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RESEARCH ARTICLE

Seasonal effect of three desert halophytes on soil microbial functional diversity

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Abstract The objective of this study was to evaluate the effect of some plant ecophysiological adaptations on soil microbial functional diversity in a Negev Desert ecosystem. Soil samples from the upper 0–10 cm layer were collected at the study site under three species of halophyte shrubs, *Zygophyllum dumosum*, *Hammada scoparia*, and *Reaumuria negevensis*. These halophytes represent the most typical cover of the Negev Desert and each of them develops complex strategies that enable greater adaptation and hence, survival. The microhabitat of the shrubs showed differences in trends and magnitude of organic matter content, electrical conductivity, total soluble nitrogen, microbial functional diversity, and C compound utilization. The trends are assumed to be driven by various mechanisms of shrub adaptation in order to be able to survive the harsh desert environment. This study provides evidence that ecophysiological strategies developed by halophytes force microbial communities (from the point of view of activity, composition, and substrate utilization) to adapt to a beneficial plant-microorganism relationship.

Keywords desert shrubs, ecophysiology, soil biota, functional diversity, desert ecosystem

1 Introduction

Desert ecosystems are characterized by their relatively simple structure, in which biological processes are controlled by water regime and its scarcity (Noy-Meir, 1973; Shmida et al., 1986). According to Powlson et al. (1987) and Kinsbursky et al. (1990), abiotic components such as climatic conditions (radiation, temperature, humidity, *etc*.), soil organic matter, and soil moisture, may influence biodiversity, including biomass and activity of soil biota.

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Biological diversity is defined as the variety in an ecosystem as well as the genetic variability within each species. According to Lynch et al. (2004), there are numerous factors that affect diversity, including trophic interactions, spatial and temporal habitat heterogeneity, disturbance, and eutrophication (Torsvik et al., 2002). In a soil ecosystem, microbial diversity is crucial to many functions, where, in the past, it was difficult to determine the major components. Therefore, this definition may limit the scope of information obtained on the interrelationships between species, where in the soil system, functional diversity, together with trophic levels and coupled with taxonomic information, appears to be a potentially valuable method for understanding the key ecological roles of soil communities (Wilson, 1988; Nannipieri et al., 2003).

The original functional diversity of a bacterial community refers to its ability to utilize a large spectrum of different compounds (substrates) occurring in plant tissue. The proportion and composition of these substrates change during decomposition (Zak et al., 1994, 1995). Ecologically, the differences are attributed to the physiological or catabolic activity of the bacterial community (Zak et al., 1994; Fliessbach and Mader, 1997) and can, therefore, provide insight into the biotic response to environmental variation, the source of organic matter, and its different decomposition stages (Zak et al., 1994, 1995).

The pattern of microbial activity in soil systems reflects the extensive heterogeneity of adaptation to climate conditions in the desert, and is dominated by the spatial organization and cover of perennial shrubs, which create favorable biological microcosms (Skujins, 1984).

Although there are usually several types of litter being returned to the soil in any plant community, the effect of litter diversity on biota and biotic processes in desert ecosystems has been largely unexplored (Whitford et al., 1986; Steinberger et al., 1990).

Based on the above, we assume that microbial functional diversity in soil samples collected in a desert ecosystem

under the shrub canopy in the vicinity of and between these three different species of halophytes (*Zygophyllum dumosum*, *Hammada scoparia*, and *Reaumuria negevensis*), representing different ecophysiological adaptations, will show differences in substrate utilization ability. The aim of this study was to understand the effect of the plant communities on soil microbial functional diversity.

2 Materials and methods

2.1 Study site

The field study was conducted at the M. Evenari Runoff Research Farm at Avdat (31°04′ N, 34°42′ E), northern Negev Desert (Israel). This area (over a 1000 ha) consists of loess plain and rocky slopes with shallow, saline, gray lithogenic calcareous soils. The soil at the study site is deep fine-textured loessial sierozem (xerosol) (Dan et al., 1972), with low amounts of organic carbon ($4.7\ g \cdot kg^{-1}$) and high amounts of carbonate (40%). The content of total N is $0.4\ g \cdot kg^{-1}$, and the pH is 7.8. The desert has a Mediterranean-type climatic cycle of mild, rainy winters (5°C–14°C in January) and hot summers (18°C–43°C in June).

The multi-annual rainfall averages 90 mm. The rainy season usually starts in October and ends in April, with most of the rainfall occurring in scattered showers between December and February. Dewfall appears in a total of 195 nights per year, with an average total of 35 mm per year. The annual potential evapotranspiration is approximately 2600 mm. The plant perennial vegetation is dominated by a desert dwarf-shrub association, in which the most common species are the three xerohalophytes: *Zygophyllum dumosum, Hammada scoparia*, and *Reaumuria negevensis* (Evenari et al., 1982). These three species of halophyte shrubs represent the most typical cover of the Negev Desert (Sarig and Steinberger, 1994; Sarig et al., 1994): *Zygophyllum dumosum*, a dwarf shrub with low-branched woody stems carrying succulent leaves surviving the summer drought in an active state; *Hammada scoparia*, a member of the goosefoot family in which the core of the branches undertakes all the photosynthesis functions that leaves have in higher plants; and *Reaumuria negevensis*, whose leaves are covered with tiny salt crystals which are actively excreted. Each of the halophytes develops complex strategies that enable greater adaptation and, hence, survival.

2.2 Soil sampling

Soil samples were collected monthly during the study period (November 2006 and October 2007) in a general area of about 5 ha, from the upper soil layer (0–10 cm), under the canopy of four individual randomly selected plants of each of the following three species: *Z. dumosum* ($n = 4$), *H. scoparia* ($n = 4$), and *R. negevensis* ($n = 4$). Soil samples taken from the exposed areas between shrubs served as controls ($n = 4$). The first sets ($n = 4$) of control samples were collected between the *Z. dumosum* and *H. scoparia*, (distance between them can range from 4 to 30 m) located at the loss plain site. Additional sets ($n = 4$) of control soil samples were collected between the *R. negevensis* shrubs, which grows on the slope in the vicinity of the other two plant species.

After sampling, the soil samples were kept in insulation boxes until their arrival at the laboratory, where they were sieved (mesh size 2 mm) and then stored at 4°C.

In the laboratory, soil moisture was determined gravimetrically by drying a known weight at 105°C, and soil organic matter was obtained by burning the dry samples in a muffle at 490°C for 8 h.

Salinity was determined in soil extracts (1∶10) and expressed as electrical conductivity ($dS \cdot g^{-1}$). Total soluble N ($NH_4^+ - N + NO_3^- - N$) was determined automatically with a Skalar Autoanalyzer (S.F.A.S., 1995).

Functional biodiversity was identified using Gram-negative BIOLOG microplates (BIOLOG Inc., CA, USA) with 96 wells (95 wells and one control) containing different substrates, with a wide spectrum of carbon sources (e.g. carbohydrates, carboxylic acids, and amino acids) metabolized by the microbial population (Vahjen et al., 1995). Each of the 95 substrate wells contained (in dried form) a low-concentration buffered nutrient medium, a tetrazolium redox dye, and a carbon substrate. A 10-g soil sample that was pre-incubated at 22°C for a period of 4 days was added to 90 mL 0.2% water agar for a final dilution of 0.1. To ensure homogenous dispersion of the soil particles in the initial dilution, the sample was shaken for 15 min at 150 r/min, and coarse soil particles were sedimented for 30 min. One-hundred μL aliquots were added to each of the 96 wells of gram-negative (GN) BIOLOG microplates. The utilization of a particular substrate was quantified by measuring the intensity of color change caused by the incorporation of tetrazolium dye into a respiring bacterial community. The microplates were incubated at 22°C and examined after 72 h, 96 h, and 7 days, until the maximum peak absorbency of tetrazolium dye was observed at 570 nm. The number of categories of utilized substrates, which were the result of microbial activity, constitutes the data set based on which functional diversity was assessed.

2.3 Data analysis

The monthly data collected was divided according to the four seasons: (1) winter (November, December, and January); (2) spring (February, March, and April); (3) summer (May, June, and July); and (4) autumn (August, September, and October). All data were subjected to General Linear Model (GLM) analysis, performed using Statistical Analysis System (SAS) software. Significance

was defined at a level of $P < 0.05$. Duncan's new multiple range test (MRT) was used since it is a multiple comparison procedure using studentized range statistics, and was used to compare sets of mean values calculated for separation of means (Sokal and Rohlf, 1981).

The substrate diversity Shannon-Weaver index (H') was determined by calculating the number of different substrates used by the microbial community. Data were processed as follows:

(1) Raw difference (RD): $X - X_0$, where X is the raw value for each well and X_0 is the OD_{570} of the blank well (A_1) used for calibration. Negative score readings were set to zero according to the control.

(2) Average well color development (AWCD): Σ RD/95, the number of utilized substrates, were the substrates with RD > AWCD.

(3) Diversity was calculated using a population ecology equation that incorporated the raw difference data (Fliessbach and Mader, 1997): $H = -\Sigma\, pi\, (\ln pi)$, where "*pi*" is the ratio for the activity on a particular substrate to the sum of activities of all substrates.

The processed data of C-compound utilization were subjected to statistical principle component analysis (PCA) using SAS. This statistical test included the three major groups of substrates (carbohydrates, carboxylic acids, and amino acids), which represent 75% of the total microbial C content.

The data obtained were also tested by computing redundancy discriminate analysis (RDA) in order to provide more information because it also took into account the environmental factors such as the three plant species, seasonality, and soil properties that were related to the samples and explained the proportion of variation (Program CANOCO, Version 4.54, October 2005—written by Ter Braak (C) 1988–2005 Biometris—Quantitative Methods in the Life and Earth Sciences, Plant Research International, Wageningen University and Research Center, Box 100, 6700 AC Wageningen, the Netherlands). The Monte Carlo Permutation (499) test was used to calculate the significance of given environmental factors and, thus, their relevance with community structure (ter Braak, 1995). Arrows pointing at similar directions indicate a positive correlation, while arrows pointing at opposite directions indicate a negative one. The longer the arrow is, the greater the significance of the relationship.

3 Results

3.1 Soil moisture

A total of 108.8 mm rainfall occurred between October and May; 71.2% of the rainfall occurred during the two months of January and February.

This rainfall pattern was reflected in the soil moisture profile. A significant difference ($P < 0.01$) was observed in soil samples taken at different dates. In winter, soil moisture was found to be significantly higher ($P < 0.01$). No differences ($P > 0.05$) were found between plant species and control (Fig. 1A and B). In January, a maximum moisture level of 7.4% was obtained in the soil samples taken under *Z. dumosum* and *H. scoparia*, while in the control samples, it reached 9%. In samples taken under *R. negevensis* and the control, moisture levels reached 7.8% and 6.9%, respectively. As the dry period progressed, a sharp decrease to a value of 1.5% was obtained at all locations. This level remained constant during the summer as well as the autumn season at each sampling location.

3.2 Soil organic matter

Significant differences ($P < 0.01$) in soil organic matter were observed in soil samples taken in the vicinity of the shrubs between different seasons, with no major effect of plant species ($P > 0.05$) and control (Fig. 1C and D). In winter, soil organic matter content was found to be significantly higher ($P < 0.01$) under *Z. dumosum* and *H. scoparia*, with an average of 10% in comparison to the seasons that followed. A sharp decrease was found toward the dry season, with organic matter content reaching 5%, and no significant differences ($P > 0.05$) were found between shrubs or locations. Soil samples collected in the vicinity of *R. negevensis* were found to be significantly higher ($P < 0.01$) in winter and summer, reaching an average of 10%, while in spring and autumn, a sharp decrease of 35% was obtained.

3.3 Electric conductivity

Soil salinity expressed as electric conductivity (EC) was found to be significantly modulated ($P < 0.01$) by the shrubs under which the samples were taken (Fig. 2A, B). The EC values under *Z. dumosum* reached a maximal value of 14.9 $dS \cdot m^{-1}$ in spring, while in winter, a minimal value of 10 $dS \cdot m^{-1}$ was obtained. The EC values under *H. scoparia* and between shrubs (as controls) reached lower values, ranging between 4.5–5.8 and 3.3–4.9 $dS \cdot m^{-1}$, respectively. Compared to these values and to control samples, the EC values under *R. negevensis* were found to be extremely high ($P < 0.01$) during all seasons throughout the study period, particularly in autumn and winter, with values of 32.9 and 29.5 $dS \cdot m^{-1}$, respectively.

3.4 Total soluble nitrogen (TSN)

A similar trend was found with total soluble nitrogen by comparing the soil samples under all shrubs (Fig. 2C and D): no significant differences were found among them. However, in summer, TSN was found to be significantly higher ($P < 0.01$) under all shrubs, and it reached 31.5, 27.4, and 23.5 $g \cdot kg^{-1}$ for *Z. dumosum*, *H. scoparia*, and

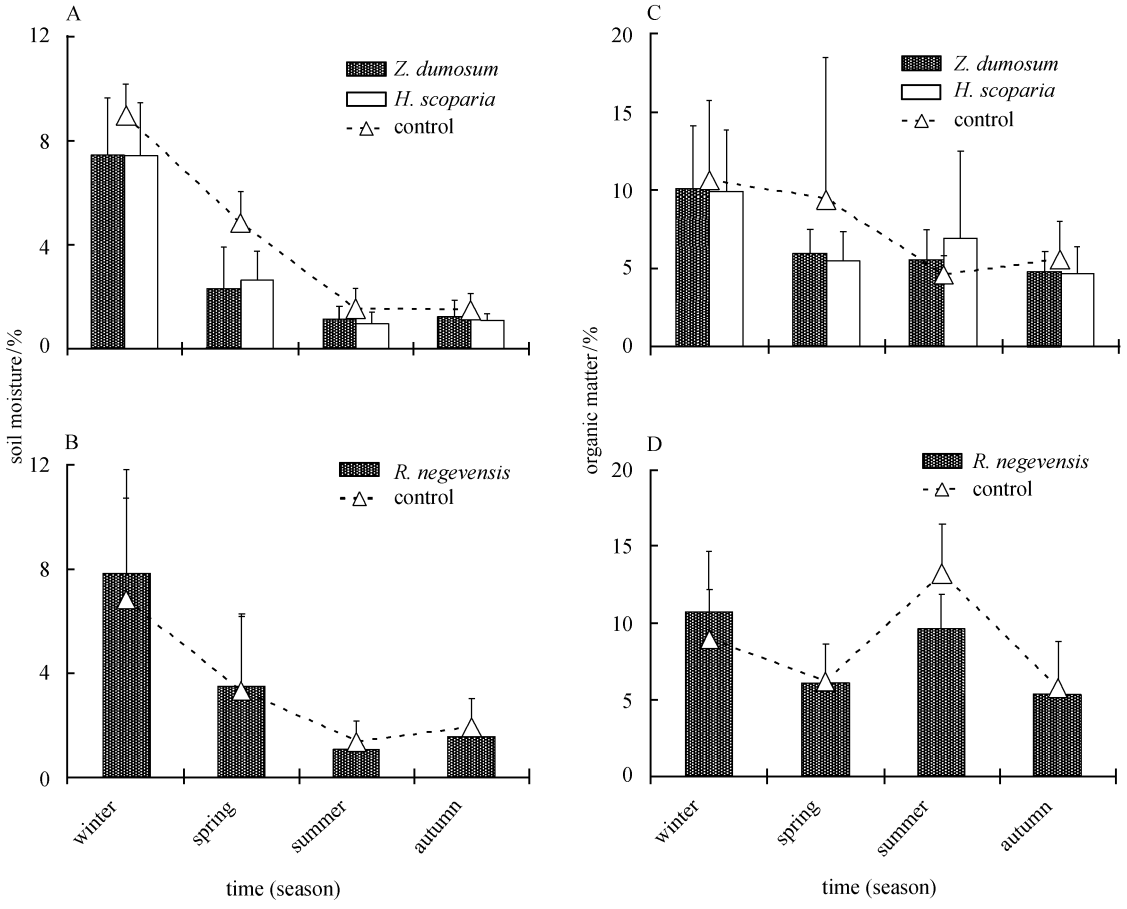

Fig. 1 Changes in mean values of soil moisture and organic matter content (%) under the canopy of *Z. dumosum*, *H. scoparia* (A, C), and *R. negevensis* and control samples (B, D), during the study period (error bars represent ± SD)

R. negevensis, respectively. During the study period, TSN values for the control samples were found to be low, ranging between 0.8 and 0.9 $g \cdot kg^{-1}$.

3.5 Functional diversity (Shannon-Weaver index)

The ability of the soil microbial community to utilize carbon substrate was expressed as the Shannon index (H'), which is a species diversity measure (Fig. 3A, B). Different patterns of microbial functional diversity were obtained for soil samples taken from different locations, with no significant differences ($P > 0.05$) in their H' values. The H'; values under *Z. dumosum*, *H. scoparia*, and the control ranged from 15×10^{-2}–17×10^{-2} and from 13×10^{-2}–17×10^{-2}, respectively, between winter and summer, with maximal values obtained in summer. A sharp decrease was obtained in autumn, reaching 7×10^{-2} (Fig. 3A). The H' values under *R. negevensis* and the control were found to reach a maximal value in autumn, 28×10^{-2}, which was significantly higher ($P < 0.05$) than those under *Z. dumosum* and *H. scoparia*. During winter, summer, and spring, the H' values were found to reach an average value of 15×10^{-2} (Fig. 3B).

3.6 Principle component analysis

The pattern of C compound utilization among three major groups of substrates (carbohydrates, carboxylic acids, and amino acids) is demonstrated by PCA, as compared to the characteristic of bacterial functional diversity among different shrubs and control open areas (Fig. 4). The results obtained for the 72-h incubation represented the highest substrate utilization levels. A very well-defined pattern demonstrates the correlation between different plant-growth zones and the utilization of carbon sources throughout the one-year study.

During the study period, a different pattern characterized the differences between microbial communities within the sites. These results indicate that microbial communities from soil samples taken in the vicinity of *Z. dumosum* (Fig. 4A) and *H. scoparia* (Fig. 4B) seemed to use different levels of the available substrates during most of the year (spring, summer, and autumn), when there was a lack of soil moisture; while in the winter, the microbial communities seemed to show similar levels of substrate use (more homogeneous handling). A different pattern was obtained for the control samples: during winter, the communities

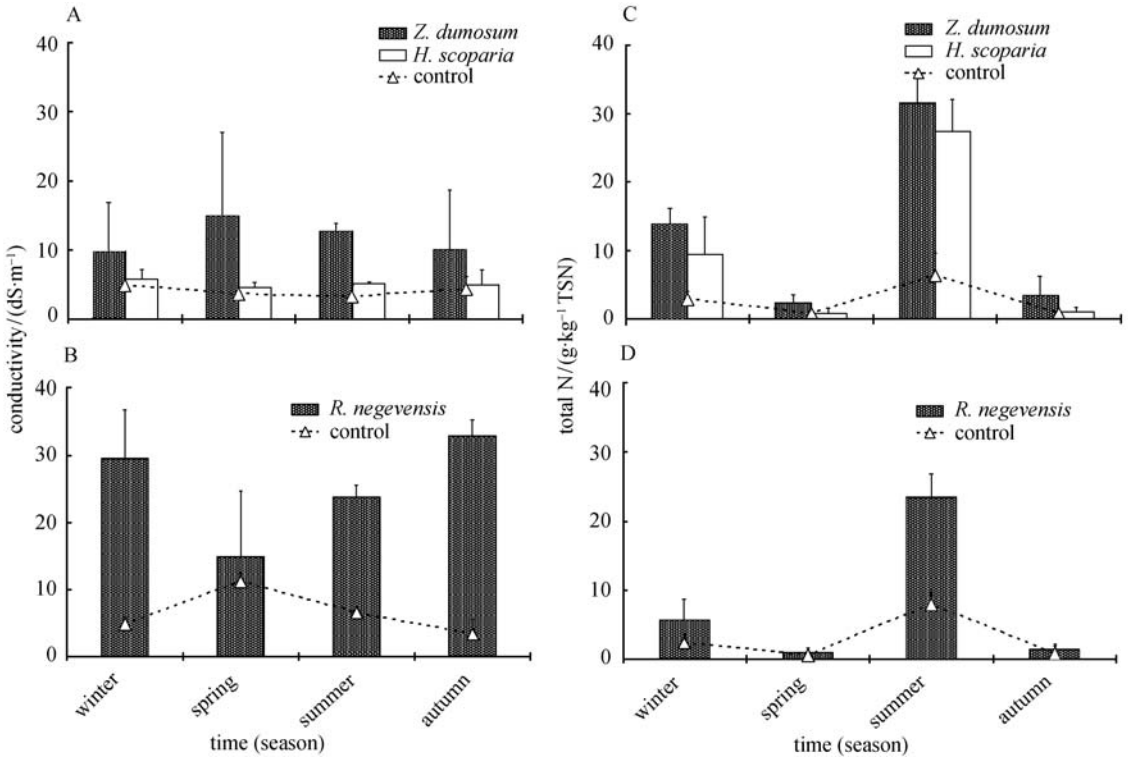

Fig. 2 Changes in mean values of soil salinity (EC) (A, B) and total soluble nitrogen (ppm TSN) (C, D) under the canopy of *Z. dumosum* and *H. scoparia* (A, C), and *R. negevensis* and control samples (B, D), during the study period (error bars represent ± SD)

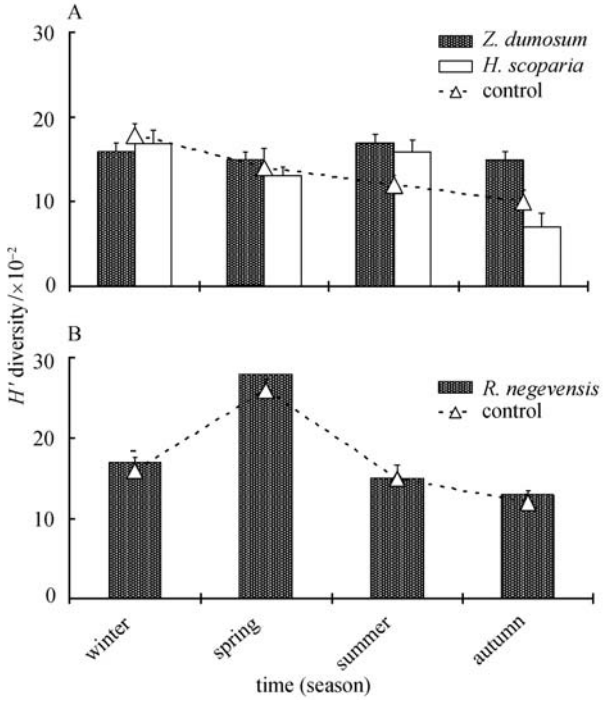

Fig. 3 Changes in mean values of microbial functional diversity according to the Shannon (*H*′) index under the canopy of *Z. dumosum* and *H. scoparia* (A) and *R. negevensis* and control samples (B), during the study period (error bars represent ± SD)

apparently acted heterogeneously, while during the remaining part of the study period, there was a trend of minor utilization in the substrates towards a homogeneous community.

Soil samples taken under *R. negevensis* (Fig. 4C) exhibited different patterns of community structure when comparing results from the different shrubs or control. During winter, the soil microbial communities provided a heterogeneous structure; while during spring, the communities became more homogenous. During summer, heterogeneous patterns were obtained, and this remained the same during autumn.

The multivariate analysis of the plant community and temporal scale showed clear discrimination between the above variables. In RDA (Fig. 5), high discrimination was found between *H. scoparia* and the control sites in comparison to the other two shrubs; while between *R. negevensis* and *Z. dumosum*, significantly less discrimination was observed. As for the measured variables, salinity was found to be affected by *R. negevensis*, with very little contribution by the *Z. dumosum* shrub. Seasonality was found to have a great effect on soil moisture availability, represented by a strong discrimination between winter and the two dry seasons, summer and autumn. However, the microbial functional diversity (*H*′) showed a strong preference for the spring season.

In RDA (Table 1), plant species and season explained 27% of the total variability, followed by the winter season with 25% of the variability for the *R. negevensis* shrub

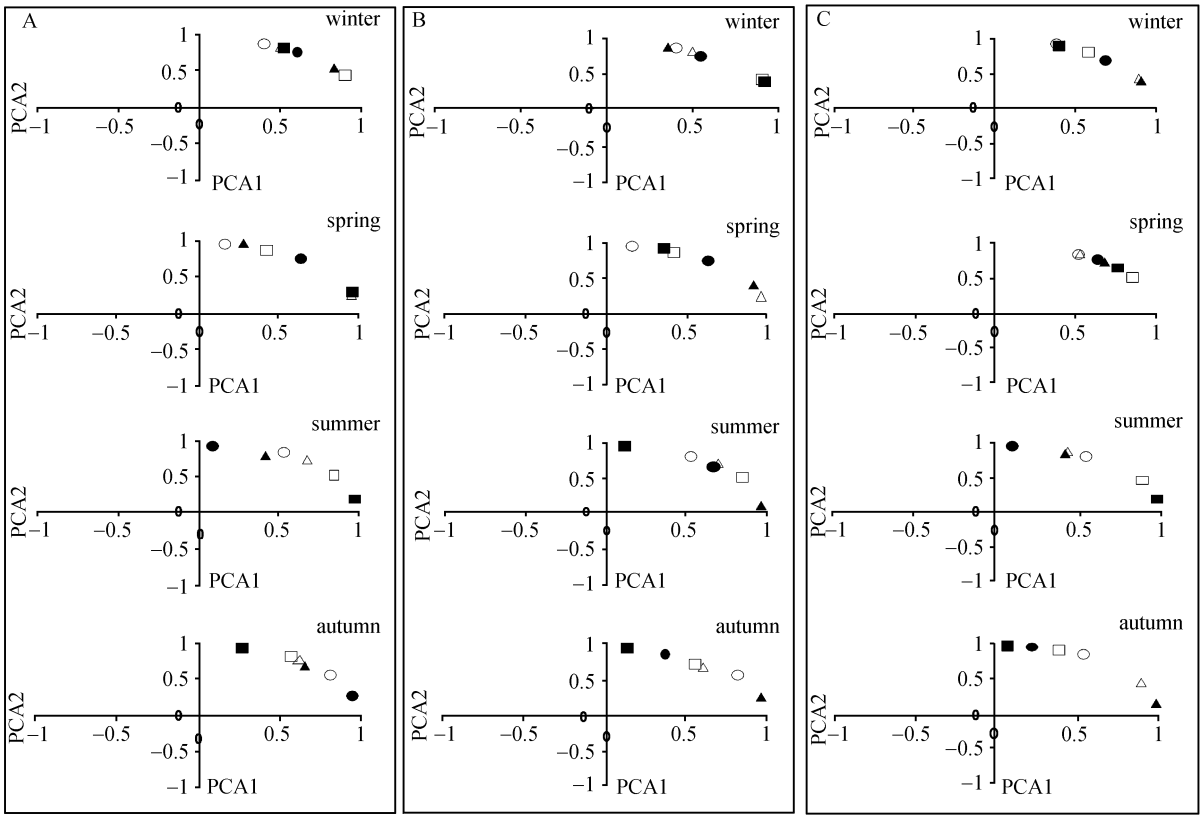

Fig. 4 Principle component analysis (PCA) under the canopy of *Z. dumosum* (●▲■) (A); *H. scoparia* (●▲■) (B); *R. negevensis* (●▲■) (C); and control (○△□) during different sampling seasons of the study period. □/■ : carbohydrate, ●/○: carboxylic acids, △/▲: amino acids.

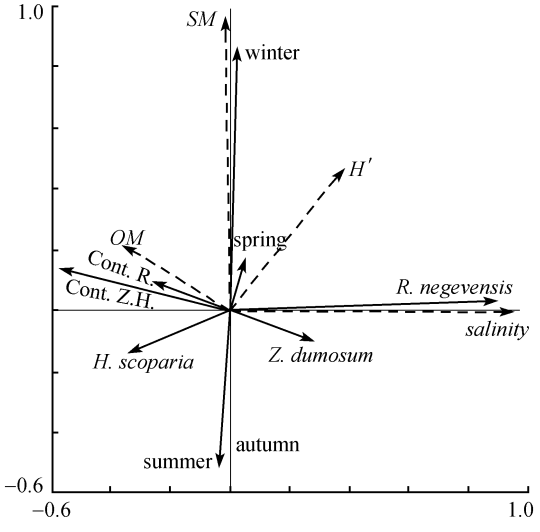

Fig. 5 RDA plot illustrating the relative positions of the different values obtained for the soil samples collected in the vicinity of the three different plant species and control samples. The ordinations are space related to seasons, salinity, soil moisture (SM), organic matter (OM), and the *H′*—Shannon Index of microbial functional diversity.

Table 1 Redundancy discriminate analysis (RDA) with specified weights of the different variables in samples obtained during the study period

tested effect	*P* value	F- ratio	extra fit*
R. negevensis	0.002	29.50	0.27
Z. dumosum	0.002	19.20	0.03
H. scoparia	0.010	4.59	0.05
control	0.006	5.70	0.03
winter	0.002	41.05	0.25
spring	0.002	20.21	0.08
summer & autumn	0.006	6.83	0.10

*Variable explained by the variables selected.

species. Both of the above variables were found to be stronger in comparison to the sum of all the other variables. However, each variable was found to have a significant level of contribution (higher than $P < 0.05$).

4 Discussion

A major characteristic of dry desert vegetation is the scattered distribution of perennial shrubs, which causes

horizontal differentiation of soil properties (Charley and West, 1978; Hadley and Szarek, 1981; Jackson and Caldwell, 1993). The spatial distribution of resources such as nutrients plays an important role not only in determining above- and below-ground primary production (West and Skujins, 1978; Noy-Meir, 1985; Whitford, 1986; Whitford et al., 1986; Fisher et al., 1988; Ashraf and McNeilly, 1994), but also in determining biotic activity, diversity, and composition. Since soil organisms are known to be some of the most sensitive biological markers, their diversity can be affected by minute changes in the ecosystem (Mills and Wasser, 1980; Kennedy and Smith, 1995).

According to Zak et al. (1994) and Lahav and Steinberger (2001), the total functional diversity of microorganisms in different soil types may be similar, and the combination of environmental and plant factors may be one of the most important factors determining which organisms are active and proliferate under different conditions.

Our results elucidate that microbial communities-microbial functional diversity–represented by carbon source utilization from soil samples collected in the vicinity of different plant species are expressed by different ratio patterns of C source utilization. This difference is induced by plant species and not by soil type, as was demonstrated by *Z. dumosum* and *H. scoparia* sharing the same biotop. The slope with *R. negevensis* where soil samples were taken is considered a different habitat. Since *R. negevensis* is a salt-exuding dwarf shrub belonging to the chloride-absorbing xerohalophytes (Evenari et al., 1982), the external salt glands on its leaves can be washed by rain and dew, thus leading to the accumulation of salt under the canopy. Our results are similar to those obtained by Garland (1996) and Westover et al. (1997), who emphasized in their study the importance of the plant rhizosphere in determining the microbial community.

Bossio et al. (1998), Marilley and Aragno (1999), and Kourtev et al. (2003) reported that structurally and functionally, distinct microbial communities develop under different plant species in humid systems. In the present study, the emphasis was on the interaction between plant ecophysiological adaptation and the microbial community, and its functionality in a xeric environment characterized by unique abiotic components. Therefore, such data contribute to the understanding of the structure and function of the soil microbial community. As a result, changes in soil organic matter content during and after the wet period can be explained by some of the processes in the field, which lead to an increase in above-ground organic detritus (leaves and flowers), root development, distribution of seeds, and germination of annual plants. All of these processes can be affected by the response of the plants to the increase in moisture throughout the seasons, providing a range of available substrates that determine biotic activity, diversity, and composition of the microbial communities. Therefore, it seems that unless the trend is similar between seasons, the composition of the microbial population can be affected by minute changes in the soil ecosystem.

The huge assortment of carbon sources on a temporal and spatial scale in a xeric environment is provided mainly by primary producers, which trigger and determine below-ground microbial functional diversity.

The findings demonstrate that the multisubstrate testing methods which allow differentiation in carbon source utilization by the microbial communities from soils taken under different plants can only be due to the presence of different microbial species that can be expressed by changes in the values of the Shannon index (H'). This diversity of microorganisms associated with the different plants may be due to the differences in carbon compounds in the litter and exudates by the plants.

In conclusion, soil microbial communities differ in both quantitative and qualitative compositions, where the populations are subjected to physicochemical changes as shown by von Wintzingerode et al. (1997). Due to the huge difficulties in determining the different organisms, microbial functional diversity is known to be one of the best tools in translating relativity in substrate utilization in microbial composition. Further studies with high detection capability tools such as PCR are needed in order to be able to amplify the small amount of DNA that may help in discovering organisms occurring in small numbers. Such studies will help us understand the complex relationship between the plants and microbial community as part of the complex food web in the soil ecosystem.

Moreover, the importance of each one of the shrub species to support its own unique community and determine its own environment was found to be strongly governed by the unpredictable xeric environmental conditions. The natural shrub community was found to be the most different in both substrate utilization and diversity, leading to different levels of dissimilarity between them. In spite of various studies that demonstrated the influence of plant species on microbial functional diversity at different sites, this study has been able to examine shrub species communities using a new approach. However, further studies are still needed to enhance the knowledge on environmental plant-soil biota functional relationships in terrestrial ecosystems.

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