



Relationships between Normalized Difference Vegetation Index (NDVI) and carbon fluxes of biologic soil crusts assessed by ground measurements

J. Burgheimer^a, B. Wilske^{b,c}, K. Maseyk^b, A. Karnieli^{a,*},
E. Zaady^d, D. Yakir^b, J. Kesselmeier^c

^a*The Remote Sensing Laboratory, Jacob Blaustein Institute for Desert Research,
Ben Gurion University of the Negev, Sede Boker Campus, Israel*

^b*The Environmental Science and Energy Research, Weizmann Institute of Science, Rehovot, Israel*

^c*Department of Biogeochemistry, Max-Planck-Institute for Chemistry, Mainz, Germany*

^d*Mitrani Department for Desert Ecology, Desertification and Restoration Ecology Research Center, Jacob Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, Sede Boker Campus, Israel*

Received 15 January 2004; received in revised form 20 March 2005; accepted 28 June 2005

Available online 15 August 2005

Abstract

The aim of this research was to study the relationships between the biological soil crusts (BSC), spectral reflectance and photosynthetic activity. Twenty field campaigns, each lasting several days, were conducted during the 2002–2003 rainy season at sand dune and loess environments in the north-western Negev desert of Israel. Simultaneous measurements of CO₂ net exchange and spectral reflectance were carried out for several types of BSC. The Normalized Difference Vegetation Index (NDVI) was derived from the BSC reflectance and correlated with their CO₂ exchange data. The relationship between NDVI and CO₂ exchange is discussed in detail with respect to environmental factors, such as soil water content, air temperature, and light intensity. Fairly good correlations were found in the rainy season. The NDVI was useful in indicating the potential magnitude and capacity of the BSC assimilation activity. Furthermore, the index corresponded well with different rates of photosynthetic activity of the different types of microphytes. The results demonstrate that spectral reflectances

*Corresponding author. Tel.: +972 8 6596855; fax: +972 8 6596704.

E-mail address: karnieli@bgumail.bgu.ac.il (A. Karnieli).

of the BSC can be related to photosynthetic activities and possesses the potential to assess the amount of carbon sequestration by these microphytes on an areal scale using satellite images. © 2005 Elsevier Ltd. All rights reserved.

Keywords: Biological soil crusts; Carbon fluxes; Remote sensing; NDVI

1. Introduction

Arid and semi-arid lands throughout the world are characterized by sparse or absence of vegetation cover. Nevertheless, the soil surface is often not bare of photoautotrophic life, but is covered by a community called biological soil crusts (BSC), known also as microphytic soil crusts, which are a complex mosaic of bacteria, cyanobacteria, green algae, microfungi, lichens, and mosses (West, 1990; Warren, 1995).

The various types of organisms that assemble the BSC share some interesting physiological traits. They are all capable of drying out and temporarily suspending physiological activities (dormant state). These types of organisms are referred to as poikilohydric. The moisture content threshold to regain activity is different for the various taxa that contribute to the biological crust and results in a certain distribution pattern (Lange et al., 1997a, 1998; Lange, 2001). BSC exist in all climates and regions. Roughly, mosses seem to favor the comparatively more mesic sites (200–300 mm of rain), lichens dominate intermediate sites (100–200 mm), and cyanobacteria favor the harshest sites (less than 100 mm). BSC may constitute up to 70% of the living cover in some plant communities, and in many arid and semi-arid areas, they are significantly more diverse than vascular plants (West, 1990; Lange, 2001).

BSC have similarities in their ecological functions (West, 1990; Johansen, 1993). They play a significant role in stabilizing soil and preventing erosion (McKenna et al., 1996; Belnap and Gillette, 1997, 1998; Evans and Johansen, 1999). They have a strong positive effect on vascular plants by fixing nitrogen. They fertilize the soil, support seed germination, influence water infiltration, increase the available water for vascular plants, and finally decrease the albedo (West, 1990; Warren, 1995).

1.1. Carbon sequestration by BSC

BSC are discussed to represent an important carbon sink on sparsely vegetated areas (Beymar and Klopatek, 1991; Lange et al., 1992; Evans and Johansen, 1999; Zaady et al., 2000). Where BSC are present, their carbon contribution provides energy for soil microbial populations (Evans and Johansen, 1999) supporting higher plant growth. Numerous studies of BSC photosynthesis showed that most of the species can be already activated even after an erratic rainfall of less than 1 mm. Furthermore, some species can use high air humidity (i.e. fog or dew) to maintain metabolic processes (Lange et al., 1990, 1992, 1994a; Veste et al., 2001). Generally,

respiration begins almost immediately after wetting, while a net carbon fixation by photosynthesis is detectable minutes to hours after wetting and varies widely depending on the BSC composition (e.g. lichens, cyanobacteria, or green algae). This variation is caused by physiological features of specific crust organisms (e.g. water capacity, chlorophyll content) and other adaptation mechanisms (e.g. CO₂-concentrating mechanisms (CCM)) combined with the different environmental conditions, i.e. light conditions and temperature (Green et al., 1993; Lange et al., 1993a, b, 1994b, 1997a, b, 1998; Zotz et al., 1998). Hence, reports of maximal rates of net photosynthesis (NP_{max}) under optimal conditions vary greatly and span the range of two orders of magnitude between 0.111 and 11.5 μmol CO₂ m⁻² s⁻¹. The latter compares to 50% of the average NP_{max} of leaves of C3 crop plants, and is substantially larger than area-related photosynthetic capacity of conifer needles (Lange, 2001). NP_{max} of soil crust lichens is often well in the upper range of maximal area-related leaf NP rates of the vascular vegetation characterizing the same site (Lange et al., 1998). In the Negev desert of Israel, crusts are reported to reach more than 20% of the daily morning NP_{max} of a coexisting desert shrub (Lange et al., 1992). Thus, the BSC are discussed to contribute substantially to the carbon budget of arid and semi-arid ecosystems where vascular plant production is low.

1.2. Remote sensing and BSC

The BSC cover vast surfaces in the arid and semi-arid deserts all over the world. Yet, despite their global extent and the expanding interest in their ecological roles, relatively few studies have been published on the use of remote sensing to detect and map their distributions and functioning (Karnieli et al., 2001).

Karnieli and Tsoar (1995) and Karnieli et al. (1996, 1999), have shown in detail the spectral reflectance of crusts and emphasize the differences from vascular plants and bare-sand spectra. Fig. 1 shows typical spectral reflectance of dry sand, dry and wet cyanobacteria soil crust, and a higher plant (*Artemisia monosperma*). The shape of the perennial plants spectrum is typical for desert vascular plants: a relatively small peak in the green region, dips in the blue and red regions due to chlorophyll absorption, and relatively higher plateau in the near infrared (NIR) region due to leaf structure reflectance. Dry BSC reflectance is generally lower than that of bare sand. Both curves are typical for soil, but the slight flattening between 600 and 700 nm in the BSC curve is due to slight absorption by photosynthetic pigments (i.e. chlorophyll *a*, assorted carotenoids and xanthophylls). Considerable change in the BSC spectral reflectance occurs when they are wet. Their reflectance is lower than that of dry crust and exhibits a significant dip in the red region (~680 nm) due to the strong absorption by photosynthetic pigments. Thus the physiological activity under wetted conditions causes a change in the spectral reflectance and more light is absorbed by the pigments (O'Neill, 1994).

Karnieli et al. (1999) conducted crust-wetting experiments, which showed that progressive physiological development, was accompanied by decreasing reflectance (both in the visible and infrared regions). Hence, spectra of well-developed crusts

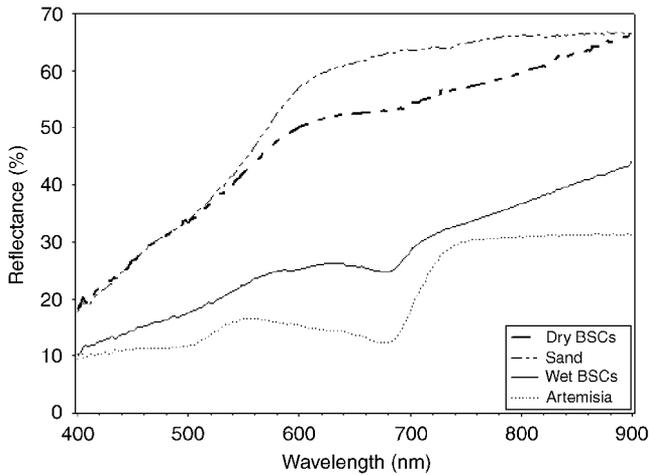


Fig. 1. Spectral reflectances of dry and wet biological soil crusts (BSC), bare sand, and a vascular plant species.

became more different from the sand/soil spectra and resembled more that of plants. However, in contrast to higher plants, neither a pronounced peak at 550 nm (except for moss species) nor a gentle increase in slope around 700 nm was found in the crusts spectra.

The Normalized Difference Vegetation Index (NDVI) and other vegetation indices have been intensively used for monitoring biophysical condition and vegetation cover from satellite and airborne sensors (Tucker et al., 1986; Running, 1990; Myneni et al., 1997; Ichii et al., 2001). Karnieli et al. (1999) tested the NDVI on BSC and found it very reliable. When crusts were dry, the NDVI value was low (0.08–0.13), a level also typical for dry soil/sand and rock (Karnieli et al., 1996). But when all these elements were wetted only the crusts showed an increase in the NDVI values. Thus, the increase in crust NDVI values (0.18–0.3) is unlikely to be due to an increase in soil moisture but can be associated with the photosynthetic activity of crust organisms. The rapid change after wetting in the physiological activity of the crusts was detected also in the NDVI values. The biggest change in the NDVI values occurred after the crust was wetted; when the crust dried out, the NDVI values declined too. Karnieli et al. (1999) found that the chlorophyll content of crusts was much higher after 7 days of incubation and showed high correlation with the NDVI values ($r = 0.89$). Furthermore, direct relationships were also found between NDVI values and organic matter, polysaccharides content, protein content, and crust thickness (Karnieli et al., 1999). Hence, NDVI can serve as an indicator for many physiological and ecological parameters concerning the BSC and can help draw conclusions on crust photosynthetic activity.

The objective of this study was to investigate the relationship between the NDVI and carbon fluxes of BSC by ground measurements and to check the potential for implementation into remote sensing studies on a larger scale.

2. Study areas

The research was conducted in two different sites in the northern Negev desert of Israel: at the Agure sand dunes and at the Sayeret Shaked long-term ecological site (SSK) (Gosz et al., 2000). In both the study sites the BSC are considered to dominate surface characteristics although the dominant crust type in each area is different. Agure sand dunes are covered mainly with cyanobacteria, while SSK, which is characterized by loess soil, has a mixture of different types of crusts.

The Agure sand dunes are located in the western Negev along the Israel–Egypt border, about 40 km south of the Mediterranean coastline (30°75'N, 34°22'E). Average annual rainfall in this area is about 95 mm, mainly during the winter (October–March). The average minimum daily temperatures are 5 and 19 °C, the average maximum temperatures reach 16 and 33 °C, in January and July, respectively (Karnieli et al., 1999). Sandy linear dunes (West–East direction) characterize the landscape. The upper part of the dune (15–20% of the region), which is exposed to wind erosion, is composed of unconsolidated sand particles (more than 95%), and it is almost void of vegetation. The dune hill slopes and interdune corridors, which occupied 80–85% of the area, have a particle size distribution of about 80% sand, 20% silt and clay (Karnieli et al., 1999; Zaady et al., 2000).

The interdunes area and the south-facing slopes are almost completely covered by a cyanobacterial crust (*Microcoleus sociatus*, *M. vaginatus*, and *Phormidium* sp.). The north-facing slopes of the dunes contain additional cyanobacterial species (*Nostoc microscopicum*, *Scytonema* sp., *Oscillatoria* sp., *Schizotrix friesii*, and *Chroococci-diopsis* sp.), cyanolichen species, green algae (*Chlorococcum* sp., *Stichococcus* sp.), and two species of mosses (*Bryum dunnense* and *Tortula brevissima*) (Karnieli et al., 1999). Perennial shrubs (e.g. *Retama raetam*, *Thymelaea hirsuta*, *Artemisia monosperma*) are scattered along the interdunes. These perennial shrubs indicate habitat stabilization provided by BSC cover and plant succession (Danin, 1991, 1996). Furthermore, the growth of the annual plants (e.g. *Senecio glaucus*, *Launaea mucronata*, *Rostraria cristata*) that appears for a few weeks after strong rain events also contribute to the dynamic stability of the sand dunes area (Danin, 1991; Kadmon and Leschner, 1995).

The Sayeret Shaked Ecological Park (SSK) is located near Beer-Sheva in the Northern Negev (31°17'N, 34°37'E). The site is a watershed that has been closed off to livestock grazing since 1987. Rainfall in this area has a long-term annual average of 200 mm and occurs only in the winter season. The 200 mm rain isohyet is considered as the transition between arid and semi-arid deserts. Average daily winter temperature is 12 °C and average daily maximum summer temperature is 25 °C. The landscape terrain is slightly hilly and consists of loessial soil with 14% clay, 27% silt, and 59% sand (Zaady et al., 2000). The area is characterized by scattered perennial shrubs (*Noaea mucronata*, *Thymelaea hirsuta*, *Pituranthos tortuosus*), and patches of annual plants (*Stipa capensis*, *Bromus fasciculatus*, *Rostraria cristata*, *Avena barbata*). The soil surface is covered with BSC

(about 70%), consisting of cyanobacteria (*Microcoleus vaginatus*, *Nostoc punctiforme*, and *Choococcus* sp.), Cyanophilous lichen (*Collema* sp.), and two main moss species (*Aloina bifrons* and *Crossidium crassinerve* var. *loevipilum*) (Karnieli et al., 1996; Zaady et al., 2001).

3. Methodology

The data were collected during the season 2002–2003 at the Agure sand dunes and the Sayeret Shaked Ecological Park (SSK). The field measurements started at the end of the summer (October), when the vegetation is still dry (except some of the perennial shrubs), continued through the winter and spring till the beginning of the summer (June). During that time 20 individual field campaigns, 3 days long each, were carried out.

Measurements of the spectral reflectance of the BSC (and bare soil/sand as a reference) were conducted by the FieldSpec-HandHeld Spectroradiometer (manufactured by Analytical Spectral Device (ASD, 2000)). This instrument measures at a wavelength of 325–1075 nm with a spectral resolution of 2 nm. High intensity contact probe device was attached with a fiber optic to the spectroradiometer. This device has an independent light source (about two-fold of the solar intensity) and made it feasible to measure under all-weather conditions. The contact probe was attached to the BSC and measured its spectral reflectance. For calculating the reflectance measurements of a white reference panel (Spectralon plat) were taken immediately before each spectral measurement.

BSC gas exchange was investigated by the use of Teflon bag cuvettes specially designed for soil-atmosphere studies (Max Planck Institute for Chemistry, Mainz). The cuvettes were topped on settled plots on a base of acrylic glass soil-borne collars ground into soil at chosen sites weeks before the measurements. CO₂ net exchange between the BSC and the atmosphere was measured under ambient air flushing and using an infrared gas analyzer (Licor, Li-7000, Lincoln, USA). These measurements were performed sequentially one treatment after the other, which allowed to measure BSC versus soil, BSC versus empty cuvette and soil versus empty cuvette. The empty cuvette was sealed towards the soil surface with Teflon film. Additionally, environmental factors such as photosynthetic active radiation (PAR), cuvette and ambient temperature, relative humidity, and gravimetric soil moisture content (g H₂O/g soil) were recorded in order to relate them to the CO₂ net fluxes. All these measurements were implemented continuously for 48 h during each campaign. For a detailed description of cuvette construction/use and gas exchange measurements see Wilske et al. (submitted for publication).

The spectral reflectance measurements of a specific crust type, corresponding to the above-mentioned treatments, were conducted shortly after the CO₂ exchange measurements. The NDVI was computed from the spectral reflectance measurements and correlated with the CO₂ net fluxes.

4. Results and analysis

4.1. The relationships between CO₂ exchange and NDVI at Agure sand dunes

Fig. 2 shows the relationships between the CO₂ net flux of the BSC and the NDVI for the second year of measurements at the sandy environment. Two main groups can be distinguished. The first group, framed by the solid eclipsoid line has NDVI values that range from 0.1 to 0.25. This group exhibits a small variation of the CO₂ exchange in comparison to the second group (dashed circle) with higher NDVI values ranging between 0.3 and 0.55. This pattern is caused by different hydrations of the BSC and environmental factors. An increasing NDVI is accompanied by an increase of the photosynthetic potential, but the realization of the latter is dependent on a complex mixture of environmental conditions. Table 1 integrates the relationships between NDVI values of the BSC and the CO₂ exchange with respect to soil moisture, light condition (PAR), and the air temperature inside the cuvette. Lower NDVI values (cases 1–7) correspond to very low soil moisture content in the soil (0.01). In this group photosynthetic activity does not occur or at least does not exceed the respiration process. Water content is the limiting factor and PAR and temperature have minor influences.

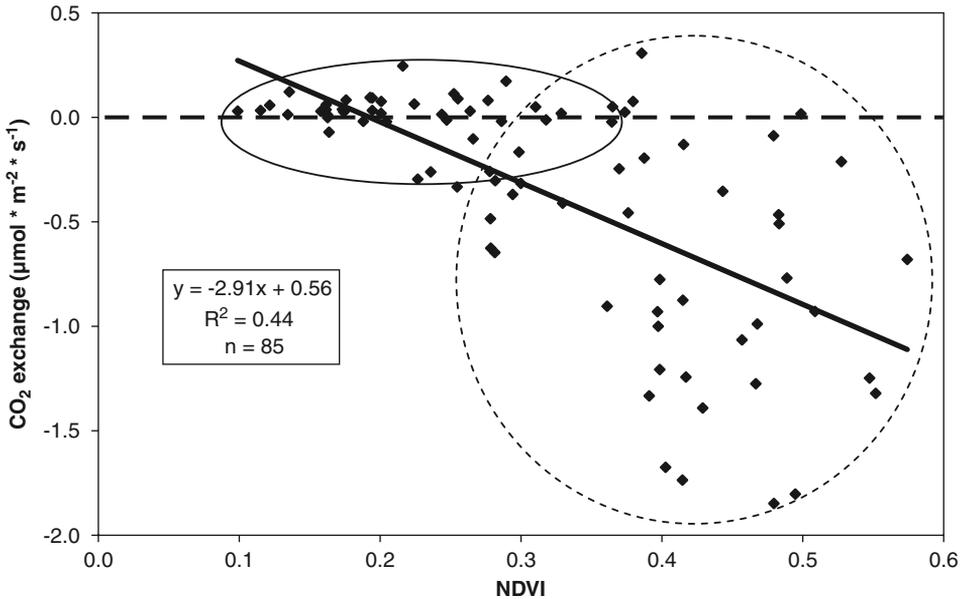


Fig. 2. Correlation between the net CO₂ fluxes of the BSC and the NDVI at the sandy environment as observed during the 2002/3 rainy season. The ellipse and the circle are suggestions to discuss different groups of activity in relation to the basic factor of soil moisture. One, the ellipse, is enclosing data within a group of low NDVI values corresponding to CO₂ exchange data around zero. The second group (circle) encloses data with increasing NDVI values accompanied by an increase of the CO₂ exchange, which is realized depending on other environmental factors such as light and temperature.

Table 1

Relationships between mixed BSC NDVI values and CO₂ exchange with respect to the environmental factors at the sand dunes site

Case no.	NDVI	CO ₂ exchange ($\mu\text{mol m}^{-2}\text{s}^{-1}$)	Soil moisture content	PAR ($\mu\text{mol m}^{-2}\text{s}^{-1}$)	Cuvette temp. (°C)
1	0.14	0.095	0.01	920	19.1
2	0.23	0.173	0.01	1690	35.0
3	0.26	-0.012	0.01	59	3.2
4	0.31	-0.022	0.01	518	19.2
5	0.31	0.051	0.01	28	13.6
6	0.32	0.5	0.01	0	6.7
7	0.27	0.019	0.01	506	12.0
8	0.32	0.076	0.03	111	8.1
9	0.42	-0.088	0.03	800	18.5
10	0.43	-0.509	0.04	1210	22.1
11	0.50	-1.321	0.04	640	13.3
12	0.34	-0.93	0.05	505	11.6
13	0.42	-1.848	0.05	992	12.5
14	0.40	-1.065	0.05	870	15.7
15	0.41	-0.989	0.07	470	6.5

Each case represents CO₂-NDVI data of a sample plot as well as the specific environmental conditions (soil moisture condition, light conditions (PAR), and cuvette air temperature) at that time.

The second group (cases 8–15) with the higher NDVI values (0.3–0.5) is also best described by higher soil moisture content (0.03–0.07), plus a large fluctuation in photosynthetic activity. In this group, several environmental factors influence the BSC activity. Light intensity (PAR) is the main factor that determines the rate of the photosynthesis when water is available and the temperature does not reach more than 30 °C (see also Lange et al., 1992; Lange, 2001). For instance, cases 12–14 have the same amount of soil moisture yet they have different rates of photosynthetic activity due to different light conditions. The rate of photosynthesis increases as the light and temperature increase (cases 12–14). The highest rate of photosynthesis was observed under high light conditions although the water content was not as high as, for example, case 15, which represents a cloudy day where light and temperature were low (PAR about 500 and temperatures around 6.5 °C). Light is the dominating parameter as soon as there is sufficient water available for the BSC. Hence, the water content in the soil is the underlying factor that explains the two main groups of activity as shown in Fig. 2. Water limitation causes the absence of or small CO₂ fluxes in group No. 1, whereas the large CO₂ flux variations in the other group are derived from effects of different light intensities under wetter conditions.

Table 2 shows the relationships between NDVI values of the pure cyanobacteria crusts and the CO₂ exchange with respect to soil moisture, light condition (PAR), and the air temperature inside the cuvette. The same pattern as found for the mixed BSC can be seen for the cyanobacterial crusts. However, NDVI values as well as the CO₂ flux magnitude (photosynthesis and respiration) are lower as compared to the

Table 2

Relationships between cyanobacteria NDVI values and CO₂ exchange with respect to the environmental factors at the sand dunes site

Case no.	NDVI	CO ₂ exchange ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Soil moisture content	PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Cuvette temp. (°C)
1	0.14	0.122	0.01	1550	19.9
2	0.12	0.033	0.01	410	10.2
3	0.19	0.093	0.01	281	15.3
4	0.17	0.038	0.01	140	10.6
5	0.25	-0.333	0.03	915	10.8
6	0.28	-0.647	0.04	1172	11.6
7	0.23	-0.296	0.04	880	12.5
8	0.30	-0.166	0.04	448	5.4
9	0.29	-0.369	0.06	466	5.9

Each case represents CO₂–NDVI data of a sample plot as well as the specific environmental conditions (soil moisture condition, light conditions (PAR), and cuvette air temperature) at that time.

mixed BSC. The reason for this is due to the structured surface of the cyanobacterial crust, which is less physiologically developed compared to the mixed BSC. As derived for the mixed crusts, the water content, reflected by the soil moisture, is the basis on which photosynthesis is regulated by light intensity. For instance, cases 6 and 9 have different rates of photosynthesis. Case 9 data were obtained under the highest soil moisture content but low light conditions, whereas case 6 data reflect the activity under lower moisture content but better light conditions. The two lowest NDVI values (cases 1–2) were measured at the end of the rainy season, which means that the cyanobacterial crusts were already drying out. The moderate NDVI values (about 0.2) were measured at the middle of the rainy season at the time between rain events and the group with the highest NDVI values (0.25–0.3) was measured at the time or very close to the rain events.

In order to observe the seasonal dynamics of the CO₂ exchange and the NDVI of the BSC, average values of these variables were calculated for each field campaign for the 2002/3 rainy season (Fig. 3). It can be seen that for the sandy environment the NDVI and the CO₂ exchange follow a similar pattern/trend in the BSC phenological cycle ($r^2 = 0.73$). A strong activity is observed at the beginning of the wet season (December). Later when the crusts are more developed, the NDVI remains relatively stable on a certain level (about 0.35; January–March) and fluctuate in close relation to the CO₂ fluxes. The end of the wet season (April–May) is characterized by a slow, but continued, decline of the NDVI. Under wetted conditions the fluctuations (amplitudes) of both NDVI and CO₂ exchange are higher than compared to dry conditions. We interpret this to result from fast changing physiological activities due to environmental conditions during the active states of the crusts.

Fig. 4 shows the correlation ($r^2 = 0.76$) between the NDVI and the CO₂ exchange of the mixed BSC averaged over 2 years of measurements. Increasing CO₂ fixation is

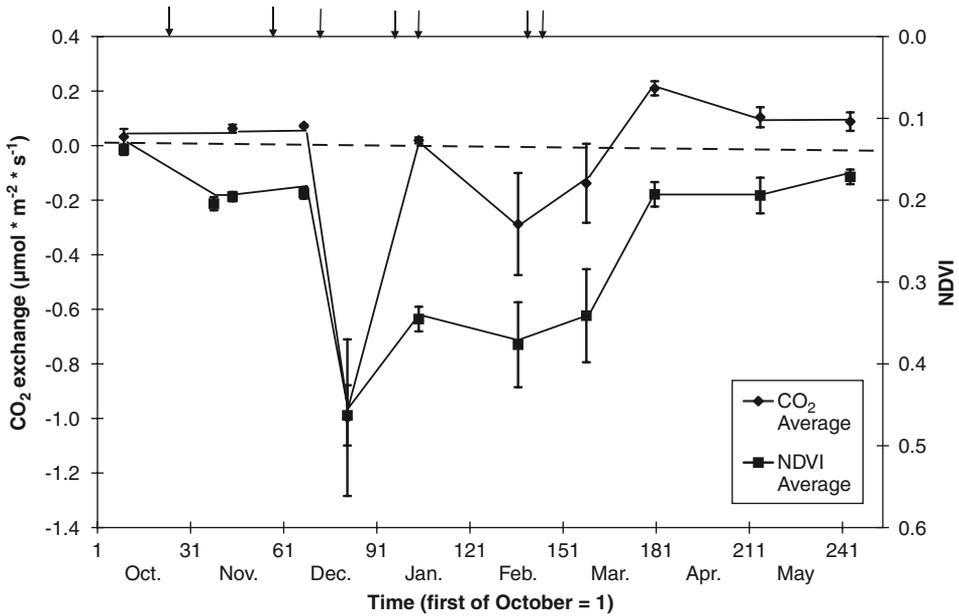


Fig. 3. Seasonal dynamics of the NDVI and the CO₂ exchange for the mixed BSC at the sandy environment at the Agure site. Negative CO₂ exchange mean carbon gain (the arrows indicate the main rain events, more than 5 mm, vertical bars indicate standard deviation $n = 21$).

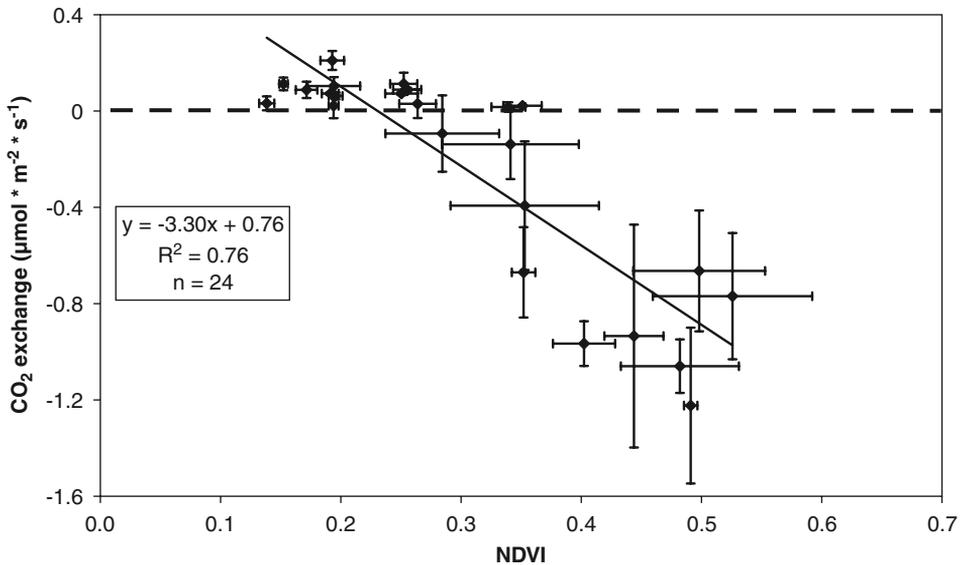


Fig. 4. CO₂ exchange as a function of NDVI for 2 years of measurements of mixed BSC at the sandy environment at the Agure site. Vertical and horizontal bars indicate standard deviations ($n = 46$).

correlated with increasing NDVI. Standard deviations (for both datasets) indicate the variability of the physiological activity, which can be high (see above and Fig. 2), as well as that of the NDVI fluctuations observed during the studies. The significant correlation points to a general potential to monitor BSC activity by remote sensing.

Fig. 5 presents the seasonal fluctuation of the NDVI and the CO₂ exchange as observed with the cyanobacterial crusts at the Agure sand dunes during the 2002/2003 rainy season. The cyanobacterial phenology cycle is similar to the mixed BSC but the amplitudes of the NDVI and CO₂ net flux are much smaller. This may be explained by the less developed morphological structures as compared with the mixed BSC accompanied by a faster drying process leaving only a short activity window for photosynthesis. The overall picture is the same as found for mixed BSC including a stabilization of the NDVI after the first rainfall and further increase and lowering in close relation to the CO₂ exchange pattern. Fig. 6 shows the correlation ($r^2 = 0.80$) between the NDVI and CO₂ exchange of the cyanobacterial crust averaged over 2 years of field measurements. The data show that the cyanobacterial crust behaves very similar as compared to the mixed crust (see Fig. 4) at this location and may be included into remote sensing observations.

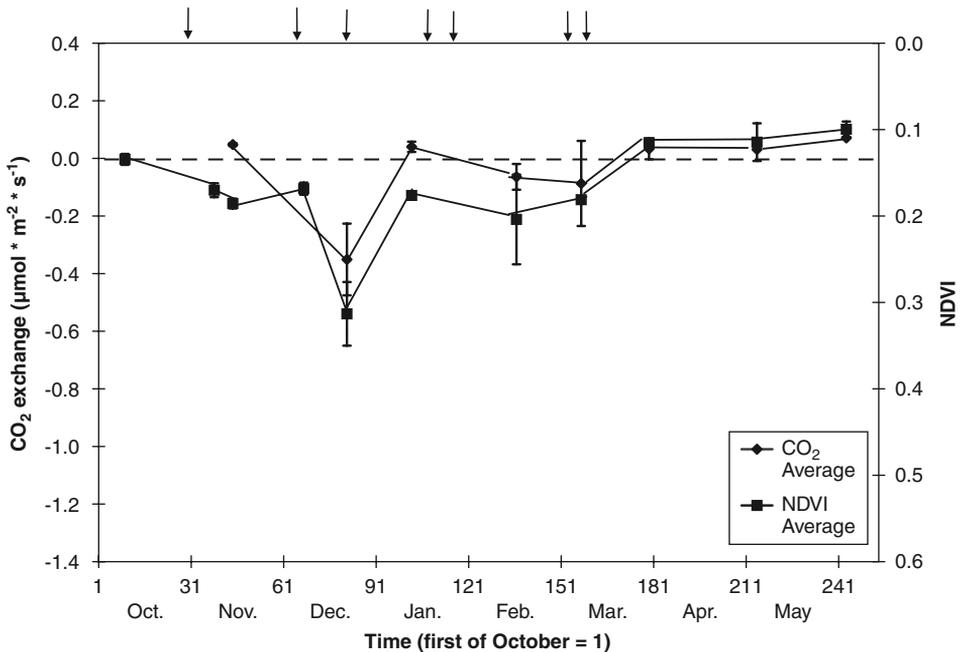


Fig. 5. Seasonal dynamics of the NDVI and the CO₂ exchange for the cyanobacteria at the sandy environment at the Agure site. Negative CO₂ exchange mean carbon gain (the arrows indicate the main rain events, more than 5 mm, vertical bars indicate standard deviations; $n = 15$).

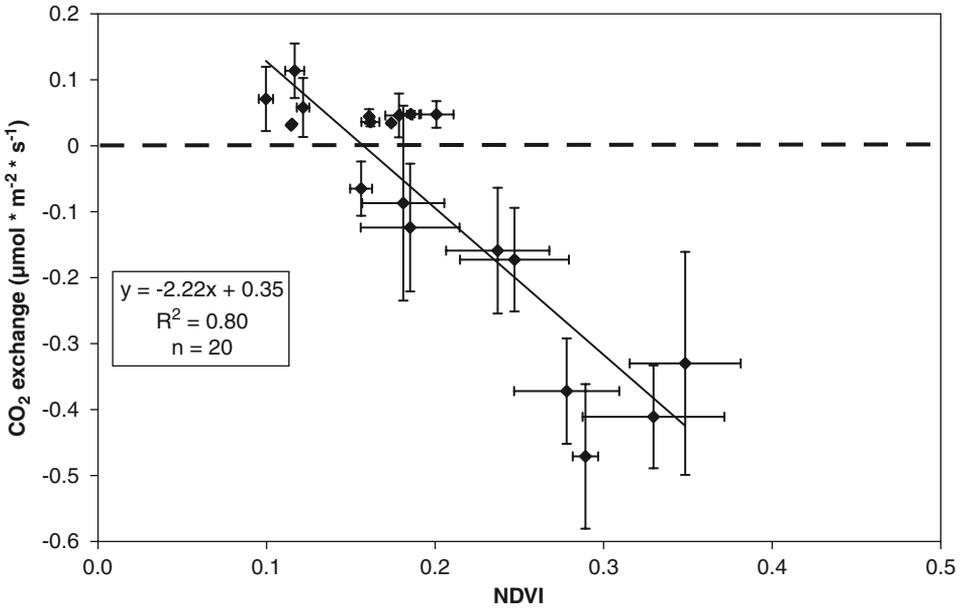


Fig. 6. CO₂ exchange as a function of NDVI for 2 years of measurements of pure cyanobacteria at the sandy environment at the Agure site. Vertical and horizontal bars indicate standard deviations ($n = 38$).

4.2. The relationships between CO₂ exchange and NDVI at the loess environment

The second site for our measurements (SSK) was characterized by loess soil environment. The data are presented in Figs. 7–9 and Table 3. Fig. 7 shows the relationship between the CO₂ net flux of mixed BSC and the NDVI as observed during the second year. The scattered pattern resembles that of the corresponding figure (Fig. 2) for the Agure site. An increase of NDVI is accompanied by an increasing potential of photosynthetic activity. The realization of the latter depends on environmental factors. SSK has only mixed BSC and lacks pure cyanobacterial crusts. This may be an explanation why the lowest NDVI values are still higher than those found at the Agure sand dunes (0.2 instead of 0.15).

Table 3 and Figs. 8 and 9 present the NDVI values of the mixed BSC at SSK in relation to the CO₂ exchange and environmental factors. The crusts growing on the loess soils show a very similar behavior as described above for the crusts at the sandy Agure site. However, we observed a less clear correlation between NDVI and CO₂ exchange when soil water content is at the lower values. This may be caused by the loess soil composition which is characterized by minerals that adsorb water, hence contributing to soil water content but not necessarily supporting NDVI and/or BSC growth (Yair, 1987; Hillel, 1998).

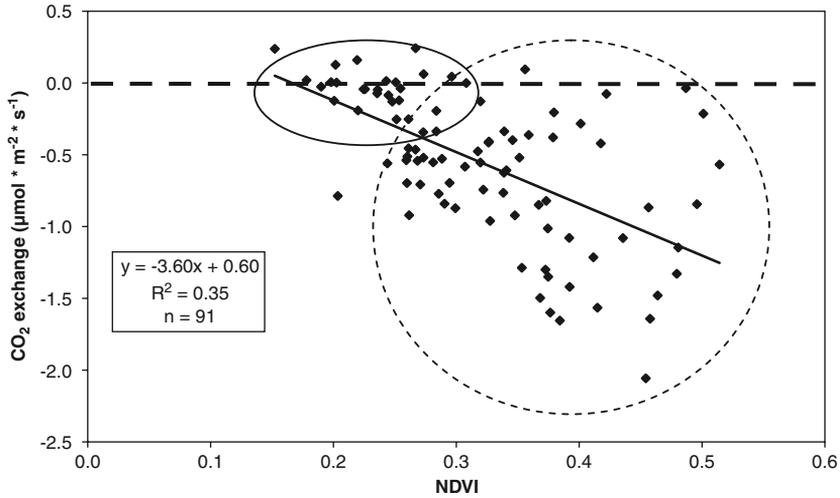


Fig. 7. Correlation between the net CO₂ fluxes of the BSC and the NDVI at the loess environment, for the 2002/3 rainy season. The ellipse and the circle are suggestions to discuss different groups of activity in relation to the basic factor of soil moisture. One, the ellipse, is enclosing data within a group of lower NDVI values corresponding to CO₂ exchange data around zero. The second group (circle) encloses data with increasing NDVI values accompanied by an increase of the CO₂ exchange, which is realized depending on other environmental factors such as light and temperature.

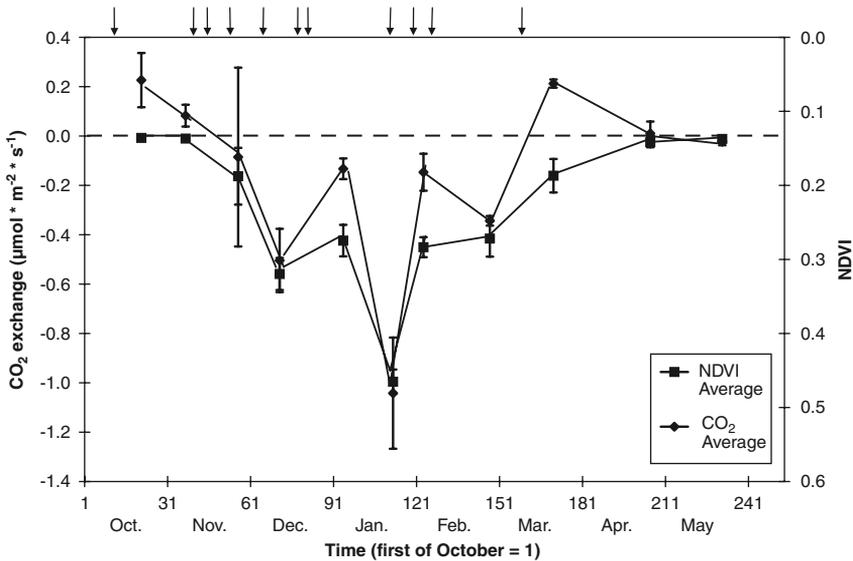


Fig. 8. Seasonal dynamics of the NDVI and the CO₂ exchange for the mixed BSC at the loess environment at SSK. Negative CO₂ exchange mean carbon gain (the arrows indicate the main rain events, more than 5 mm, vertical bars indicate standard deviation; $n = 20$).

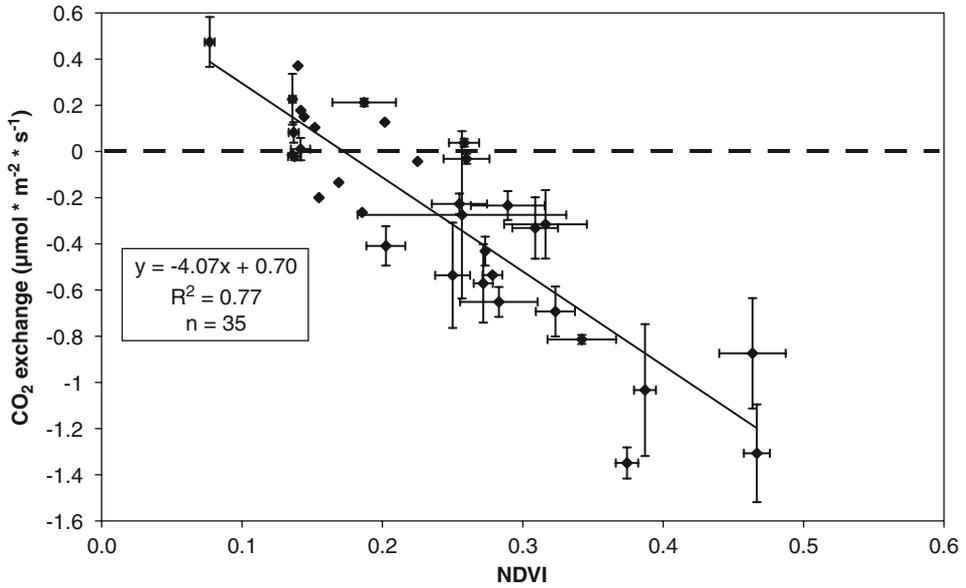


Fig. 9. CO₂ exchange as a function of NDVI for 2 years of measurements of mixed BSC at the loess environment at SSK. Horizontal or vertical bars indicate standard deviation; *n* = 52).

Table 3
Relationships between mixed BSC NDVI values and CO₂ exchange with respect to the environmental factors at SSK

Case no.	NDVI	CO ₂ exchange (µmol m ⁻² s ⁻¹)	Soil moisture content	PAR (µmol m ⁻² s ⁻¹)	Cuvette temp. (°C)
1	0.18	0.02	0.02	726	11.8
2	0.24	0.014	0.04	230	6.1
3	0.29	-0.772	0.05	1330	17.8
4	0.15	0.238	0.05	1053	16.9
5	0.20	-0.787	0.06	506	8.4
6	0.22	-0.191	0.06	1080	19.4
7	0.31	0	0.06	220	6.6
8	0.25	0.005	0.06	730	13.9
9	0.31	-0.583	0.06	580	9.9
10	0.33	-0.415	0.06	720	11.7
11	0.36	-0.362	0.08	330	5.1
12	0.49	-0.036	0.1	140	13.4
13	0.48	-1.146	0.12	550	17.8
14	0.46	-1.642	0.13	1330	19.6
15	0.50	-0.214	0.14	80	8.4

Each case represents CO₂– NDVI data of a sample plot as well as the specific environmental conditions (soil moisture condition, light conditions (PAR), and cuvette air temperature) at that time.

5. Discussion

The ecological functions of BSC have been investigated and discussed in many studies. It was found that soil crusts contribute to the maintenance of the ecosystems and assist in catalyzing the succession level of a certain area (West, 1990; Warren, 1995). Their contributions are significant in particular for the vascular plants in harsh environments (i.e. arid and semi-arid deserts), where essential sources (i.e. water, nutrients) are limited (Belnap and Harper, 1995; Evans and Johansen, 1999). With respect to carbon fixation, BSC were found to represent a carbon sink, which can in some cases exhibit CO₂ assimilation rates as found with higher plants (Lange, 2001). Taking into consideration that these organisms cover huge arid and semi-arid areas around the world, and that the weaker part in the global carbon budget are the terrestrial ecosystems (Wigley and Schimel, 2000), an investigation of the BSC contribution to the global carbon budget is of general interest. Ground-based studies that cover the seasonal development (Wilske et al., submitted for publication) deliver basic information. Closely related investigations of the BSC spectral behavior may help to deliver the calibration for remote sensing approaches (i.e. satellite or airborne images) on a larger scale. As a first step for achieving this goal we investigated the relationships between spectral reflectance (e.g. NDVI) and direct CO₂ measurements of the BSC on a seasonal basis for sites in the Negev desert of Israel.

Our studies on BSC at two different sites showed that NDVI and the physiological activity of the crusts are related to each other, although a distinct calibration between reflectance and CO₂ uptake needs further investigation. NDVI values can be categorized into two general ranges, which indicate the physiological status and activity of the BSC. Furthermore, these two ranges vary with respect to the type of crusts that are measured (mixed BSC or cyanobacteria). The two NDVI ranges that were identified for the mix BSC, both at the sandy and loess environments, are 0.15–0.3 and 0.3–0.5.

The first NDVI range indicates (for most of the cases) that the BSC are dry and do not perform any carbon exchange. These values are achieved at the beginning and at the end of the wet season (October–November and March–May, respectively). The low NDVI values under these dry conditions may be explained by either a low chlorophyll content or a by cytological structural disorganization preventing a signal. This condition is described by only very few data points (Figs. 3 and 8); therefore further measurements are needed. Nevertheless, it can be discerned from the following NDVI features which are reached.

After first rainfalls, NDVI values typically increase to range between 0.25 and 0.3. This state can be named as a “hold position” where the mixed BSC achieved a good physiological condition after a few rain events. The missing physiological activity under these conditions can be regarded as a result of lacking water, preventing the initiation of photosynthetic activity. Crusts in a “hold position” wait for the next rain event, to start their metabolic processes immediately. The other option, in this NDVI value range, is to reach a moderate level of photosynthesis (up to 1 $\mu\text{mol m}^{-2} \text{s}^{-1}$; see Tables 1 and 3), depending on the availability of an additional small amount of water, a typical situation for few days after a rain event. This view is

in accordance with Karnieli et al. (1999), who found that BSC, wetted and measured after 7 days of incubation were fully morphologically developed and had a NDVI value of about 0.3 that corresponds to the “hold position”. Hence, some rain events at the beginning of the rainy season with some breaks of sunny days can activate the BSC to reach a waiting (hold) position with a relatively stable NDVI around 0.3. They will immediately switch over into a physiologically active state with high rates of photosynthesis with the next rainfall events. This stage, with NDVI values above 0.3, describes well-developed and fully active crusts when enough water is available. Under these conditions photosynthesis with high rates ranging between 0 and $2 \mu\text{mol m}^{-2} \text{s}^{-1}$ can be observed, depending on light conditions.

The descriptions above are valid for both mixed BSC in sandy as well as loess environments. However, at the loess areas the discrimination between the two lower NDVI groups (up to 0.3) are less obvious than in the sandy environment. The loess particles, because of their arrangement in the soil profile, may absorb water, which is not available for the crust components (Yair, 1987; Hillel, 1998). Thus the amount of soil moisture needed to initiate the photosynthesis activity (especially when the soil is dry) is higher than in the sandy environment. This may cause a large variation both in the CO_2 exchange and in the NDVI values, which interferes with the differentiation between the two NDVI groups. Hence, using remote sensing tools to monitor BSC activity at this area should be interpreted with caution.

Also in the case of cyanobacteria the NDVI values are characterized by two general ranges. However, due to the lower concentration of pigments low NDVI values were observed, which corresponded to the low photosynthetic activity rates ($0\text{--}0.6 \mu\text{mol m}^{-2} \text{s}^{-1}$). The NDVI ranges for the cyanobacteria are 0.1–0.2 and 0.2–0.3. The interpretations of these groups are the same as for the mixed BSC. The lowest value indicates dry and inactive cyanobacteria, the intermediate level (0.15–0.2), is the “hold position” stage, and the high NDVI level is related to rain events with water available for the cyanobacteria crusts to perform photosynthesis activity depending on the light conditions.

Contrasting the mixed BSC, the cyanobacterial crusts have less obvious visual color changes. When the cyanobacteria are wet they appear like moist sand (brown color) and when they are dry their color is bright gray. The “hold position” is visually not so obvious as it is for the mixed BSC, but it can be identified by the NDVI values.

A good correlation between the BSC CO_2 exchange and the NDVI was found with datasets averaged to field campaign resolution. As the NDVI parameter does not change as fast as the carbon fluxes, the daily average seems to be a better scale for linking between these two parameters. This scale of resolution successfully demonstrated the seasonal phenology pattern of the BSC to be tracked by NDVI.

6. Summary

This research investigated the relationships between the NDVI and the CO_2 exchange. It is well known that chlorophyll is a dominant contributor to the NDVI

signal of biological soil crusts. Hence, influences on the spectral features of chlorophyll by subcellular structural changes or by production and decomposition as well as wetting may have a significant influence on the signal. CO₂ exchange of the BSC is coupled to the chlorophyll content and conditions, but the rates of photosynthesis may fluctuate between zero and high fixation rates when the pigment is in an “activated” state as reported by high NDVI values. This may be due to several reasons such as the influence of temperature and in particular light, which may cause large amplitude of CO₂ exchange rates.

Fairly good relationships between NDVI and CO₂ exchange of the mixed BSC were found, when NDVI values are between 0.15 and 0.25, the BSC are dry and at the beginning or the end of their phenological cycle, depending on the time of the measurements. NDVI values between 0.25 and 0.3 can indicate a good physiological condition but lack of water preventing the initiation of photosynthetic activity. If a small amount of water is available they might perform photosynthesis activity till a moderate level of $1 \mu\text{mol m}^{-2} \text{s}^{-1}$. NDVI values above 0.3 describe well-developed and fully active crusts with high rates of photosynthesis ranging between 0 and $2 \mu\text{mol m}^{-2} \text{s}^{-1}$, depending on light conditions.

The cyanobacteria crusts showed the same pattern of relationship. However, due to the lower concentration of pigments, low NDVI values were observed, which corresponded to the low photosynthetic activity rates ($0\text{--}0.6 \mu\text{mol m}^{-2} \text{s}^{-1}$).

A good correlation between the BSC CO₂ exchange and the NDVI was found with datasets averaged to field campaign resolution. This scale of resolution successfully demonstrated the seasonal phenology pattern of the BSC to be tracked by NDVI.

Using the NDVI–CO₂ exchange relationships that were found in this research, BSC photosynthetic activity and their derived CO₂ fluxes will be able to be assessed on an areal scale by using satellite images. However, it has to be noted that with the onset of the higher plants’ phenology, satellite-derived NDVI may lose any BSC signal because of the reflectance attributes of the annuals and perennials. Nevertheless, BSC surfaces and activity is still present during higher plant development, and could be estimated from the early season survey. The key to both, the more accurate resolution of the CO₂ exchange, and the estimate of “under-cover” BSC activity, must be a remote sensing signal independently tracking the soil surface water status.

Further areas of investigation should be to study the alteration between the dry and the “hold-position” that might be observed by the NDVI during early morning hours when a little increase in water availability might induce a CO₂ exchange.

Acknowledgements

This study was supported by Minerva fellowship to Burkhard Wilske, and by the International Arid Lands Consortium (IALC). We also gratefully acknowledge the fundamental financial support by the Max Planck Society.

References

- ASD, 2000. Hand Held Spectrometer User's Guide. FieldSpec UV/VNIR. Analytical Spectral Devices Inc., Boulder, USA.
- Belnap, J., Gillette, A., 1997. Disturbance of biological soil crusts: impacts on potential wind erodibility of sandy desert soils in Southeastern Utah. *Land Degradation & Development* 8, 355–362.
- Belnap, J., Gillette, D.A., 1998. Vulnerability of desert biological soil crusts to wind erosion: the influences of crust development, soil texture, and disturbance. *Journal of Arid Environments* 39, 133–142.
- Belnap, J., Harper, K.T., 1995. Influence of cryptobiotic soil crusts on elemental content of tissue of two desert seed plants. *Arid Soil Research and Rehabilitation* 9 (1), 107–115.
- Beymar, R.J., Klopatek, J.M., 1991. Potential contribution of carbon by microphytic crusts in pinyon-juniper woodlands. *Arid Soil Research and Rehabilitation* 5 (2), 187–198.
- Danin, A., 1991. Plant adaptations in Desert dunes. *Journal of Arid Environments* 21 (2), 193–212.
- Danin, A., 1996. *Plants of Desert Dunes*. Springer, Berlin, New York.
- Evans, R.D., Johansen, J.R., 1999. Microbiotic crusts and ecosystem processes. *Critical Reviews in Plant Sciences* 18 (2), 183–225.
- Gosz, J.R., French, C., Sprott, P., 2000. The International Long Term Ecological Research Network. University of New Mexico, Albuquerque, NM 109pp.
- Green, T.G.A., Büdel, B., Heber, U., Meyer, A., Zellner, H., Lange, O.L., 1993. Differences in photosynthetic performance between cyanobacterial and green algal components of lichen photosymbiodemes measured in the field. *New Phytologist* 125, 723–731.
- Hillel, D., 1998. *Environmental Soil Physics*. Academic press, London, pp. 443–465.
- Ichii, K., Matsui, Y., Yamaguchi, Y., Ogawa, K., 2001. Comparison of global net primary production trends obtained from satellite based normalized difference vegetation index and carbon cycle model. *Global Biogeochemistry Cycles* 15, 351–364.
- Johansen, J.R., 1993. Cryptogamic crusts of semiarid and arid land in North America. *Journal of Phycology* 29, 140–147.
- Kadmon, R., Leschner, H., 1995. Ecology of linear dunes: effect of surface stability on the distribution and abundance of annual plants. *Advances in GeoEcology* 28 (1), 125–143.
- Karnieli, A., Tsoar, H., 1995. Spectral reflectance of biogenic crust developed on desert dune sand along the Israel-Egypt border. *International Journal of Remote Sensing* 16 (2), 369–374.
- Karnieli, A., Shachak, M., Tsoar, H., Zaady, E., Kaufman, Y., Danin, A., Porter, W., 1996. The effect of microphytes on the spectral reflectance of vegetation in semiarid regions. *Remote Sensing of Environment* 57 (1), 88–96.
- Karnieli, A., Kidron, G.J., Glaesser, C., Ben-Dor, E., 1999. Spectral characteristics of Cyanobacteria soil crust in semiarid environment. *Remote Sensing of Environment* 69 (1), 67–75.
- Karnieli, A., Kokaly, R.F., West, N.E., Clark, R.N., 2001. Remote sensing of biological soil crusts. In: Belnap, J., Lange, O.L. (Eds.), *Biological Soil Crust: Structure, Function, and Management*. Springer, New York, pp. 431–455.
- Lange, O.L., 2001. Photosynthesis of soil-crust biota as dependent on environmental factors. In: Belnap, J., Lange, O.L. (Eds.), *Biological Soil Crusts: Structure, Function and Management*. Springer, New York, pp. 217–240.
- Lange, O.L., Meyer, A., Zellner, H., Ullmann, I., Wessels, D.C.J., 1990. Eight days in the life of desert lichen: water relations and photosynthesis of 'Teloschistes capensis' in the coastal fog zone of Namib Desert. *Madoqua* 17 (1), 17–30.
- Lange, O.L., Kidron, G.J., Budel, B., Meyer, A., Kilian, E., Abeliovich, A., 1992. Taxonomic composition and photosynthetic characteristics of the 'biological soil crusts' covering sand dunes in the western Negev Desert. *Functional Ecology* 6, 519–527.
- Lange, O.L., Budel, B., Meyer, A., Kilian, E., 1993a. Further evidence that activation of net photosynthesis by dry cyanobacterial lichens requires liquid water. *Lichenologist* 25 (2), 175–189.
- Lange, O.L., Budel, B., Heber, U., Meyer, A., Zellner, H., Green, T.G.A., 1993b. Temperate rainforest lichens in New Zealand: high thallus water content can severely limit photosynthetic CO₂ exchange. *Oecologia* 95 (3), 303–313.

- Lange, O.L., Meyer, A., Zellner, H., Heber, U., 1994a. Photosynthesis and water relation of lichen soil crusts: field measurements in the coastal fog zone of the Namib Desert. *Functional Ecology* 8 (3), 253–264.
- Lange, O.L., Meyer, A., Budel, B., 1994b. Net photosynthesis activation of a desiccated cyanobacterium without liquid water in high air humidity alone. Experiments with ‘*Microcoleus sociatus*’ isolated from desert soil crust. *Functional Ecology* 8 (1), 52–57.
- Lange, O.L., Belnap, J., Reichenberger, H., Meyer, A., 1997a. Photosynthesis of green algal soil crust lichens from arid lands in southern Utah, USA: role of water content, on light and temperature responses of CO₂ exchange. *Flora* 192 (1), 1–15.
- Lange, O.L., Green, T.G.A., Reichenberger, H., Hesbacher, S., Proksch, P., 1997b. Do secondary substances in the thallus of lichen promote CO₂ diffusion and prevent depression of net photosynthesis at high water content. *Oecologia* 112, 1–3.
- Lange, O.L., Belnap, J., Reichenberger, H., 1998. 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. *Functional Ecology* 12, 195–202.
- McKenna, C.N., Maxwell, C.D., Boulton, J.W., 1996. Wind transport of sand surface crusted with photoautotrophic microorganisms. *Catena* 27, 229–247.
- Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G., Nemani, R.R., 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386 (6626), 698–702.
- O’Neill, A.L., 1994. Reflectance spectra of microphytic soil crusts in semi-arid Australia. *International Journal of Remote Sensing* 15 (3), 675–681.
- Running, S.W., 1990. Estimating terrestrial primary productivity by combining remote sensing and ecosystem simulation. In: Hobbs, J.R., Mooney, H.A. (Eds.), *Remote Sensing of Biosphere Functioning*. Springer, New York, pp. 65–86.
- Tucker, C.J., Fung, I.Y., Keeling, C.D., Gammon, R.H., 1986. Relationship between atmospheric CO₂ variations and a satellite-derived vegetation index. *Nature* 319, 195–199.
- Veste, M., Littmann, T., Friedrich, H., Breckle, S.W., 2001. Microclimate boundary conditions for activity of soil lichen crusts in sand dunes of the north-western Negev desert, Israel. *Flora* 196, 465–474.
- Warren, S.D., 1995. Ecological role of microphytic soil crusts in arid ecosystems. In: Allsopp, D., Hawksworth, D.L., Colwell, R.R. (Eds.), *Microbial Diversity and Ecosystem Function*. Cab International, London, pp. 199–209.
- West, N.E., 1990. Structure and function of Microphytic soil crusts in wildland ecosystems of arid and semi-arid regions. *Advances in ecological Research* 20, 197–223.
- Wigley, T.M.L., Schimel, D.S., 2000. *The Carbon Cycle*. Cambridge University Press, Cambridge.
- Wilske, B., Burgheimer, J., Karnieli, A., Zaady, E., Yakir, D., Kesselmeier, J., submitted for publication. The CO₂ exchange of biological soil crusts in a semiarid shrub-grassland at the northern transition zone of the Negev desert, Israel, *Soil Biology & Biochemistry*.
- Yair, A., 1987. Environmental effects of loess penetration into the northern Negev desert. *Journal of Arid Environments* 13 (1), 9–24.
- Zaady, E., Kuhn, U., Wilske, B., Sandoval-Soto, L., Kesselmeier, J., 2000. Patterns of CO₂ exchange in biological soil crusts of successional age. *Soil Biology & Biochemistry* 32, 959–966.
- Zaady, E., Offer, Z.Y., Shachak, M., 2001. The content and contributions of deposited aeolian organic matter in a dry land ecosystem of the Negev Desert, Israel. *Atmospheric Environment* 35 (4), 76.
- Zotz, G., Büdel, B., Meyer, A., Zellner, H., Lange, O.L., 1998. In situ studies of water relations and CO₂ exchange of the tropical macrolichen, ‘*Sticta tomentosa*’. *New Phytologist* 139, 525–535.