exchange measurements: The CO₂ exchange was investigated using an infrared gas analyser (IRGA, LI-7000, LICOR, Lincoln, USA) in differential mode with negative fluxes representing CO₂ deposition due to CO₂ uptake by BSC photosynthesis, and positive fluxes representing emission due to BSC respiration and/or soil CO₂ efflux. BSC-related CO₂ fluxes were obtained by measuring one BSC sample versus one soil sample. Hence, soil CO₂ efflux was subtracted instantaneously. Soil CO₂ efflux was obtained from differences between a soil sample and a blank collar (C_a). Enclosures were alternated between three to four BSC- and two soil samples. The precision of measurements was regularly checked by measuring the blank-cuvette offset (C_a vs. C_a). Results from direct differential measurements were checked with results from BSC vs BSC, BSC vs blank compared with soil vs blank, soil vs soil, and change of IRGA channels. The basic 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.

(5) 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 $\leq 0.05 \mu\text{mol mol}^{-1} \text{CO}_2$ 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.

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To calculate 15-h fluxes, data gaps were filled using stepwise regression.

(6) Environmental conditions: Three to five 30-mm soil cores were sampled for gravimetric soil moisture content 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, Effeltrich, 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). Precipitation and temperature records showed

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42% of annual PPT occurred in conjunction with the lowest monthly mean 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). While 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

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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, data for day and night time fluxes were short by three and six hours, respectively. 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). This reduced the net deposition by BSC to 3.3 mmol m^{-2} per 300 h.

3.2 Flux triggering conditions

CO_2 fluxes with hydrated BSC were triggered by light and temperature. The CO_2 exchange of activated BSC reached the light compensation at PAR values of $35\text{--}40 \mu\text{mol m}^{-2} \text{ s}^{-1}$ at T_{sa} $1\text{--}5^\circ\text{C}$, and $55\text{--}60 \mu\text{mol m}^{-2} \text{ s}^{-1}$ at T_{sa} $10\text{--}15^\circ\text{C}$. Average CO_2 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 $1\text{--}5^\circ\text{C}$ and $10\text{--}15^\circ\text{C}$, respectively. Temperature-related maximum CO_2 deposition was derived from regressions including at least four of the highest deposition rates with optimally hydrated BSC, such as given immediately after precipitation and between decreased CO_2 uptake owing to water suprasaturation and decrease due to dry out (e.g., 17 December 2001, 8–20 January 2002). Maximum CO_2 deposition at T_{sa} 5°C , 10°C , and 18°C (each $\pm 0.5^\circ\text{C}$) were -0.67 , -0.26 , and $-0.08 \mu\text{mol m}^{-2} \text{ s}^{-1}$ per $100 \mu\text{mol m}^{-2} \text{ s}^{-1}$ PAR, respectively (Fig. 4). From non-gap-filled data, more than 90% of the BSC-related CO_2 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 $920 \mu\text{mol m}^{-2} \text{ s}^{-1}$ PAR per 10 min and frequent rains led repeatedly to water films on BSC surfaces, which caused large changes in CO_2 fluxes within the averaging periods (Fig. 3e).

On the other hand, changing cloud cover and the associated light fluctuation resulted

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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).

5 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
10 0.5-mm.

3.3 CO₂ flux pattern relative to moisture supply

Under dry conditions, the CO₂ flux from BSC samples and soil plots was the same (10-min mean difference $\leq 0.01 \mu\text{mol m}^{-2} \text{s}^{-1}$), which indicated that BSC were inactive and did not contribute to the flux (e.g., Fig. 3c, 7 January 2002). Net CO₂ fluxes
15 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). To evaluate potential effects of the type of moisture supply on the magnitude of daily BSC-related CO₂ deposition fluxes, we compared gap-filled daily periods from the most consistent data set (00:00 to 15:00 h) (Table 1). BSC-related CO₂ flux
20 yielded the highest 15-h total of $-17.56 \text{ mmol m}^{-2}$ with recurrent rain events during daytime of the 21 January 2002 (Table 1). Similarly, the third largest 15-h deposition of $-13.82 \text{ mmol m}^{-2}$ was obtained from a day with frequently recurring drizzle (8 January 2002, PPT day total 2.7 mm). However, the second ($-16.16 \text{ mmol m}^{-2}$) and fourth largest ($-11.31 \text{ mmol m}^{-2}$) 15-h totals of BSC-related CO₂ deposition were obtained
25 from days where BSC activity was supplied only by massive dew in the morning (Table 1, 14 and 15 January 2002). The comparison of days with highest BSC-related deposition showed that rain and dew can result in similar time periods with BSC ac-

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tivity maintaining significant CO₂ uptake (Table 1). Contrastingly, CO₂ deposition after 2.6 mm PPT was surprisingly low in November (22 November 2001) as compared with the yield of daily deposition upon even lower precipitation at later times during the rainy season. Erratic rain at the end of the rainy season even resulted in a 30-min emission burst, although it provided less than 0.1 mm PPT and affected only minor parts of the sample (Fig. 3i, 16 April 2002). Thus, the type of moisture supply per se was less indicative for the magnitude of BSC-related CO₂ deposition. However, formation of massive dew was only observed subsequent to repeated rain events when soil moisture was high and VPD was low. For example, massive dew formed on the 14 January 2002 but not on the 7 January 2002 despite similar low mean T_{soil} of -3.4 and -2.4°C during the preceding nights, respectively. While the last precipitation prior to the 7 January 2002 occurred three days before, daily recurring precipitation accumulated to a total of 16 mm during the six days preceding the 14 January 2002. Increased SWC (see Fig. 2) also delayed the desiccation of BSC (Fig. 3d, Table 1: 14–15 January 2002), but low SWC as single water source resulted only in net respiration and CO₂ emission (Fig. 3g, 24–25 February 2002).

Before the peak of the rain season, when soil moisture was still low (December 2001), dew formation occurred on dry grass blades from the last vegetation season, on outcropping stones, and in two of the sample collars. Droplets formed on grass blades and trickled down wetting surrounding BSC, while larger patches of BSC surfaces without standing grass matter were visually dry. BSC-related CO₂ deposition during the two consecutive 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.

In order to test a potential effect of soil moisture on the photosynthetic uptake of BSC, we correlated both the amount of PPT and its frequency (i.e., PPT records from 15-min intervals) on BSC-related CO₂ fluxes (Fig. 6). Maximum correlation between daily BSC-related CO₂ fluxes and PPT was found for the frequency of PPT, which reflected the preceding three days ($r^2=0.78$), while correlation with the amount of PPT was

similar reflecting the last two ($r^2=0.70$) and three days ($r^2=0.69$). This result points to an important influence of the short-term history of moisture on BSC-related CO₂ fluxes.

We also tested the predictability of BSC-related CO₂ deposition based on moisture-indicating parameters that could be provided from the nearby LTER weather station. CO₂ fluxes were calculated for three 3-h day periods (07:00–10:00, 10:00–13:00, 13:00–16:00) and correlated with respective discrete amounts of PPT, as well as averages of relative air humidity (RH), VPD and soil moisture at 50 mm. As expected from the result above, CO₂ deposition did not correlate well with distinct amounts of PPT. VPD and soil moisture yielded the best prediction of BSC-related CO₂ deposition. 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 soil moistures 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 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 60–120 mg g⁻¹, and the emission

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decreased with increasing temperature at the highest SWC (Fig. 8). The irregular pattern at higher SWC indicated that at different times the moisture gradient changed and different parts of the soil column contributed to the fluxes. In addition, it seemed that the short-term measured fluxes were also subjected to gas dilution in and 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.

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 (as mentioned 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 in the periods November–January, February–May, and November–May, respectively.

4 Discussion

4.1 Soil efflux and BSC-related CO₂ fluxes

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-shrub steppe. Consistent with the 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 very similar between the soil in SE Spain (ca. <0–58 μmol m⁻² s⁻¹, mean + SE) (Maestre and Cortina, 2003) and in Sayered Shaded (0.15–0.58 μmol m⁻² s⁻¹). Similarly consistent, soil CO₂ effluxes showed a clipping of the upper half of the previous flux range (0.33–0.43 μmol m⁻² s⁻¹) within a Mediterranean savanna ecosystem in California during the

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dry season (Tang et al., 2003). The slightly broader range of soil CO₂ efflux in the present study is explained by the larger changes in conditions from the cold and wet to the hot and dry season.

BSC-related net deposition compensated only 2.6% of the concurrent soil CO₂ efflux during the sum of measurement periods. However, our data show that the soil-dwelling BSC represent 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 reported values from 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 $500 \mu\text{mol m}^{-2} \text{s}^{-1}$, T_{sa} 22°C) (Zaady et al., 2000). We measured $-1.44 \mu\text{mol m}^{-2} \text{s}^{-1}$ (10-min mean) under similar light conditions but at lower temperature two hours after 0.2 mm PPT during the peak of the rain season (20 January 2002, T_{sa} 13°C, PAR $540 \mu\text{mol m}^{-2} \text{s}^{-1}$). The difference of 9°C under which the fluxes were measured indicates a lower temperature adaptation of BSC in the field than in the laboratory. A lower temperature optimum is also 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 also 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 from their components, particularly if such calculations were based on concurrent optima of

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light, temperature and hydration, which cannot play a significant role for BSC-related CO₂ deposition under field conditions. For instance, maximum net CO₂ deposition to BSC dominated by the lichen species *Collema tenax* and *Microcoleus* 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 could be expected from the moss contribution in our samples.

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

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individual amounts ensues also from the upper limit of PPT, which 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 until the early winter season may represent an alternative water source for soil-dwelling BSC in semiarid grasslands 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

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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 hydrate and 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 to 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). However, as 42% PPT of the year's total was occurring in January more measurements in January were retrospectively justified. The conjunction of rain frequency and conditions delaying the dry out of BSC surfaces (e.g., low solar radiation and VPD) suggest furthermore that CO₂ deposition occurred during two third of the days in January. At the same time, the area was still free from grasses, and even at the low elevation of the sun in January, BSC were not deprived of incoming light. 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.

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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. Wilske. 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.

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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.

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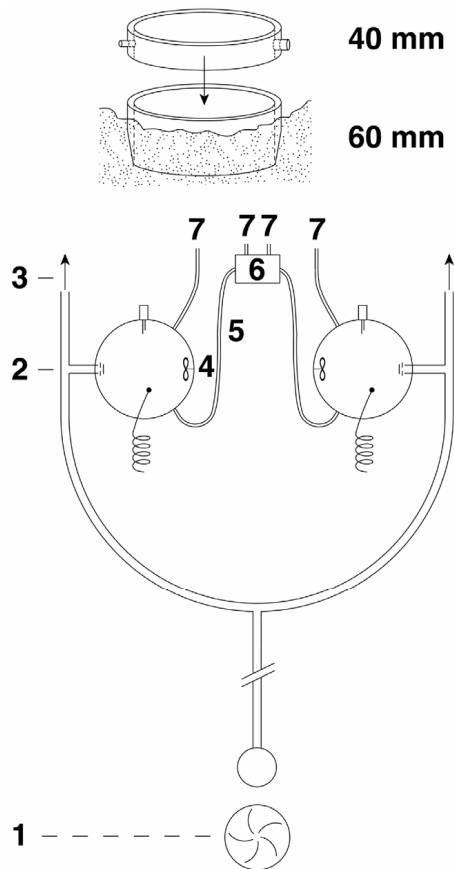


Fig. 1. Twin-cuvette system to measure BSC-related net CO₂ flux: (1) radial fan on 25.4-mm Teflon tubing, (2) 25.4-mm to 12.7-mm Teflon connection to cuvette, (3) 25.4-mm open end tubes, (4) cuvette fan, (5) 6.4-mm connection, (6) infrared gas analyzer, (7) flow control and pumps. Cuvette top height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

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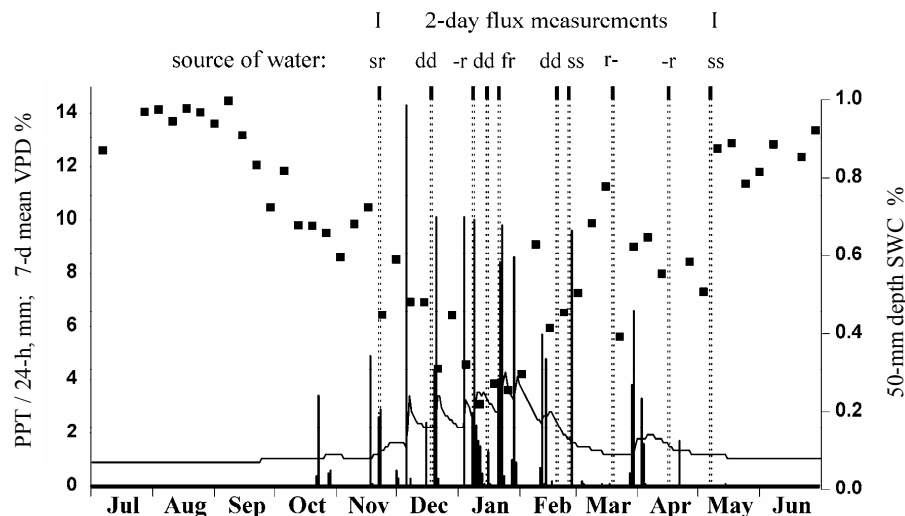


Fig. 2. Moisture parameters and periods of flux measurements during the hydrological year 2001–2002 in SSK-LTER. Bottom X-axis: month from 1 June 2001–30 May 2002; top X-axis: periods of measurements (vertical dot line); left Y-axis: 7-d averages of vapour pressure deficit, % (v , cut-off at 15%), and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

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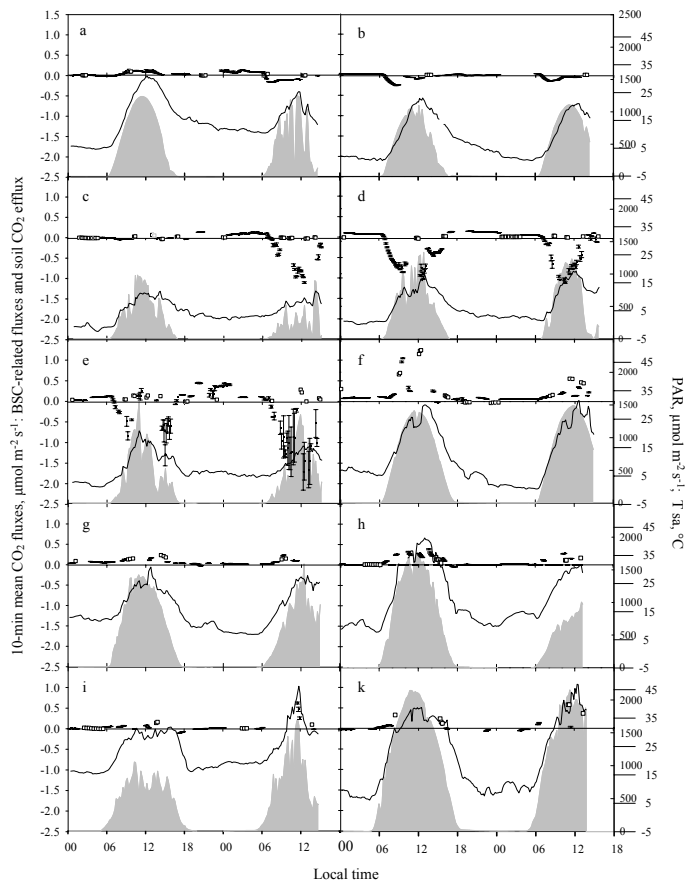


Fig. 3. (a–k) BSC-related net CO₂ flux ($\mu\text{mol m}^{-2} \text{s}^{-1}$, 10-min mean bars + 90 confidence, emission positive), soil CO₂ efflux (\square , 10-min mean), photosynthetically active radiation (PAR, grey) and air temperature in the enclosure (T_{sa} , thin line) during 10 field campaigns including two consecutive days from beginning to end of the wet season 2001/2002 at LTER-SSK.

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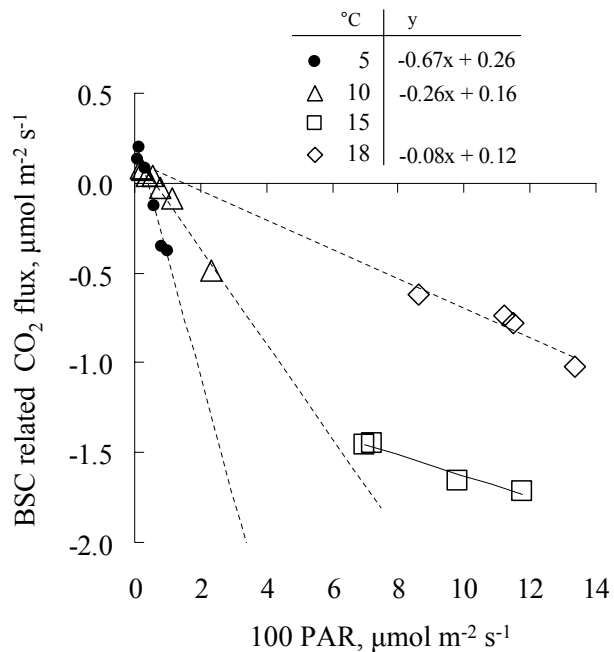


Fig. 4. Temperature-related maximum CO₂ deposition to BSC. Regressions based on at least the four highest deposition rates (10-min mean) to well hydrated BSC, i.e., after precipitation and between decrease in uptake owing to water suprasaturation and due to desiccation.

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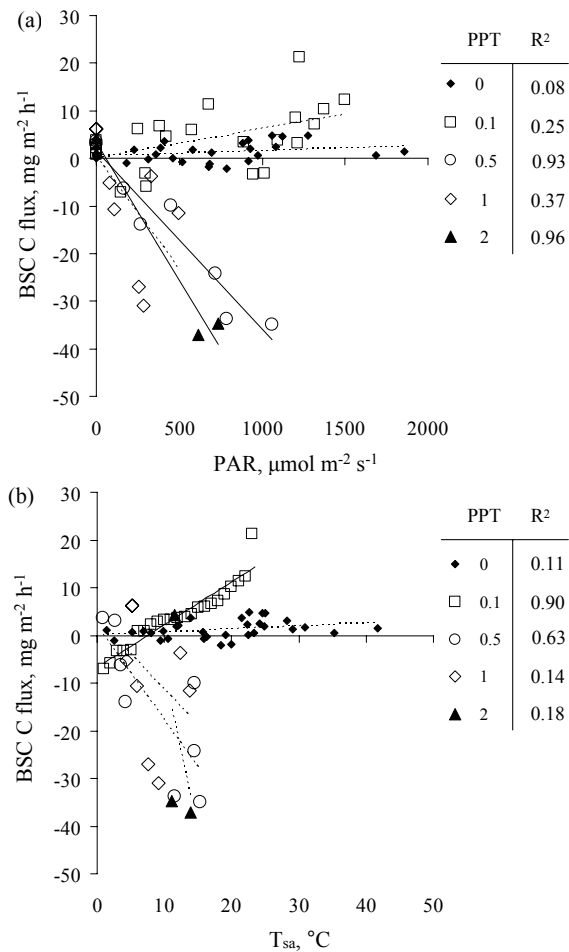


Fig. 5. Correlation of BSC-related CO₂ fluxes with (a) light and (b) temperature separated into categories of PPT received (mm).

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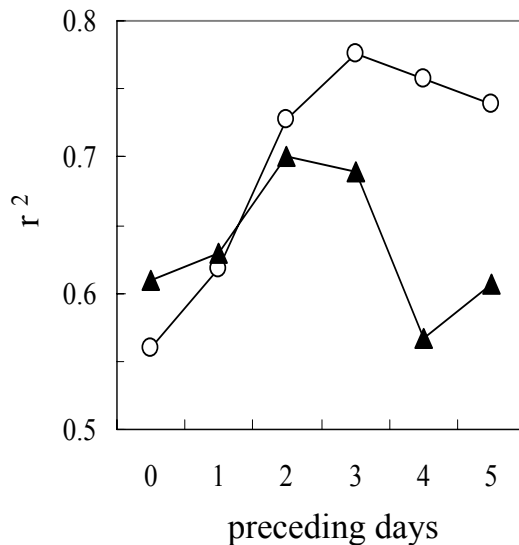


Fig. 6. Correlation coefficients between daily BSC-related CO₂ deposition (15 h) and amount (▲)/frequency (○) of PPT for the same day (0) and the preceding 5 days.

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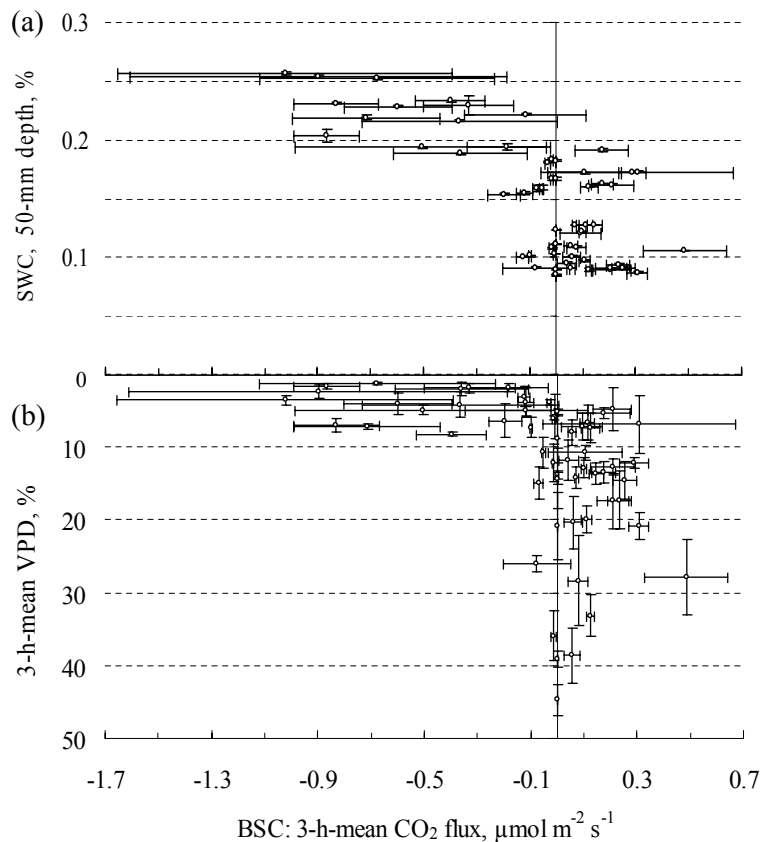


Fig. 7. BSC-related net CO₂ fluxes ($\mu\text{mol m}^{-2} \text{s}^{-1}$) versus VPD (%) and SWC at the 50-mm level (%). Values represent 3-h means \pm SD of three daytime periods (07:00–10:00, 10:00–13:00, 13:00–16:00) for fluxes, VPD, and SWC. VPD<10% and >10%, was related with 90% of net deposition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

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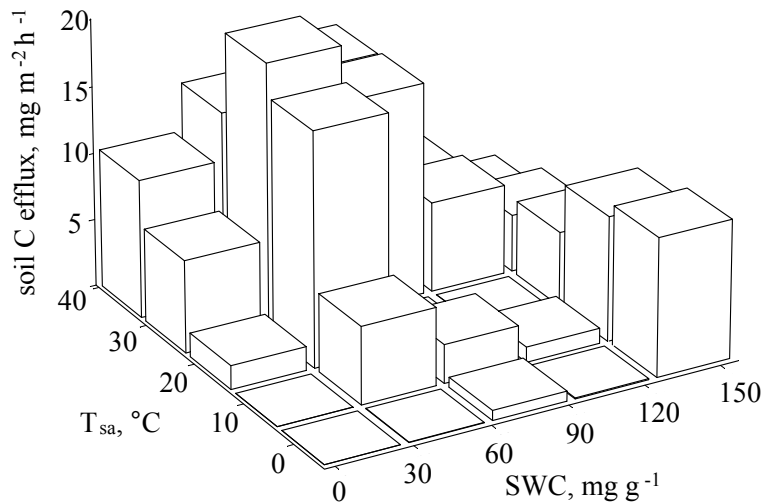


Fig. 8. Soil CO₂ effluxes (in mg C) based on air temperature in the sample enclosure (T_{sa}) and gravimetric soil water contents (SWC) from soil samples at the site.

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