

Ground and space spectral measurements for assessing the semi-arid ecosystem phenology related to CO₂ fluxes of biological soil crusts

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Abstract

This paper reports on ranges of carbon dioxide (CO₂) activity in biological soil crusts (BSC) correlated with different ranges of the BSC's spectral reflectance throughout the phenological cycle of the year. Methodology is based on surface CO₂ exchange measurements, ground spectral measurements, and satellite images interpretation. Thirty-nine field campaigns, each of duration of 3 days, were conducted over the course of 2 years at a sand dunes and a loess environment of the northwestern Negev desert in Israel, in order to relate the CO₂ fluxes and the spectral signals to the seasonal phenology. The Normalized Difference Vegetation Index (NDVI) was derived from ground measurements of the BSC's reflectance and correlated with their CO₂ exchange data. A linear mixture model, incorporating the different contributions of the sites' ground features, was calculated and compared with SPOT-HRV data. From the ground measurements, fairly good correlations were found between the NDVI and the CO₂ fluxes on a seasonal scale. Hence, the NDVI successfully indicates the potential magnitude and capacity of the BSC's assimilation activity. The linear mixture model successfully describes the phenological cycles of the BSC, annual, and perennial plants and corresponds well to the satellite data. Moreover, the model enables annual changes of the phenology cycle and the growing season length to be distinguished. Both the linear mixture model and the derived NDVI values recorded the recovery of the BSC at the beginning of the wet season before annuals had germinated. Finally, it is concluded that a combination of CO₂ exchange measurements, linear mixture model, and NDVI values is suitable for monitoring BSC's productivity in arid regions.

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1. Introduction

Arid and semi-arid lands throughout the world are characterized by sparseness or absence of vegetation cover. Nevertheless, the soil surface is often not lacking of photoautotrophic life, but is covered by a community of soil surface covering organisms, able to tolerate dehydration and thus adapted to aridity. These communities are referred

to as biological soil crusts (BSC), known also as microphytic soil crusts, comprising a complex mosaic of bacteria, cyanobacteria, green algae, microfungi, lichens, and mosses (Belnap & Lange, 2001; Warren, 1995; West, 1990).

The various types of organism that make up the BSC share some unique physiological traits. They are all capable of drying out and temporarily suspending physiological activities (dormant state). These types of organism are referred to as poikilohydric. Most of the species will be activated even after an erratic rainfall of less than 1 mm. Furthermore, some species can use high air humidity (e.g., fog or dew) to maintain metabolic processes (Lange et al.,

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1992; Lange & Meyer, 1990; Lange et al., 1994; Veste et al., 2001). Hence, BSC are considered to represent an important carbon sink on sparsely vegetated areas (Beymar & Klopatek, 1991; Evans & Johansen, 1999; Lange et al., 1992; Zaady et al., 2000). This carbon contribution provides energy for microbial soil populations (Evans & Johansen, 1999), thus supporting higher plant growth. Reports of maximal rates of net photosynthesis (NP_{max}) under optimal conditions vary greatly and span the range of two orders of magnitude, between 0.1 and 11.5 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. The latter value is of a similar magnitude to that of higher vegetation, and indicates the potential importance of crust organisms in ecosystem carbon dynamics, particularly in stressed environments (Lange, 2001). As the relative area covered by the crust communities is often much larger than that of the higher plants, the biological soil crusts are considered to contribute substantially to the carbon budget of arid and semi-arid ecosystems, where vascular plant production is low.

The vast distribution of microphytes in drylands and their fast photosynthetic response to wetting have encouraged several researchers to use spectroscopic and remote sensing applications for investigating the BSC (Karnieli et al., 2001; Karnieli & Tsoar, 1995). Karnieli et al., (1999, 1996) have shown in detail the spectral reflectance of crusts and emphasize its difference from those of vascular plants and bare-sand spectra.

The Normalized Difference Vegetation Index (NDVI), and other vegetation indices, have been intensively used for monitoring biophysical condition and vegetation cover from air- and space-borne sensors (e.g., Ichii et al., 2001; Myneni et al., 1997; Running, 1990; Tucker et al., 1986). Karnieli et al. (1999) calculated the NDVI from BSC's spectra under various wetting conditions and found that when crusts were dry, the NDVI values were low (0.08–0.13), a level also typical for dry soil/sand and rock. However, under wetting conditions, the crusts showed relatively high NDVI values (0.18–0.3). The biggest changes in the NDVI values occurred minutes after the crusts were wetted, while, as the crust dried out, the NDVI values declined. Karnieli et al. (1999) found that the chlorophyll content of crusts was much higher after 7 days of growth after wetting. Moreover, a correlation was found between the NDVI values and the chlorophyll content. Furthermore, direct relationships were also found between NDVI values and organic matter, polysaccharides content, protein content, and crust thickness. Hence, the NDVI can serve as an indicator for many physiological and ecological parameters of the BSC and can help draw conclusions on crust photosynthesis activity (Karnieli et al., 1999).

Karnieli et al. (1996) and Karnieli and Tsoar (1995) point out that high NDVI values in dry lands can lead to false interpretation of higher vegetation biomass or productivity. Previous studies have shown that when vegetation cover is less than 30%, the soil background contributes significantly

to the spectral signal (Huete et al., 1985; Huete & Tucker, 1991). Hence, satellite images that are taken from areas that are dominated by a wet and hence, active, BSC will exhibit high NDVI values with dominant contributions by the crusts and not by higher plants.

Considerable efforts have been spent in investigating the relationships between NDVI and net primary production (NPP), based on empirical results with horizontally uniform canopies (e.g., Bartlett et al., 1990; Hatfield et al., 1984; Kumar & Monteith, 1981) and model predictions (Asrar et al., 1984; Sellers, 1985, 1987; Sellers et al., 1992). These studies indicate that NDVI is related to fractional intercepted, or absorbed photosynthetically active radiation (F_{IPAR} or F_{APAR}), and thus related to the net CO_2 uptake under non-stressed conditions. However, despite the extensive research on global NPP and its distribution, most researchers have failed to consider desert areas as important contributors to NPP, due to the scattered higher vegetation and productivity estimates of less than 200 $\text{g C m}^{-2} \text{ year}^{-1}$ (Cramer et al., 1999). Although BSC cover vast areas of dry lands, to the best of our knowledge, no large-scale research has been conducted to assess their carbon sequestration potential. These microphytes might affect the arid ecosystem NPP and should be examined for their share within desert productivity estimates. Consequently, the objectives of the current study were: (1) to relate the CO_2 exchange of the BSC to ground spectral measurements throughout the wet season in two semi-arid ecosystems; and (2) to upscale these plot measurements to a regional scale, by interpreting space-borne imagery in terms of NDVI.

2. Study areas

The research was conducted in two different ecosystems in the northern Negev desert of Israel: the Agure Sand Field (ASF) and the Sayeret Shaked (SSK) Long-Term Ecological Research site (Gosz et al., 2000). In both sites, the BSC are considered to dominate surface characteristics. However, the substrate of each site is different, comprising sand dunes and loessial soil in the ASF and SSK, respectively.

The Agure sand dunes are located along the Israel–Egypt border, about 40 km southeast of the Mediterranean coastline (30°45'N, 34°13'E). Average annual rainfall in this area is about 95 mm during the winter (October–March) (Karnieli et al., 1999). Sandy linear dunes (West–East direction) characterize the landscape. The upper part of the dunes (15–20% of the region), which is exposed to wind erosion, is composed of unconsolidated sand particles (more than 95%) and it is almost devoid of vegetation. The dune hill slopes and the interdune corridors, which occupy 80–85% of the area, have a particle size distribution of about 21% sand, 55% silt, and 24% clay (Zaady et al., 2000).

The interdune area and the south facing slopes are almost completely covered by a cyanobacterial crust (*Microcoleus sociatus*, *Microcoleus vaginatus*, and *Phormidium* sp.). The north facing slopes of the dunes contain additional cyanobacterial species (*Nostoc microscopicum*, *Scytonema* sp., *Oscillatoria* sp., *Schizotrix friesii*, and *Chroococcidiopsis* sp.), cyanolichen species, green algae (*Chlorococcum* sp., *Stichococcus* sp.), and two species of moss (*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's cover and plant succession (Danin, 1991, 1996). Furthermore, the growth of the annual plants (e.g., *Senecio glaucus*, *Launaea mucronata*, *Rostraria cristata*), which appear for a few weeks after strong rain events, also contributes to the dynamic stability of the sand dunes area (Danin, 1991; Kadmon & Leschner, 1995).

The Sayeret Shaked Ecological Park (SSK) is located 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 semi-arid and sub-humid climatic zones. 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*, *T. hirsuta*, *Pituranthos tortuosus*) and patchy growth of annual plants (*Stipa capensis*, *Bromus fasciculatus*, *R. cristata*, *Avena barbata*). The soil surface is covered with a BSC (about 70%) consisting of cyanobacteria (*M. vaginatus*, *Nostoc punctiforme*, and *Choococcus* sp.), cyanophilous lichen (*Collema* sp.), and, mainly, two moss species (*Aloina bifrons* and *Crossidium crassinerve* var. *loevipilum*) (Karnieli et al., 1996; Zaady et al., 2001).

3. Methodology

Thirty-nine field campaigns, each of duration of 3 days, were conducted over the course of 2 years at the sand dune and loess environments of the northwestern Negev desert in Israel. The gas exchange of the BSC was investigated by using Teflon bag cuvettes (one empty reference plus one sample cuvette), designed especially for soil–atmosphere studies by the Max Planck Institute for Chemistry, Mainz, Germany. The cuvettes were topped on settled plots on a base of acrylic glass soil-borne collars ground into the soil at sites chosen weeks before the measurements. The empty cuvette was sealed towards the soil surface with Teflon film. CO₂ net exchange between the BSC and the atmosphere was measured under ambient air flushing and using an infrared gas analyzer (Licor, Li-7000) in the differential mode. Measurement protocols included BSC

versus soil, BSC versus empty cuvette, and soil versus empty cuvette. For details see Wilske et al. (submitted for publication).

The spectral reflectance measurements of any specific crust surface were conducted immediately after the CO₂ exchange measurements of the BSC, along with spectral measurements of the annuals, dry annuals, perennials, and bare soil/sands. These measurements were implemented with the FieldSpec-HandHeld Spectroradiometer (manufactured by Analytical Spectral Device (ASD), 2000), at wavelengths of 325–1075 nm with a spectral resolution of 2 nm. A High Intensity Contact Probe device with a fiber optic was attached to the spectroradiometer. This device had an independent light source, which made it feasible to take measurements under all weather conditions. The contact probe was attached to the BSC's surface and measured its spectral reflectance. Measurements of a white reference panel (Spectralon plate, Labsphere Inc.) were taken immediately before each spectral measurement.

The percentage cover for each ground feature was measured separately. The perennials' aerial cover was measured, using the McAuliffe method (McAuliffe, 1990), developed especially for rapid estimation of density and cover of perennial vegetation in arid environments. In addition, several random plots of 1 m² were photographed with a digital camera for measuring the percentage cover by BSC, annuals, and dry annuals. These photographs were used for the supervised classification, using the ERDAS IMAGINE software (Richards, 1993).

Twenty-eight Satellite Pour l'Observation de la Terra (SPOT) images of 20 m resolution were acquired over the course of the 2 years of research, in order to scale up the field measurements to a regional perspective. These images were subject to radiometric, atmospheric, and geometric correction procedures.

NDVI values were calculated, both from the ground spectral measurements and the satellite images, by using the following equation (Rouse et al., 1974):

$$\text{NDVI} = (\rho_{\text{NIR}} - \rho_{\text{R}}) / (\rho_{\text{NIR}} + \rho_{\text{R}}) \quad (1)$$

where ρ_{NIR} and ρ_{R} are the reflectances in the near infrared and red bands, respectively, corresponding to SPOT spectral bands No. 3 (0.79–0.89 μm) and No. 2 (0.61–0.68 μm).

A linear mixture model (Ichoku & Karnieli, 1996; Settle & Darke, 1993) was applied to the ground data from the two study sites. In order to assess the weighted NDVI (NDVI_w) from the relative NDVI contribution of each end-member (j), the commonly used linear mixture model was reformulated as:

$$\text{NDVI}_w = \sum_{j=1}^n (f_j * \text{NDVI}_j) \quad (2)$$

in which the NDVI_w is the sum of the products of the NDVI and the respective percentage areal cover (f) for

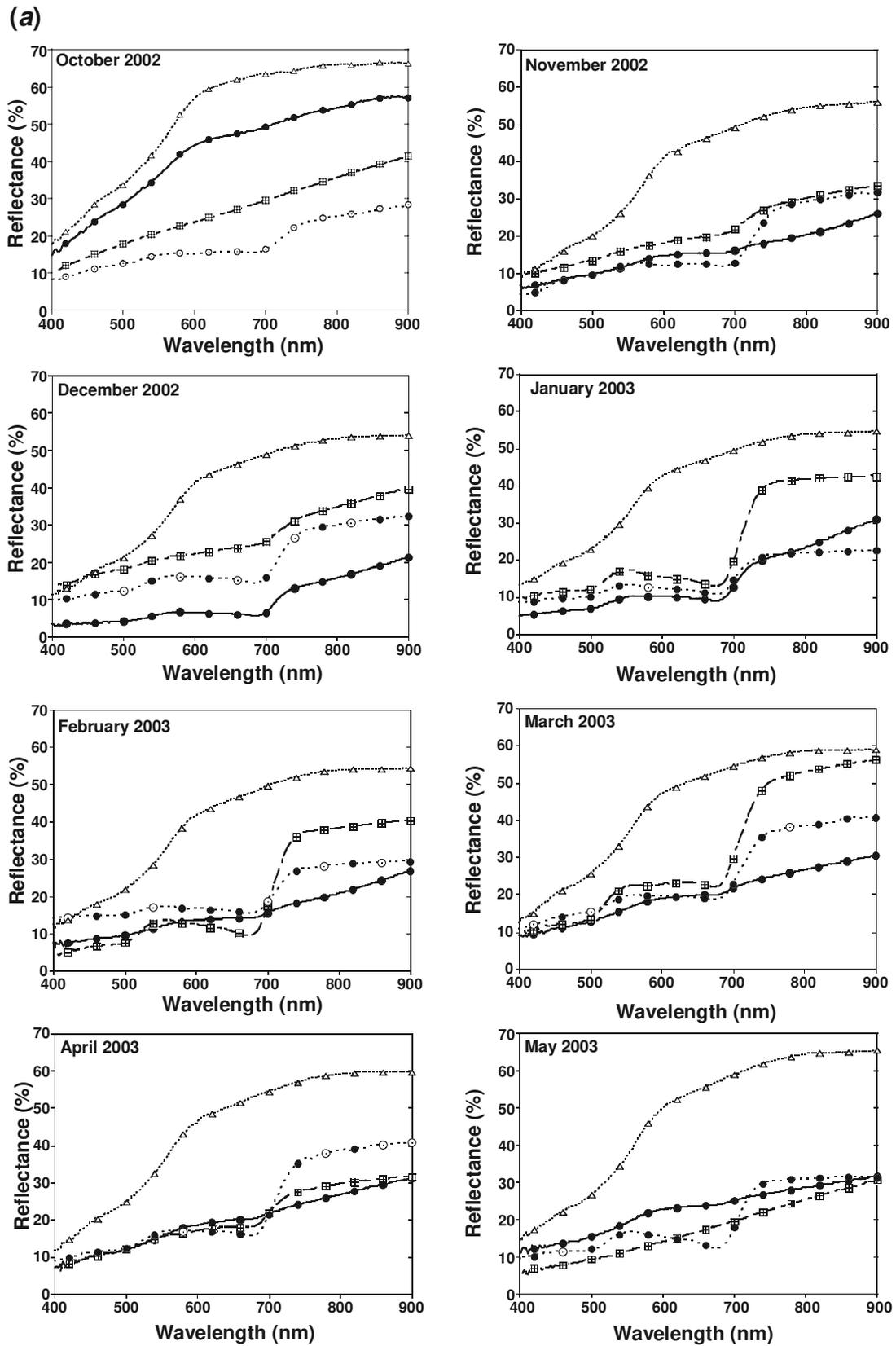


Fig. 1. Spectral reflectance of the end-members: BSC (—■—), Annuals (—□—), Perennials (—○—), Bare Sand/Soil (—△—), (a) at the sand dunes and (b) at the loess environment.

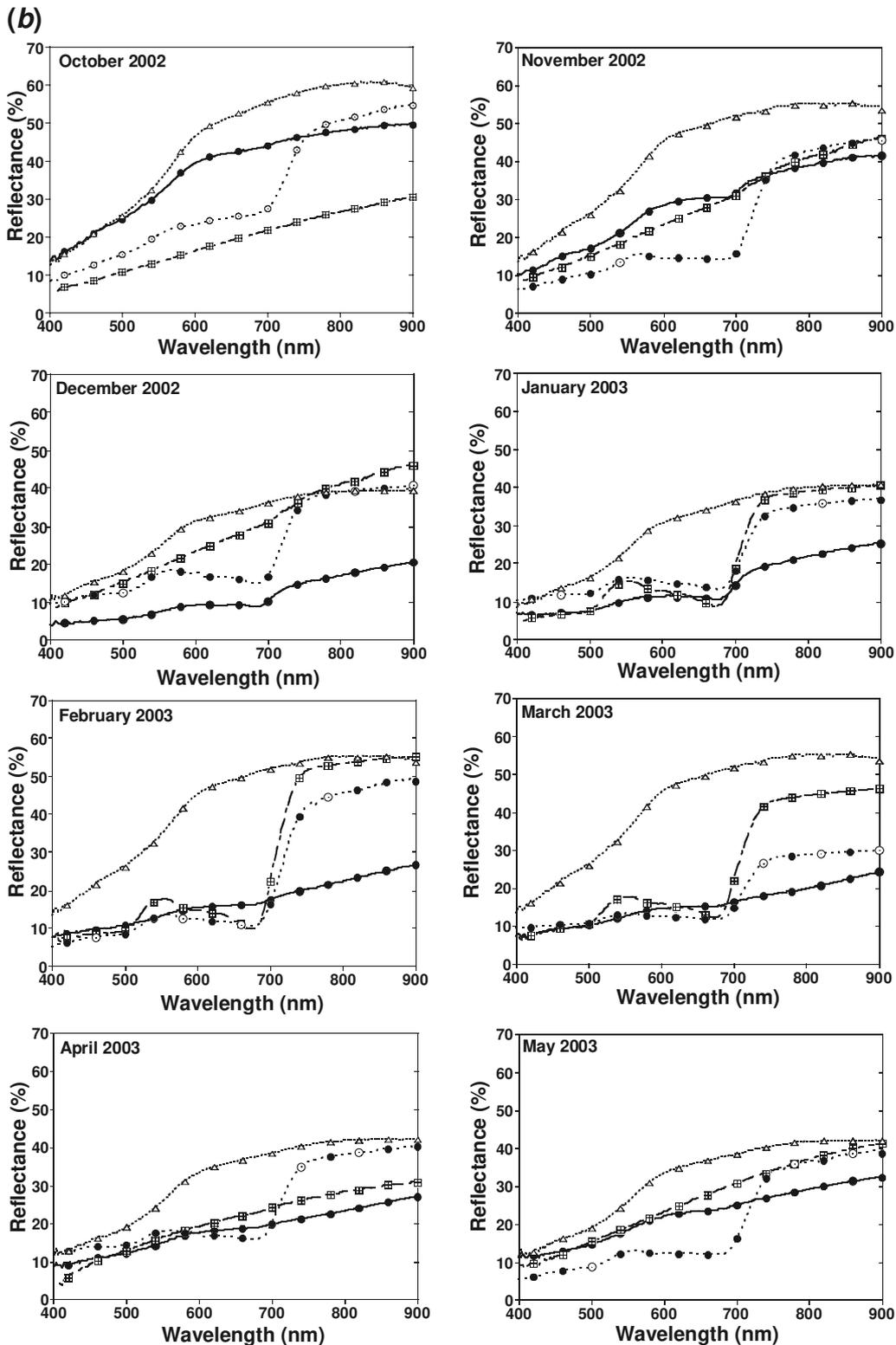


Fig. 1 (continued).

each of the n ground features (Karnieli, 2003). This calculation was performed for each of the field campaigns. According to the basic assumption, the NDVI extracted from the SPOT images should match the weighted NDVI

calculated from the ground measurements. Good agreement between the two would indicate an accurate representation of the state of all single contributors found in the study area.

4. Results and analysis

4.1. Spectral reflectance

The spectral reflectance dynamics of the ground features during the 2002/2003 wet season, at the sand dunes and at the loess environment, are presented in Fig. 1. Despite the differences in environmental conditions, both sites show a basic similarity within the spectra of each contributing element throughout the year. By itself, the spectral reflectance is expected to indicate the physiological activity of the vegetal elements, as expressed by the dip of the reflection in the upper 600 nm spectral region. These graphs show continuous activity throughout the year for perennials, whereas the BSC and annuals are active from December to February and January to March, respectively. The bare soils/sands are characterized by the highest reflectance, decreasing slightly during the wet season due to wetting, but without changing their general spectral shape.

4.2. NDVI of the different ground features

Table 1 presents the relative contribution of each ground feature to the overall NDVI signal at the sand dunes and at the loess environment, for the hydrological year 2002/2003. At both sites, the BSC and the annuals exhibit the most dynamic variation in their NDVI values, whereas the

Table 1

Average values of NDVI for each ground feature during the study year (a) at the sand dunes environment and (b) at the loess environment

(a)					
Date	BSC	Annuals	Dry annuals	Perennials	Bare sand
09 Oct. 02	0.08	0	0.15	0.32	0.06
07 Nov. 02	0.13	0	0.15	0.30	0.08
14 Nov. 02	0.14	0.20	0	0.29	0.09
07 Dec. 02	0.16	0.22	0	0.31	0.09
19 Dec. 02	0.28	0.21	0	0.35	0.09
01 Jan. 03	0.24	0.34	0	0.31	0.08
11 Jan. 03	0.25	0.40	0	0.28	0.10
14 Feb. 03	0.23	0.35	0	0.41	0.09
07 Mar. 03	0.22	0.24	0	0.35	0.09
29 Mar. 03	0.15	0.22	0	0.36	0.09
02 May 03	0.16	0.17	0	0.37	0.08
31 May 03	0.16	0	0.13	0.37	0.08
(b)					
Date	BSC	Annuals	Dry annuals	Perennials	
21 Oct. 02	0.12	0	0.15	0.29	
06 Oct. 02	0.14	0.24	0.15	0.33	
25 Nov. 02	0.15	0	0.15	0.30	
12 Dec. 02	0.23	0	0.16	0.29	
01 Jan. 03	0.33	0.30	0.15	0.34	
20 Jan. 03	0.33	0.33	0	0.31	
30 Jan. 03	0.32	0.34	0	0.34	
22 Feb. 03	0.25	0.37	0	0.37	
18 Mar. 03	0.18	0.36	0	0.36	
10 Apr. 03	0.13	0.35	0.15	0.38	
23 Apr. 03	0.14	0.21	0.15	0.38	
20 May 03	0.14	0	0.14	0.39	

Table 2

The percentage cover of each of the ground features (a) at the sand dunes environment and (b) at the loess environment for the hydrological year 2002/2003

(a)				
Date	BSC	Annuals	Perennials	Bare sand
09 Oct. 02	69.95	0	11.05	19.00
07 Nov. 02	69.95	0	11.05	19.00
14 Nov. 02	69.92	0.03	11.05	19.00
07 Dec. 02	69.78	0.05	11.17	19.00
19 Dec. 02	63.67	5.38	11.95	19.00
01 Jan. 03	58.35	10.13	12.52	19.00
11 Jan. 03	57.17	11.25	12.58	19.00
14 Feb. 03	56.15	11.39	13.46	19.00
07 Mar. 03	53.26	12.95	14.79	19.00
29 Mar. 03	60.40	6.35	14.25	19.00
02 May 03	65.06	2.05	13.89	19.00
31 May 03	66.64	0	14.36	19.00
(b)				
Date	BSC	Annuals	Dry annuals	Perennials
21 Oct. 02	60.31	0	37.95	1.75
06 Oct. 02	61.23	9.04	27.99	1.75
25 Nov. 02	60.48	0	37.78	1.75
12 Dec. 02	61.18	0	37.01	1.81
01 Jan. 03	53.22	44.87	0	1.90
20 Jan. 03	51.11	46.84	0	2.05
30 Jan. 03	43.56	54.27	0	2.17
22 Feb. 03	33.77	63.91	0	2.32
18 Mar. 03	27.49	70.16	0	2.35
10 Apr. 03	24.62	37.87	34.88	2.64
23 Apr. 03	25.27	10.63	61.17	2.93
20 May 03	28.56	0	68.19	3.25

perennials and the bare sands (only at the sand dunes) are almost constant all year round. The BSC contribute strongly to the overall NDVI, mainly at the beginning of the wet season, whereas the annuals contribute from the middle of the winter to the end of the springtime. The perennials have high NDVI values throughout the year, with a slight increase after the main rain events (February–May). The highest overall NDVI values are reached at the time when the growth of the BSC and annuals approach their maximum (January–February).

In general, the NDVI values of the vascular plants are higher than those of the BSC. Of the seasonal average, the annuals and the perennials at the sand dunes contributed about 28% and 41%, respectively, whereas the BSC contributed about 21% to the component sum NDVI. At the loess environment, the annuals and the perennials contributed about 32% and 41%, respectively, and the BSC contributed about 24%. These values can imply on the differences in the photosynthetic rates between these elements.

4.3. Percentage cover of the different ground features

The percentage cover is an important variable for computing the weighted NDVI on which the linear mixture model is based. Table 2 presents the proportion of the ground features to the total cover at the two sites, for the hydrological

year 2002/2003. The dominance of BSC cover can be identified at both sites. However, in contrast to the relatively constant cover of all contributing elements at the sand dunes, the loess area exhibits the appearance of an extensive cover of annuals in the seasonal cycle causing a dramatic change in the land cover. From January to the beginning of April, the contribution of the annuals exceeds that of the BSC. Later in the year, towards the hot season, the annuals dry out and the BSC once again takes over. These considerably different dynamics at both sites have a significant influence on the outcome of the linear mixture model.

4.4. Linear mixture model and satellite image analysis

Relating the NDVI of the different end-members to their respective covers provides the weighted NDVI that is used in the linear mixture model (Eq. (2)). The model is used to assess the phenological cycle of the field components and to relate the field measurements to the data acquired from the satellite.

The phenological cycle of the different cover elements, given as the weighted NDVI for the sand dunes for 2001/2002, is presented in Fig. 2a. The BSC peak is in January, after the main rain events, while the annuals reach their moderate peak only in the middle of February. The perennials contribute on a low level, but show a slight increase towards the end of the rainy season. The dominance of the BSC is obvious: although they reach their phenological peak early in the wet season, they continue to constitute a substantial part, even when they dry out, whereas the annuals reach their peak, dry out, and vanish. This leads to the conclusion that the cover domination of the BSC is the reason for their high weighted NDVI.

The upper line in Fig. 2a represents the cumulative NDVI weighted elements in the field and it should resemble the NDVI values acquired from the SPOT satellite. One can see that, although there are some small variations along the year, a meaningfully good agreement was achieved between the values derived from the ground-based measurements and those from the satellite. The correlation between the two sets of data has an $r^2=0.94$. Hence, the linear mixture model closely follows the SPOT-derived NDVI data, detailing its components and their annual intensity. The same general phenological pattern was found in the second year of measurements 2002/2003 (Fig. 2b). Again, the domination of the BSC can be seen. Furthermore, the SPOT satellite NDVI data and the weighted NDVI cumulative curve are again very similar, with a high correlation of $r^2=0.88$.

Another alternative for evaluating the “goodness of fit” between the weighted NDVI values ($NDVI_w$), compiled by the linear mixture model, and the satellite-derived NDVI values ($NDVI_s$) exists via the root mean square deviation (RMSD) (Gao et al., 2003):

$$RMSD = \sqrt{\frac{1}{n} \sum_{i=1}^n (NDVI_w - NDVI_s)^2} \quad (3)$$

The RMSD reveals a very small variation from year to year, 0.146 ± 0.007 and 0.142 ± 0.013 in 2001/2002 and 2002/2003, respectively. Hence, the model in both years closely resembles the satellite view.

Comparing the years 2001/2002 and 2002/2003 (Fig. 2a and b), a delay of about one month in the overall phenological cycle is observed. This trend can be explained by the rainfall distribution. In the first year, the total amount of rain was lower than the annual average (74 mm) and was mainly concentrated around the month of January. The second year was characterized by higher rainfall amounts (126 mm), evenly distributed throughout the season, thus allowing for a more advantageous scenario for vegetation growth and development. Therefore, in the first year, the BSC reached their peak only at the end of January, compared to a peak in the middle of December in the following year. Annuals showed a similar pattern, reaching their maximal development in February, while in the following year they had already reached their peak by the beginning of January. This corresponds well with the time of germination of the seeds of the annuals, which also occurred 1 month earlier (December) than in the first year. The cycle of the annuals ended completely by the end of April/beginning of May in both years. Hence, the length of the growing season was also influenced by the beneficial rain distribution in the second year. However, while we detected different cycle lengths during the two data sets, the apparent physiology cannot be related to these phenological aspects. The low amount of water needed by the organisms of BSC makes it more difficult to clearly delimit the cycle, as can be done, for example, in the case of annuals.

The phenological cycle of the ground features at the loess environment for 2001/2002 is presented in Fig. 2c. Similar phenology to the sand dunes can be observed. However, in contrast to the dominance of the BSC at the sand dunes, we can discern two phenological cycles in the loess area: (1) a clear maximum at the beginning of the wet season for the BSC; and (2) a maximum caused by the annuals in the middle of the wet season.

The temporal patterns of the summarized, weighted, ground-based NDVI and the SPOT NDVI are similar, showing a high correlation ($r^2=0.73$). Hence, the linear mixture model again successfully mirrors the satellite NDVI data and specifies its components and their strength on a temporal scale. The same general pattern was found for the second year of measurements (Fig. 2d), with a correlation factor of $r^2=0.92$. The RMSD analysis was 0.20 ± 0.011 and 0.23 ± 0.019 for the 2001/2002 and 2002/2003 years, respectively.

Further comparison between the two linear mixture models (Fig. 2c and d) reveals that despite the large difference in the total amounts of rainfall, 138 and 238 mm in 2001/2002 and 2002/2003, respectively, which have a strong influence on the phenology cycle length of each element (particularly for the higher plants), the NDVI data

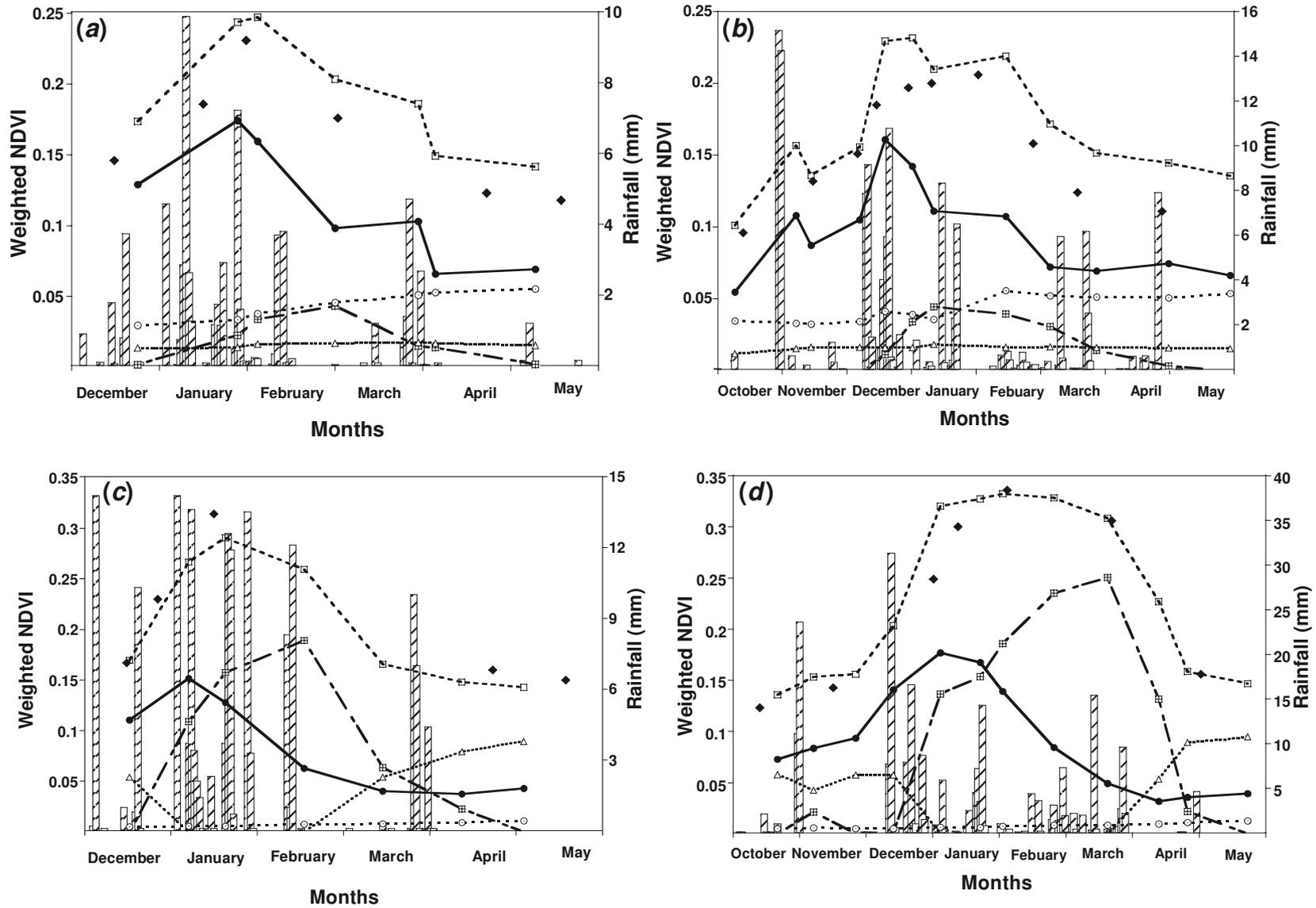


Fig. 2. NDVI linear mixture model of the end-members: BSC (—■—), Annuals (—■—), Bare Sand/Dry annuals (—△—), Perennials (—○—), Cumulative (—□—), SPOT (◆), Precipitation (▨) at the sand dunes and loess environment for the year 2001/2002 (a and c) and 2002/2003 (b and d), respectively.

derived from the SPOT satellite fits the model well. Furthermore, a high correlation was found when combining the data for both years, i.e., the cumulative linear mixture curves and the SPOT NDVI data ($r^2=0.86$). This finding substantiates the claim that the linear mixture model is a good tool for representing the satellite view.

4.5. NDVI and CO₂ analysis

In order to get a seasonal overview of the relationships between the NDVI and the CO₂ exchange, the two variables were averaged over the available data points per field campaign. Fig. 3 shows the seasonal dynamics between NDVI and CO₂ net fluxes for the BSC at the sand dunes and at the loess environment. On a seasonal scale a similar pattern can be observed between the NDVI and the CO₂ exchange. A strong increase of the NDVI at the beginning of the wet season (December) is observed. Once the crusts are developed, the NDVI remains

relatively stable at a certain level (about 0.3), and changes in a way similar to the CO₂ fluxes, according to the availability of moisture (January–March). Hence, if the rain is well distributed, the crusts grow, develop, and stay in a good physiological condition during most of the winter season. The standard deviations for both variables grow when the physiological activities increase (during and after rainfall events). This scatter can be related to rapid changes (within a few days) of photosynthetic activities, in close accordance with drying out processes (Burgheimer et al., submitted for publication; Wilske et al., submitted for publication). The correlation between the two variables on this scale of resolution was $r^2=0.73$ and $r^2=0.80$ for the sand dunes and for the loess area, respectively.

The potential of the NDVI to detect BSC’s photosynthetic activity on different time scales have been addressed by Burgheimer et al. (submitted for publication) and Wilske et al. (submitted for publication). In Fig. 4, the

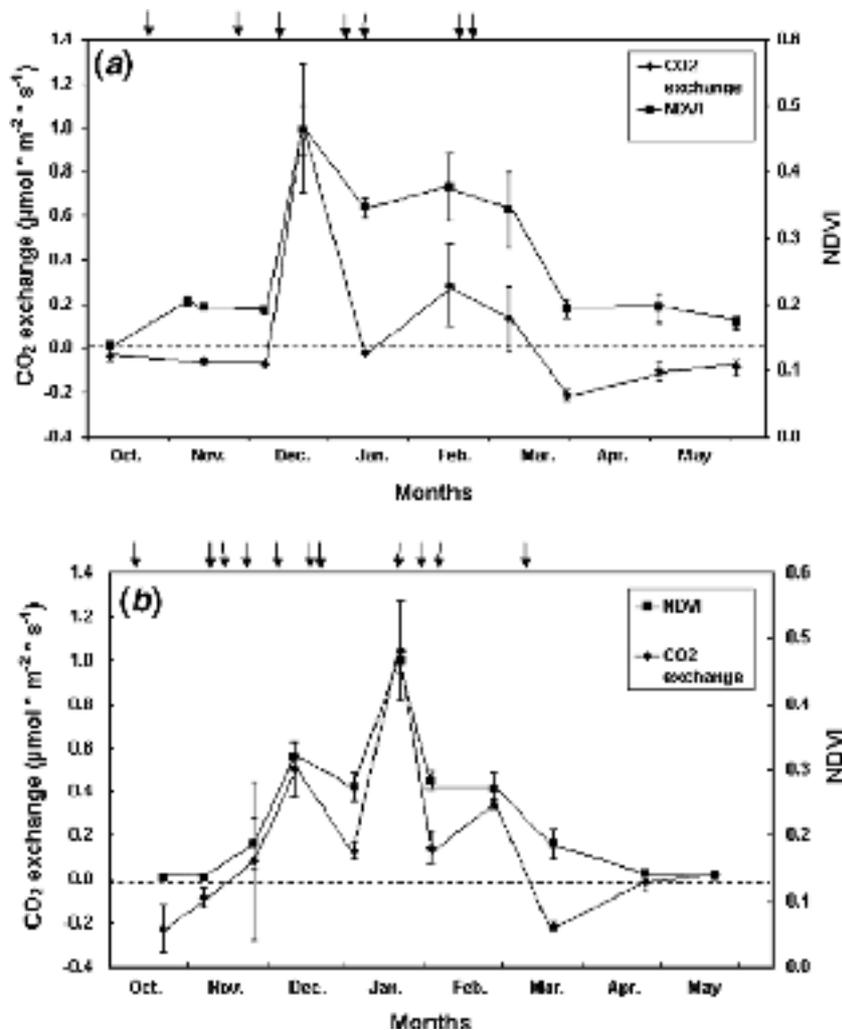


Fig. 3. Seasonal dynamics of the NDVI and the CO₂ exchange for the mix BSC (a) at the sand dunes and (b) at the loess environments. Positive rate of CO₂ exchange mean carbon sequestration. (The arrows indicate the main rain events, more than 5 mm; the vertical bars indicate standard deviation.) Modified from Burgheimer et al. (submitted for publication).

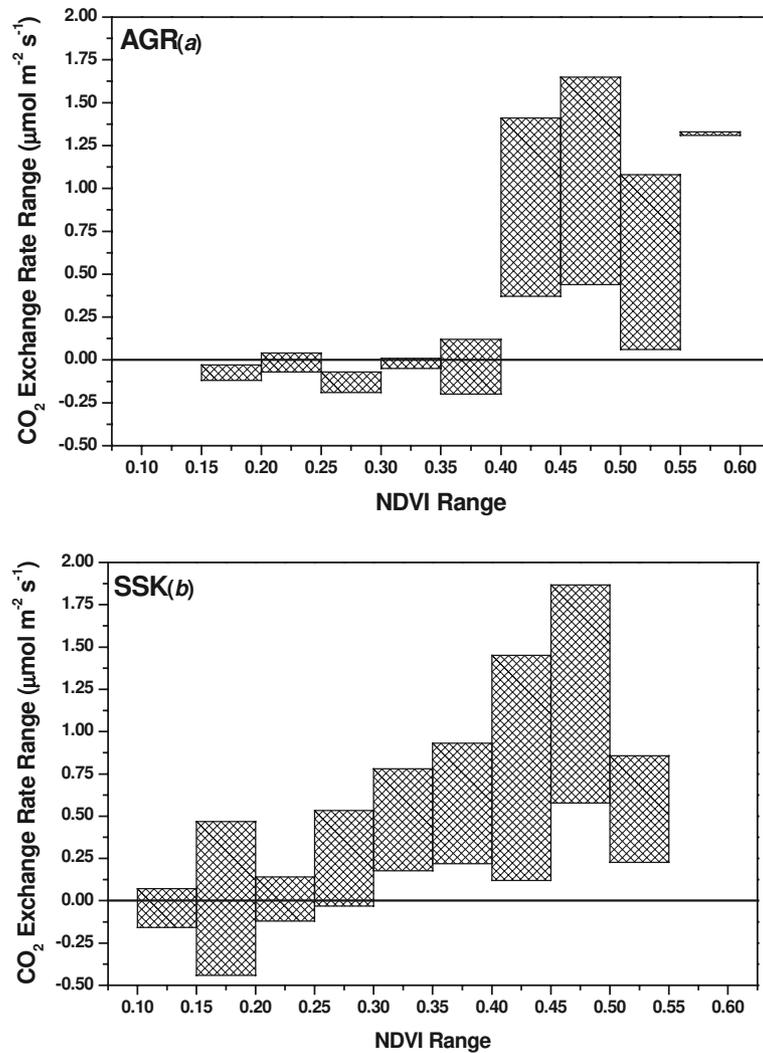


Fig. 4. Relationship between the NDVI and the BSC's CO₂ exchange (a) at the sand dunes and (b) at the loess environments for the hydrological years 2001–2003.

NDVI data are grouped (time independent) into small ranges (of 0.05 units) and the CO₂ exchange rates associated with each NDVI value in the narrow range averaged. For both of the study sites, the increase of the photosynthetic rate was associated with the increase in NDVI, but this was also associated with large potential of CO₂ exchange rates. This pattern is due to the nature of the BSC's CO₂ exchange behavior, which is highly sensitive to local moisture dynamics, whereas the NDVI represents an accumulation of simultaneous biophysical parameters (Running, 1990; Tucker et al., 1986; Tucker and Sellers, 1986) and responds more slowly to drying-out process. Including the moisture regime data will help to obtain more accurate information on the CO₂ exchange–NDVI relationship.

When the two sites are compared, large differences can be seen at the lower end of the NDVI values, where the CO₂ exchange range is larger within the SSK graph. This pattern is likely to be related to the moisture holding capacity of the two soil types.

5. Discussion

The ecological function of BSC has been investigated and discussed in many studies. It was found that these microphytic soil crusts contribute to the maintenance of ecosystems and assist in catalyzing the successional level of a certain area (Warren, 1995; West, 1990; Zaady et al., 2000). Their contributions are particularly significant in growth environments that are harsh for vascular plants (i.e., arid and semi-arid deserts), where the essential sources for growth are limited (i.e., water, nutrients, soil) (Belnap & Harper, 1995; Evans & Johansen, 1999). With respect to carbon assimilation, BSC were reported to assimilate CO₂ at rates similar to C3 plants (surface to leaf surface) under optimal conditions (Belnap & Lange, 2001). Taking into consideration the fact that these BSC organisms cover vast arid and semi-arid areas around the world (Karnieli et al., 2001) and that our understanding of the global carbon budget, concerning the different terrestrial ecosystems, is insufficient (Wigley & Schimel, 2000), an investigation of

the contribution of BSC to the global carbon budget is of particular interest.

A feasible way to investigate BSC on a large scale is by using remote sensing approaches (i.e., satellite or airborne images). The first step in establishing a BSC's NDVI–CO₂ exchange relationship, on the basis of ground-based measurements in the western Negev of Israel has been recently reported (Burgheimer et al., submitted for publication). The authors found that the NDVI has the potential to roughly indicate the range of magnitude and capacity of the BSC's assimilation activity, which is significantly influenced by environmental factors (i.e., soil water content and light intensity) at any particular moment. In addition, the index was found to be a good tool for representing the BSC's seasonal photosynthetic activity (Fig. 3). Gamon et al. (1995) reported a positive correlation between the seasonal pattern in maximum net CO₂ uptake of semi-deciduous shrubs and their NDVI. Hence, the NDVI may be regarded as a sufficiently reasonable parameter in estimating the range of photosynthetic activity and its capacity along the BSC's phenological cycle within a certain range of errors.

The linear mixture model that was applied to both sandy and loess environments was found to be a good tool for representing the dynamic phenological cycles of the different ground features in the field, over the course of the year. Furthermore, good correlations and RMSD were found between the NDVI extracted from the satellite images and the linear mixture model (cumulative weighted NDVI). Thus, the model is a useful tool that can be used to understand the components contributing to the NDVI values derived from satellite data. One crucial problem is that the dominant and permanent BSC cover at the studied sand dunes site affected the accuracy of the linear mixture model, and caused an increased discrepancy with the satellite NDVI data, especially toward the end of the wet season.

At both sites, the BSC exhibited a phenological cycle with an early peak at the beginning of the wet season, before the germination of the annuals. Hence, the high NDVI value extracted from the satellite images at this time can be attributed to the initializing of BSC's activity earlier than that of other competitors. This is in agreement with Schmidt and Karnieli (2002), who used NOAA AVHRR images with a low resolution of 1 km. Thus, even at a low resolution, the satellite can distinguish and detect the BSC's phenological cycle.

The linear mixture model could also prove to be a good tool for monitoring varying lengths of the phenological cycle from year to year. Changes in these cycles over extended time periods may be interpreted to indicate processes, such as desertification or other trends caused by global climate change. Therefore, monitoring phenological cycles via remote sensing techniques could be an important tool for determining biological responses to climate change in semi-arid and arid ecosystems of the world.

Large differences in the amount of precipitation between the 2 years of this survey strongly influenced the pheno-

logical cycle length of the biological competitors. Among the ground features, the BSC's phenology cycle was less affected, as their initial water requirements for activity is low. Hence, the crusts develop immediately with the early rain, reach their phenology peak within a month of the highest precipitation, and then start to decline slowly. As stated by Karnieli et al. (2002), the rainfall and its scatters are the key to understanding the dynamic phenology shifting of the ground features. In conclusion, despite the disparity in the rainfall pattern between the 2 years, the linear mixture model reliably described the dynamic phenological changes that occurred in each year and offered a good relationship with the satellite data.

Relating these linear mixture models to the seasonal dynamics of the BSC's CO₂ exchange (Fig. 3) demonstrates the potential for using remote sensing methods to estimate BSC's assimilation activity. At both sites, the phenology peak of the BSC corresponds well to the time when the highest BSC CO₂ activity was observed, December and January at the sand dunes and loess environments, respectively. Similar relationships with the vascular plants will lead to the ability to draw reasonable conclusions on the entire ecosystem productivity, by means of remote sensing applications.

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