PLANT MICROBE INTERACTIONS

Are Biological Effects of Desert Shrubs More Important than Physical Effects on Soil Microorganisms?

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Abstract Vegetation cover plays a major role in providing organic matter and in acting as a physical barrier, with both together contributing to the formation of "fertile islands," which play an active role in prolonging biological activity in desert ecosystems. By undertaking this study, a long-term research, we designed an experiment to separate the two components—the physical and biotic parts of the perennial plants—and to identify the factor that contributes the most to the ecosystem. The study site was located in the northern Negev Desert, Israel, where 50 *Hammada scoparia* shrubs and 50 artificial plants were randomly marked. Soil samples were collected monthly over 3 years of research at three locations: under the canopy of *H. scoparia* shrubs, in the vicinity of the artificial plants, and between the shrubs (control). The contribution to microbial activity was measured by evaluation of the microbial community functions in soil. The functional aspects of the microbial community that were measured were CO_2 evolution, microbial biomass, microbial functional diversity, and the physiological profile of the community. The results of this study are presented in two ways: (1) according to the three locations/treatments; and (2) according to the phenological situation of the vegetation (annual and perennial plants) in the research field: the growing phase, the drying process, and the absence of annual plants. The only parameters that were found to affect microbial activity were the contribution of the organic matter of perennial shrubs and the growth of vegetation (annual and perennial) during the growing seasons. The physical component was found to have no effect on soil microbial functional diversity, which elucidates the important contribution of the desert shrub in enhancing biological multiplicity and activity.

Introduction

Water availability is one of the main limiting factors that largely determine community functions in desert ecosystems [1–4]. In the Negev Desert, rain events are usually relatively short and scattered over long periods of time during the winter season (November–April) [1]. Dew formation is an additional and important source of water that triggers and prolongs biological activity during the long dry season [5, 6]. Because precipitation is scarce, soil microbial activity episodes are described by the pulse-reserve model [7].

The spatial structure of arid ecosystems has been described as a mosaic of plant-centered "islands of fertility" [8]. These islands are defined by a concentration of organic matter originating from primary production and from nutrients that exceed those of the surrounding soil and provide loci for biogeochemical activity. In deserts, primary production is based mainly on perennial plants that have access to essential moisture and nutrients due to their wide range of ecophysiological adaptations [1, 9]. One of the main ecophysiological adaptations of the perennial plants in desert ecosystems is a reduction in the area of their transpiring surface when soil moisture becomes limiting. This occurs when they shed some of their parts (leaves, stems, branches, roots, etc.) in order to keep the remaining parts alive and active [1] toward the summer months—the dry season.

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The above- and belowground components of terrestrial ecosystems essentially depend on each other since plants provide carbon sources for the soil fauna. Perennial shrubs allow soil microbial communities to increase and prolong their above- and belowground activities [9–14]. Soil microorganisms are of great importance for long-term sustainability of ecosystems [15], since they play key roles in organic matter decomposition, nutrient cycling, and maintenance of soil structure.

The contribution of the perennial plants can be divided into two components: biological and physical contributions. The organic component includes the litter, fruits, and seeds and roots exudates. These products supply the microbial communities in the soil with a large diversity of carbon sources [16–19]. The physical component is the barrier that protects the below-shrub area from high radiation and decreases wind velocity, which together contribute to improving water balance and to an increase in litter and seed accumulation below the canopy [20, 21]. Plants and microbial community structure and diversity are known to be closely correlated [22] through the utilization of dead cells, root exudates, and litter, resulting in an interwoven interaction between them [16, 19, 23]. Considerable information is available on the effect of plant diversity on the microbial community [17, 24]. However, the difference between the physical and biological contributions of perennial plants on the microbial community is not understood.

The aim of this study was to examine the physical and organic contributions of perennial shrubs to the microbial community over 3 years in a Negev Desert ecosystem. By undertaking such a long-term research, we expected to be able to distinguish between the two components—the physical and the biotic (organic) contributions of the perennial plants by using the functional aspects of the active bacterial community such as CO_2 evolution, microbial biomass, physiological profile, and functional diversity. These parameters were monitored in the vicinity of *Hammada scoparia* shrubs, representing the physical and biotic effects of perennial plants, and in the vicinity of artificial shrubs, representing only the physical influences of the perennial shrubs.

Based on the above discussion, we hypothesized that soil microbial activity represented as CO_2 evolution, microbial biomass, physiological profile, and functional diversity would be regulated by the dual roles of the perennial shrub. We predicted that both components of perennial shrubs would positively affect the soil community biomass, CO_2 evolution, and functional diversity and enhance microbial activity. Isolation of the two perennial shrub features at the Avdat Farm Research Station in the Negev Desert Highlands, Israel, in this study, enabled a better understanding of the importance of perennial shrubs as long-term moderators of soil microbial activity.

Material and Methods

Study Site

The field study site is about 600 m above sea level. The area has a temperate desert climate with hot summers (mean maximum air temperature 32°C; mean minimum air temperature 17.7°C, in June) and cool winters (mean maximum temperature 14.8°C; mean minimum temperature 5.4°C, in January). The multiannual mean rainfall is 90 mm at Avdat Station and occurs in scattered showers only during the winter season (November–April). An additional source of moisture is dew, which falls heavily during the autumn months (September–November) [1]. The soils are brown, shallow, rocky, desert soils (brown lithosols), loessial, and gray desert soils (loessian sierozems) [25]. The vegetation is a mixture of perennial shrub communities with a large variety of annuals. Predominant perennials at the research site are *H. scoparia*, *Zygophyullum dumosum*, *Artemisia sieberi*, and a variety of annual plants and geophytes.

Experimental Setup

Fifty *H. scoparia* shrubs were randomly marked at the study site within a 10,000-m² fenced area. Fifty artificial shrub-like plants made of plastic were also placed randomly in the study area (with about 2 m between both shrub types). The artificial plants were chosen in order to emulate *H. scoparia*'s physical contribution, and they looked similar to the natural shrubs in the field (same size and proportions—about 45 cm high and 40 cm in diameter).

Soil samples were collected from depths of 0–10 cm starting immediately after setup of the experiment and continuing for a period of 3 years (December 2005 to November 2008). The samples were collected monthly ($n=$ 4) from three locations/treatments: (1) under the canopy of *H. scoparia*; (2) under the canopy of the artificial plants; and (3) from the interspace between the shrubs (control samples). The soil samples were placed in individual plastic bags and transported in a cooler to the laboratory. All soil samples were sieved (mesh size 2 mm) in order to remove root particles and other organic debris and were kept at 4°C until biological and chemical analyses were performed.

The results of this study are presented in two ways: according to the three locations/treatments (under the canopy of *H. scoparia* shrubs, in the vicinity of the artificial plants, and control—between the shrubs) and according to the phenological situation of the vegetation (annual and perennial plants) in the research field. The phenological characteristics are divided into three categories of vegetation processes that were observed throughout the 3 years of study: the first is a growing phase, in which

both annual and perennial plants are green and productive aboveground=growing biomass (G.B.; between December and May—which could be different in length, dependence on rainy season, and its distribution); the second phase is the drying process, in which all annuals are still aboveground but dry=dry aboveground biomass (D.A.B; between March and Jun—which could be different in length following the wet period); and the third phase is when all the annual vegetation disappears and perennial plants are the only reproductive vegetation in the field=no aboveground biomass (N.A.B.; between July and November, differ each year depends on the two phases).

Methods

Soil moisture was determined gravimetrically by drying samples at 105°C for 48 h and was expressed as percentage of dry weight.

Organic matter content was determined by igniting samples at 490°C for 8 h.

Total soluble nitrogen (TSN) was determined by chemical extraction and color reactions using a Skalar autoanalyzer [26] that measures NH_4 and NO_3 content.

Microbial functional diversity and community level physiological profile (CLPP) were detected using the MicroResp^{TM} plate [27]. Fifteen different carbon sources of carbohydrates, carboxylic acids, amino acids, and aromatic carboxylic acids (Table 1) were added to whole soil samples (0.33 g in each well) in deep well plates. CO_2 evolution was measured by dye plates—a colorimetric reaction using absorbent alkali with the ability to measure carbon dioxide evolution. The plates were read twice in a spectrophotometer at 590 nm: just before the plates were placed on the deep wells containing the soil samples (time 0), and after 6 h of soil respiration (time 1). During that time, the plates were incubated in the dark at 27°C. The result for each well was calculated compared to the 16th well, which contained the same soil sample and water, measuring the basal respiration with no added carbon source

Microbial functional diversity was determined using the Shannon–Weaver index (H'): $H'=-\sum Pi (\ln Pi)$, where Pi is

the ratio of the activity of a particular substrate and the sum of activities of all substrates [28].

Microbial biomass and CO_2 evolution were measured by dye plates—a colorimetric reaction using absorbent alkali with the ability to measure carbon dioxide evolution. Water was added to whole soil samples in deep well plates covered by the dye plates in order to measure respiration. Glucose was added to determine microbial biomass according to the substrate-induced respiration method. CO_2 values were measured after 6 h of soil respiration [29].

Statistics

All the data obtained in the study were subjected to statistical analysis of variance using the SAS model (analysis of variance (ANOVA), Duncan's multiple range tests, and Pearson correlation coefficient) and were used to evaluate differences between separate means. ANOVA was followed by Tukey's Honestly Significant Differences test to establish the significance of differences between plot areas using the statistical package Statistica 4.3. Differences obtained at levels of $P<0.05$ were considered significant. Significant differences ($P<0.05$) between parameters are represented by small letters in the body of the figures.

Redundancy discriminate analysis (RDA) is a direct ordination method based on linear regression, essentially the canonical form of principle component analysis [30]. The data were tested by carrying out RDA for each treatment and phenological phase of the vegetation in order to provide more information, allowing environmental factors and properties related to the results to be proportionally explained (program CANOCO version 4.54, October 2005—written by ter Braak [31]. The Monte Carlo permutation test (499 permutation was used for the test) was used to calculate the significance of a given environmental factor and its relevance to results obtained during the study period [32]. The figure presented is a simple graphical output for a complex change in many variables simultaneously. Arrows pointing in roughly one direction indicate a high positive correlation, whereas, arrows pointing in the opposite direction indicate a high negative correlation. The arrows of the environmental and biotic

Table 1 The different carbon sources added to soil using MicroRespTM divided into chemical groups

Aromatic carboxylic acids	Carboxylic acids	Carbohydrates	Amino acids
3,4-Dihydroxybenzoic acid (protocatechuic acid)	L-alanine	L-arabinose	Citric acid
	Arginine	D-fructose	L-malic acid
	L-cysteine HCI	D-galactose	Oxalic acid
	γ-Amino butyric acid	D-glucose	
	L-lysine	Trehalose	
	N-acetyl-glucosamine		

variable are long and exhibit greater influence than the shorter ones, which are of an inferred correlation.

Results

Precipitation

The total amounts of rainfall from each rainy season during the study period varied significantly between the 3 years of the study, ranging from 58.8 to 175.6 mm (Fig. 1). During the first rainy season (November 2005–April 2006), rainfall totaled 58.8 mm, which represents 65% of the multiannual average, with 85% of the rain falling during two of the four rainy months (46% and 39% in February and April, respectively). In April 2006, the total rainfall was 57.3 mm, representing 64% of the multiannual average. In the second rainy season (October 2006–May 2007), the amount of rainfall was more than three times that of the previous year, with a total of 175.6 mm. In April 2007, the total rainfall was 57.3 mm, representing 64% of the multiannual average. In the third rainy season (December 2007–February 2008), 70 mm of the rain fell during three rainy months, compared to eight rainy months in the second season.

Soil Moisture

Rainfall patterns of the three rainy seasons were reflected in soil moisture. Soil moisture levels measured in samples collected monthly at the different locations during the 3 years of the study are presented in Fig. 2. The amounts of rainfall led to significant ($P<0.05$) differences between the three phenological phases observed at all locations during the 3 years of study ($n=100$). Soil moisture measured during the growing biomass (annual and perennial plants) stage was significantly ($P<0.05$) higher compared to other phenological steps (Fig. 2a). The second highest soil moisture level was found during the drying process, in which all annuals were dry and dead aboveground (D.A.B.). The lowest soil moisture was observed during the third phenological phase—the

absence of annuals from aboveground (N.A.B.)—at all locations during the 3 years of the study. However, during all 3 years, there were no significant differences in the soil moisture levels that were detected between the three locations (Fig. 2b).

Soil Organic Content and Total Soluble Nitrogen

Soil organic content ($n=300$) and changes in TSN ($n=250$) were found to be significantly correlated and strongly affected ($P<0.0001$) by sampling location and time (Fig. 3). The drying phenological phase of annual plants (D.A.B.) represents the highest levels of organic content and TSN measured at all three locations during the 3 years of study (Fig. 3a). Organic content was lowest ($P<0.0001$) during the absence period, when annuals were decomposed (N.A.B.), while the lowest TSN values ($P<0.05$) were measured during the growing periods (G.B.). Organic content and TSN values were highest under the canopy of *H. scoparia* shrubs ($P<0.0001$) during all 3 years of the study (Fig. 3b) reaching mean values of 2.76% and 6.91 µg TSN $\times$ g^{-1}, respectively. No significant differences were found between control areas and the vicinity of the artificial plants.

CO$_2$ Evolution

CO2 evolution was found to be strongly affected by the growing season (G.B.; $n=1,200$), with highest ($P<0.0001$) mean values of 0.085 µg CO$_2$–C g dry soil^{-1}h^{-1} measured during this period (Fig. 4a). The lowest values of CO$_2$ evolution were obtained during the drying season, when all annual plants were aboveground in a dry state (D.A.B.) and during the absence phase (N.A.B.), when no annual plants were detected in the field. Significant differences ($P<0.0001$) were found between microbial biomass values in soil samples collected from the vicinity of the *H. scoparia* shrubs ($n=1,100$; mean of 0.1 µg CO$_2$–C g dry soil^{-1}h^{-1}) compared to the control and artificial plant soil samples (0.076 and 0.077 µg CO$_2$–C g dry soil^{-1}h^{-1}, respectively; Fig. 4b).
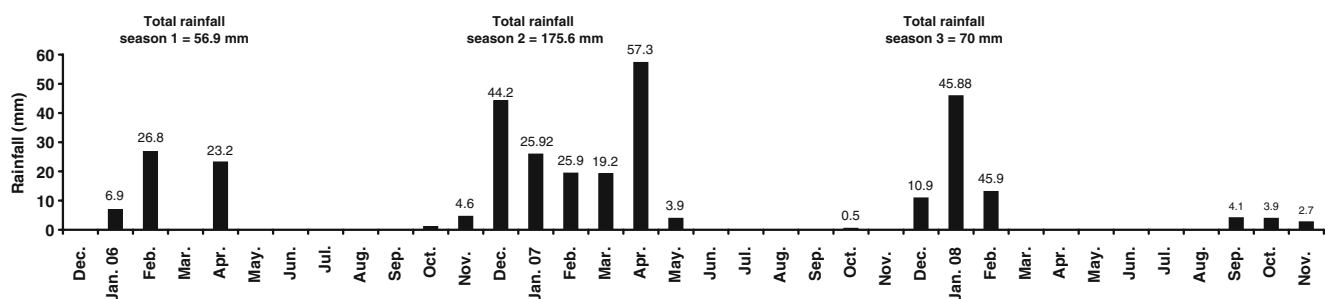

Figure 1 Monthly rainfall in the research area during the study period (November 2005 to May 2008)
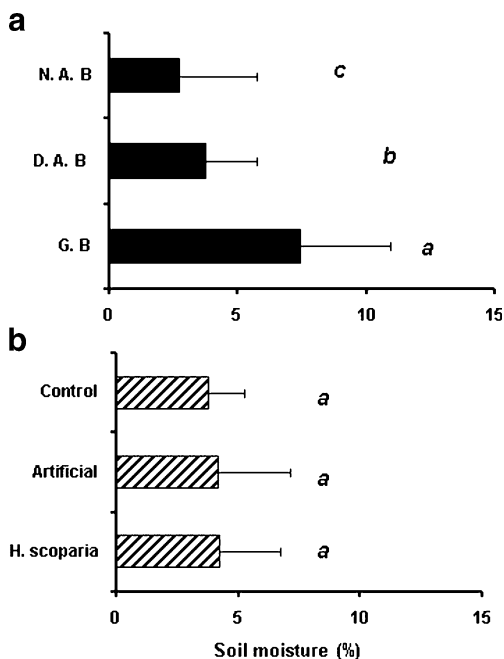
Figure 2 **a** Changes in mean values of soil moisture (%) during the three phenological phases observed at all locations during all 3 years of study: the growing biomass (G.B.), the dry aboveground biomass (D.A.B.), and the no-aboveground biomass (N.A.B.). The *letters in italics* represent statistically significant differences ($P<0.05$) between the three locations. **b** Changes in mean values of soil moisture (%) during all 3 years of study at three different locations: under the canopy of *H. scoparia*, under the canopy of the artificial plant, and in the open areas between the shrubs (control). The *letters in italics* represent statistically significant differences ($P<0.05$) between the three locations

Microbial Biomass

Microbial biomass exhibited a pattern similar to CO_2 evolution: on a temporal basis, the highest mean values (9.02 µg C g dry soil^{-1}; $P<0.001$) were recorded during the growing season (G.B.) and decreased during the annual plant dry period (D.A.B.), reaching a minimum value during the absence period (N.A.B.), with values of 6.13 and 4.71 µg C g dry soil^{-1}, respectively ($n=1,100$; Fig. 4A).

The levels of microbial biomass in soil samples collected from the bare soil and beneath the canopy of the artificial plants were found to be significantly ($P<0.001$) lower than at the other sampling sites (Fig. 4B).

Microbial Functional Diversity (H')

The Shannon index was used to determine the microbial functional diversity (H') of substrate utilization (Micro-Resp^{TM}). Significant differences ($P<0.001$) were found between the three sampling locations, with the lowest values found in soil samples collected at the control site and under the artificial plants (0.67 and 0.71, respectively),

while the highest mean value of $H'=0.85$ was found under the canopy of *H. scoparia* shrubs (Fig. 4B). However, no significant differences in microbial functional diversity were detected during the three phenological periods during the 3 years of study ($n=300$; Fig. 4a). Microbial functional diversity was found to be strongly associated ($r=0.71$) with microbial biomass.

Community Level Physiological Profile

All detected carbon groups (aromatic acids, aromatic carboxylic acids, amino acids, and carbohydrates) were not found to exhibit any significant differences on a temporal basis (Fig. 5a). The utilization rate of each substrate was similar during all three phenological phases (G.B., D.A.B., and N.A.B.). However, soil samples collected under *H. scoparia* shrubs exhibited a relatively higher ($P<0.05$) utilization rate than those from the other sampling sites ($n=900$; Fig. 5b).
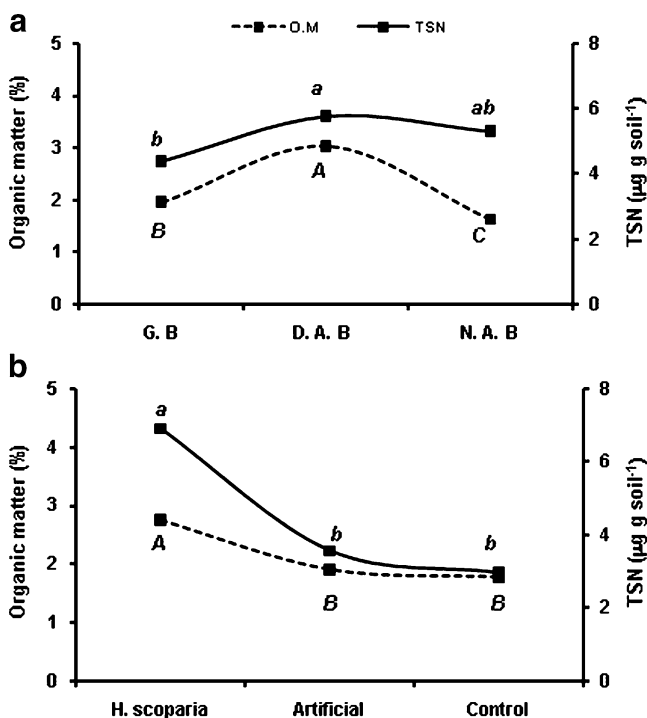

Figure 3 **a** Changes in mean values of organic content (%) and total soluble nitrogen (TSN) during the three phenological phases observed at all locations during all 3 years of study: the growing biomass (G.B.), the dry aboveground biomass (D.A.B.), and the no-aboveground biomass (N.A.B.). The *letters in italics* represent statistically significant differences ($P<0.05$) between the three locations. **b** Changes in mean values of organic content (%) and total soluble nitrogen (TSN) during all 3 years of study at three different locations: under the canopy of *H. scoparia*, under the canopy of the artificial plant, and in the open areas between the shrubs (control). The *letters in italics* represent statistically significant differences ($P<0.05$) between the three locations
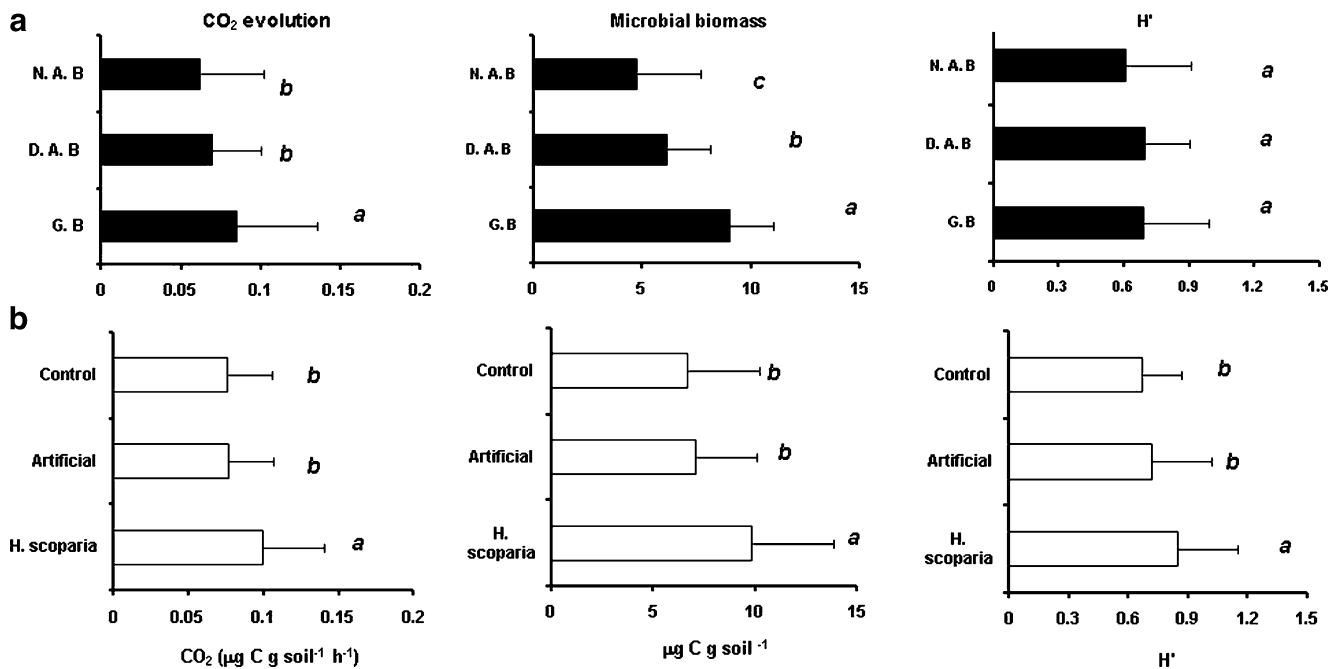
Figure 4 a Changes in mean values of CO_2 evolution microbial biomass and soil microbial functional diversity (H') during the three phenological phases observed at all locations during all 3 years of study: the growing biomass (G.B.), the dry aboveground biomass (D. A.B.), and the no-aboveground biomass (N.A.B.). The *letters* in *italics* represent statistically significant differences ($P<0.05$) between the three locations. b Changes in mean values of CO_2 evolution microbial biomass and soil microbial functional diversity (H') during all 3 years of study at three different locations: under the canopy of *H. scoparia*, under the canopy of the artificial plant, and in the open areas between the shrubs (control). The *letters* in *italics* represent statistically significant differences ($P<0.05$) between the three locations

The highest carbon utilization rate was found under the *H. scoparia* shrubs for aromatic carboxylic acids, with a mean of 0.555 μg CO_2–C g dry $soil^{-1}h^{-1}$, compared to amino acids, which were found to be six times lower (0.083 μg CO_2–C g dry $soil^{-1}h^{-1}$). The lowest values ($P<0.05$) of carbon utilization rate were measured under the artificial plant canopy and in the control areas for all four carbon groups, with no significant differences between the two locations.

Redundancy Discriminate Analysis

Environmental conditions and the phenological state of primary production (growing, drying, and absence) together with the soil-sampling locations were found to have a major effect ($P<0.001$) on soil abiotic (SM, OM, and TSN) components and microbial parameters—biomass (MB), CO_2 evolution, and H' variables (Fig. 6). As seen in this graph, both physical and biological components were found between the drying (D.A.B) and the growing (G.B.) phenological seasons, when the G.B. phase was found to have a great and significant ($P<0.001$) effect on the collected variables. The effect of *H. scoparia* shrub represented by the longest arrow shows a significant ($P<0.001$) effect and strong correlation with the abiotic and biotic variables, while the artificial plant site and the control

treatments were found to be reflected by opposite trends—no related to biotic and abiotic parameters measured. Moreover, the growing and drying annuals seasons were found to have the opposite orientation compared to the absence (N.A.B) of annuals seasons in the field, reflecting the relative importance of biotic and abiotic components (Fig. 6).

Discussion

Organisms in desert ecosystems have been found to cope with the harsh environment by using behavioral, phenological, and physiological adaptations. One of the most important triggers of microbial activity that determines the success of their survival is moisture availability, which is unpredictable in time and space. Evenari et al. [1], Noy-Meir [33], Whitford [9], and Coleman and Crossley [34] emphasized the importance of moisture availability to soil biotic activity and its contribution to nutrient accessibility for primary production.

Vegetation cover plays a major role in providing organic matter and a physical barrier. Both contribute together to the formation of "fertile islands," which play an active role in "prolonging biological activity" [5, 16, 20, 21, 35].
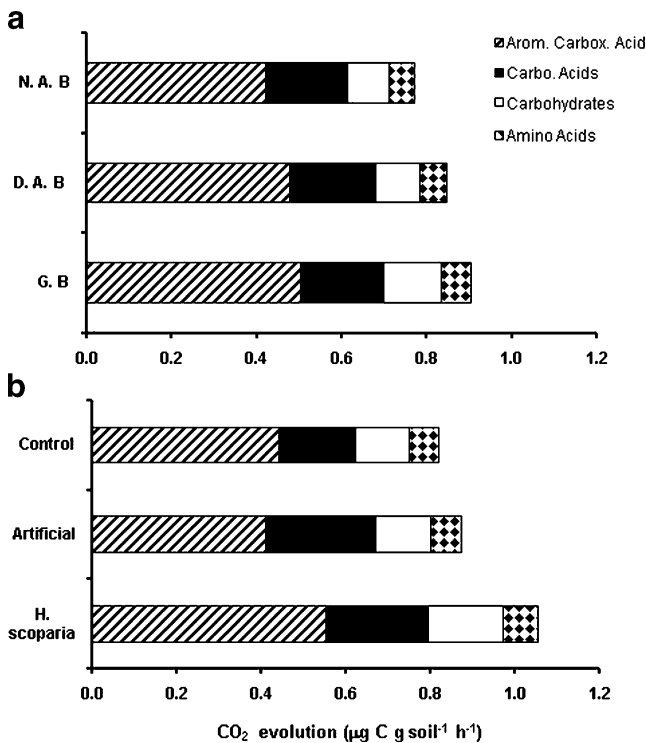
Figure 5 a Changes in utilization ability of four carbon groups, carbohydrates, amino acids, carboxylic acids, and aromatic carboxylic acids during the three phenological phases observed at all locations during all 3 years of study: the growing biomass (G.B.), the dry aboveground biomass (D.A.B.), and the no-aboveground biomass (N. A.B.). **b** Changes in utilization ability of four carbon groups: carbohydrates amino acids, carboxylic acids, and aromatic carboxylic acids during all 3 years of study at three different locations: under the canopy of *Hammada scoparia*, under the canopy of the artificial plant, and in the open areas between the shrubs (control)

Soil organic matter values were found to be significantly different between the three sampling sites (under shrubs, artificial plants, and control), with the highest values found in the vicinity of the *H. scoparia* shrubs, similar to results obtained by Parker et al. [36], Steinberger et al. [37], Freckman et al. [38], and Whitford [9]. Moreover, all functional aspects of the microbial community that were measured in the present study (CO_2 evolution, microbial biomass, functional diversity, and CLPP) exhibited the same pattern, with high values in the vicinity of *H. scoparia* greater than artificial canopy/control, with no difference found between the artificial and control samples. Our results were found to be similar to the trend presented by Insam and Haselwandter [39], who suggested that the presence of live shrubs and their organic input is the main factor affecting microbial activity. Similar findings that support the findings of the present study, emphasizing the importance of soil organic substances in determining biological activity, were reported by Campbell et al. [40], Priha et al. [41], Grayston et al. [42], Shmueli et al. [23], and Wichern et al. [19],

emphasizing the fact that carbon resources of different parts of the plants regulate microbial activity.

Data accumulated during the 3-year study period, based on monthly sampling, allowed us to examine the impact of environmental climate conditions such as rainfall and its distribution, which differed significantly throughout the years and to distinguish between the parameters that influence the microbial community. During this study, we observed massive vegetation pulses in the rainy year, with a double decrease in the drier years. The difference in rainfall distribution and amount elucidated the importance of rainfall as one of the major triggers for primary production. Moreover, primary production was found to have a stimulating effect by increasing litter contribution, enriching soil organic matter, and triggering biological activity, similar to trends reported by Parker et al. [36].

Organic matter and total soluble nitrogen were found to be highly correlated with the different sampling locations. Soil samples collected from the control and artificial plants showed low organic matter followed by lowest levels of TSN. However, on a temporal basis, during three years of study, TSN levels followed the organic matter values, where the highest levels of TSN and organic matter were measured during the period of dry aboveground biomass (D.A.B.), as reported by Elkins and Whitford [43], Zaady [44], and Steinberger et al. [45].

Furthermore, under conditions of the absence of aboveground annual biomass and low soil organic matter, the TSN
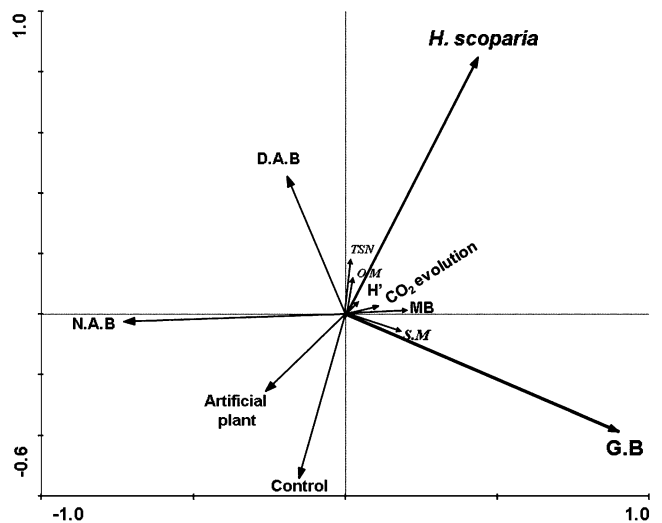

Figure 6 Redundancy analysis (RDA) representing four parameters: the three sampling locations—under the canopy of *H. scoparia*, under the canopy of the artificial plant, and in the open areas between the shrubs (control); soil abiotic factors (*SM* soil moisture, *OM* organic matter, *TSN* total soluble nitrogen); microbial activity parameters (CO_2 evolution, microbial biomass, and soil microbial functional diversity—*H'*); and the phenological phases observed during all 3 years of study (growing biomass (G.B.), dry aboveground biomass (D.A.B.), and no-aboveground biomass (N.A.B.)

was found to be relatively high as a result of higher microbial activity, as shown by Broughton and Gross [24], Kalbitz et al. [46], Laakso et al. [47], and Saetre and Stark [48].

The physiological profiles (CLPP) of the microbial populations were found to support the concept of the role of "fertile islands" in increasing organic matter content in the vicinity of perennial shrubs. The relatively high abundance of aromatic carboxylic acid utilizers (can utilize lignin) by the soil microbial community in the vicinity of *H. scoparia* can be explained by the presence of plant litter accumulation containing relatively high lignin content. However, no significant differences were found during the 3 years of study in the physiological profile of the microbial community in the different phenological phase results, which elucidate the fact that the profile of the community remained constant over time but varied according to sites.

RDA was performed in order to summarize the results and fully understand all parameters examined in this study and their relative contribution to the microbial functional diversity in this desert ecosystem. RDA was found to be the most appropriate for integrating all the results, illuminating the two main forces affecting microbial activity in desert soils: (1) the temporal axis, as detected by the phenological phase of primary production; and (2) patch type parameter, as detected by the locations of the soil samples, i.e., the canopy effect of the *H. scoparia* perennial shrubs.

RDA enabled us to determine the importance of *H. scoparia* canopy on the functional diversity of the microbial community, while other physiological parameters—CO_2 evolution and microbial biomass—were equally affected by the location and the phenological stage of the primary producers (G.B.). Moreover, the artificial plants, which represent the physical obstacle of perennial shrubs, had no effect on either the biotic (microbial activity) or abiotic (TSN, organic matter, and soil moisture) components.

Our data suggest that the aboveground vegetation biomass, divided into perennial plants (which create an "island of fertility" during the entire year) and annual plants as major component of primary producers during the growing seasons (especially in rainy years) determines soil microbial activity and community physiological profile. The microbial activity regulates nutrient availability for primary producers as represented by the TSN and organic matter results. The findings of the present study do not support the hypothesis of the dual role of perennial plants as suppliers of organic matter and moderators of abiotic variables (e.g., as a physical barrier against wind and radiation) that affect microbial activity in desert soils. The only parameter found to control microbial activity was the contribution of organic matter by perennial shrubs and the growth of vegetation (annual and perennial) during the growing seasons.

The results obtained in the present study elucidate the importance of the interplay between rainfall and its impact upon vegetation in general as a physical barrier on the one hand and organic matter accumulation below perennial shrubs on the other hand. Together, they contribute to the establishment of spatial and temporal activity and composition of the soil microbial community. This article contributes to a better understanding of desert ecosystems, which are characterized by harsh environmental conditions for plant cover and soil microbial communities. The physical component was found to have no effect on soil microbial functional diversity, and our conclusions are that the most effective factor in arid systems is the living shrub.

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