

Vertical Distribution and Activity of Soil Microbial Population in a Sandy Desert Ecosystem

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Abstract

The vertical distribution of a microbial community on a temporal and spatial (vertical) scale under the *Tamarix aphylla* salt-resistant plant was studied. The uniqueness of this plant is in the creation of “islands of salinity” beneath the plant, due to salt excretion and leaf shedding at the plant base. Our working hypothesis was that the activity and biomass of the soil microbial population and the ratio between bacterial biomass and fungal biomass will decrease toward the driest season. Soil samples were collected beneath and between plants under the *T. aphylla* canopy down to the 0- to 50-cm depth at 10-cm intervals. The substrate-induced respiration method was used to estimate the total soil microbial biomass (MB), CO₂ evolution, metabolic quotient (qCO₂) index, and MB of both the fungal and bacterial communities. A significant difference was observed ($p < 0.05$) in MB and qCO₂ index between the different soil layers in the control samples, whereas there was no significant difference in the soil samples in the vicinity of the plant ($p > 0.05$) between the depths, due to the plant rhizosphere effect.

Introduction

Desert habitats are characterized by a combination of extreme abiotic conditions, low and unpredictable amounts of moisture, nutrients, and organic matter availability [7, 14]. Water and organic matter are among the major variables limiting primary production and determining biota activity. As a result, biological activity is strongly affected in time and space by these variables. In a sandy soil desert, temperature and moisture availability are even more acute as a result of the physical and

chemical characteristics of sand texture, which strongly determine biological activity and vertical distribution. Because of the presence of over 80% quartz, known to have low specific heat (0.199), the sandy soil surface can reach temperatures as high as 75°C in the hot summer season, whereas in the winter soil surface temperature falls below 0°C. These harsh climatic conditions lead to heat stress in organisms that live above and in the upper soil layers. Sandy soil serves as a good insulator, because of the large amount of air trapped between the quartz grains, decreasing heat conduction from the soil surface toward the deeper layers, thus maintaining a constant temperature at a depth of ~30 cm and below. As a response to these extreme abiotic factors, the plant community has been found to develop ecophysiological adaptations by developing adventitious roots.

Water availability (essential for biotic life functions) in the sandy desert soil undergoes extreme fluctuations, mainly in the upper soil layer. Alon and Steinberger [1] showed that soil microbial biomass (MB) increases with the increase in soil moisture, which mediates nutrient turnover for short periods [8, 21, 23].

Soils in this desert system are extremely dry for more than 90% of the year, leading to nutrient deficiency and frequently also to the accumulation of salts. The occurrence of annual as well as perennial vegetation in this habitat will be determined by abiotic variables and soil biota [7]. Salt-resistant plants create “islands of salinity” [9, 22], causing a spatial and temporal differentiation between the habitats in the study area. These islands are created by the *Tamarix aphylla* plants in the sandy system because of their ecophysiological adaptation, where the plants absorb salts through their root system, translocate them to leaves, and deposit them on the ground [6]. Therefore, soil biotic communities in these systems are exposed to an extreme saline microhabitat in addition to moisture and temperature fluctuations. Salt levels in the soil increase moisture availability

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and create a unique environment for biological activity. Moreover, plant ecophysiological adaptation strongly influences abiotic conditions in the soil beneath the plants, affecting temporal and spatial (vertical) distribution of soil biota. Under these extreme environments, a “window activity” cycle is created throughout the year. In this cycle, the microbial community, which is composed mainly of bacteria and fungi, can fulfill all its biological functions.

The present study was carried out to determine the effect of *T. aphylla*, which is known to be one of the most widely dispersed plant covers in the sandy system, on the temporal and spatial (vertical) dynamics of the soil microbial community. We hypothesized that abiotic conditions are harsh in this habitat, and the activity and biomass of the microbial population and the ratio between bacterial and fungal biomass will decrease toward the driest seasons [26].

Study Site

Soil samples were collected from February 2003 to February 2004 at Ramat-Negev, a sandy desert soil system in the northern Negev Desert, Israel, approximately 20 km south of Beer-Sheva. The site has a semiarid climate, with an average multiannual rainfall of 150 mm. Precipitation fluctuates between 90 mm in a drought year and 250 mm in an extremely rainy year. The rainy season usually begins in October and ends in late April, with most of the rainfall occurring in scattered showers between December and February. An additional source of moisture is dew, which contributes 35–37 mm year⁻¹ during 210 days, with heavy dew occurring during late summer and autumn. The multiannual temperatures are 19–21°C (10–12°C in January and 26–28°C in August). The potential annual evaporation rate is 1600–1800 mm year⁻¹. The topographic relief of the area is level, except for sand dunes, which are stable. The perennial vegetation in this area is dominated by *Carex pachystylis* and *Nuerad procumbens*.

Materials and Methods

Soil Sampling. Soil samples were collected by using a 7-cm-diameter soil auger in the early morning from two locations: under the canopies of four randomly selected individual *T. aphylla* plants and from open spaces between the selected plants as control. The samples were collected seasonally during the study period at five depths: 0–10, 10–20, 20–30, 30–40, and 40–50 cm, with four replicates from each of the two locations and each of the five depths ($n = 40$ month⁻¹). The soil samples were placed in individual plastic bags and then transported in an insulated container to the laboratory, where they were stored at 4°C. These soil samples were sieved (2-mm

mesh size) before biological and chemical analyses to remove root particles and other organic debris.

Laboratory Analysis. Soil moisture, organic matter, total soluble nitrogen (TSN), CO₂ evolution, and MB were determined in the laboratory.

A 5-g sample from each of four replicates from each depth was weighed and dried at 105°C to a constant weight for gravimetric determination of its water content. Soil organic matter (SOM) was determined by dichromate oxidation in the presence of H₂SO₄, without the presence of external heat [19].

TSN and nitrate in soil was determined in a 5-g subsample that was agitated (2 h, RT) with 50 mL CaCl₂ (0.01 M) [11]. The filtrate was analyzed by using a Skalar Autoanalyzer Unit [20], which determines TSN and nitrate amounts via chemical and color reactions (up to 0.5 ppm N).

Total microbial, bacterial, and fungal biomass was determined using substrate-induced respiration (SIR). The SIR method was used to evaluate the biological MB and chemical inhibitors were used to estimate soil microbial activity. The SIR method [2, 3] is based on using selective inhibitors [2], which allow quantification of the fungal (eukaryotic) and bacterial (prokaryotic) contributions to the MB. The method used is designed for soil samples that are moisture-adjusted to 40% of the water-holding capacity (WHC), and is based on the assumption that the addition of glucose (substrate) maximizes the initial respiratory response and the use of antibiotics maximizes inhibition of the fungal and/or bacterial groups. It also ensures that the inhibitor concentration is sufficiently high not to be used as a substrate, but also not high enough to affect nontarget organisms. Therefore, the initial respiration will differ significantly between the bacteria and fungi. The amounts of streptomycin (for the bacterial population) and cyclohexamide (for the fungal population) added to the soil samples (dry weight equivalents) were determined experimentally from quantitative analyses by using Infra Red Gas Analyzer (IRGA). Data obtained from preliminary studies indicate that 1000 ppm glucose or streptomycin and 3000 ppm cyclohexamide are needed to maximize the response of selective respiratory inhibition for a 25-g dry soil sample. Soil respiration rates were monitored in four replicates for 10 h. Four different CO₂ evolution curves (a total of 16 SIR readings) were measured during this period: (1) control (with glucose); (2) bacterial population (with streptomycin); (3) fungal population (with cyclohexamide); and (4) total effect (glucose + streptomycin + cyclohexamide). A fifth curve was calculated for the sum of the single inhibitors, e.g., (1) – [(1 – 2) + (1 – 3)].

The calculated curve should afford the same value as the fourth curve. If the value obtained is identical, the

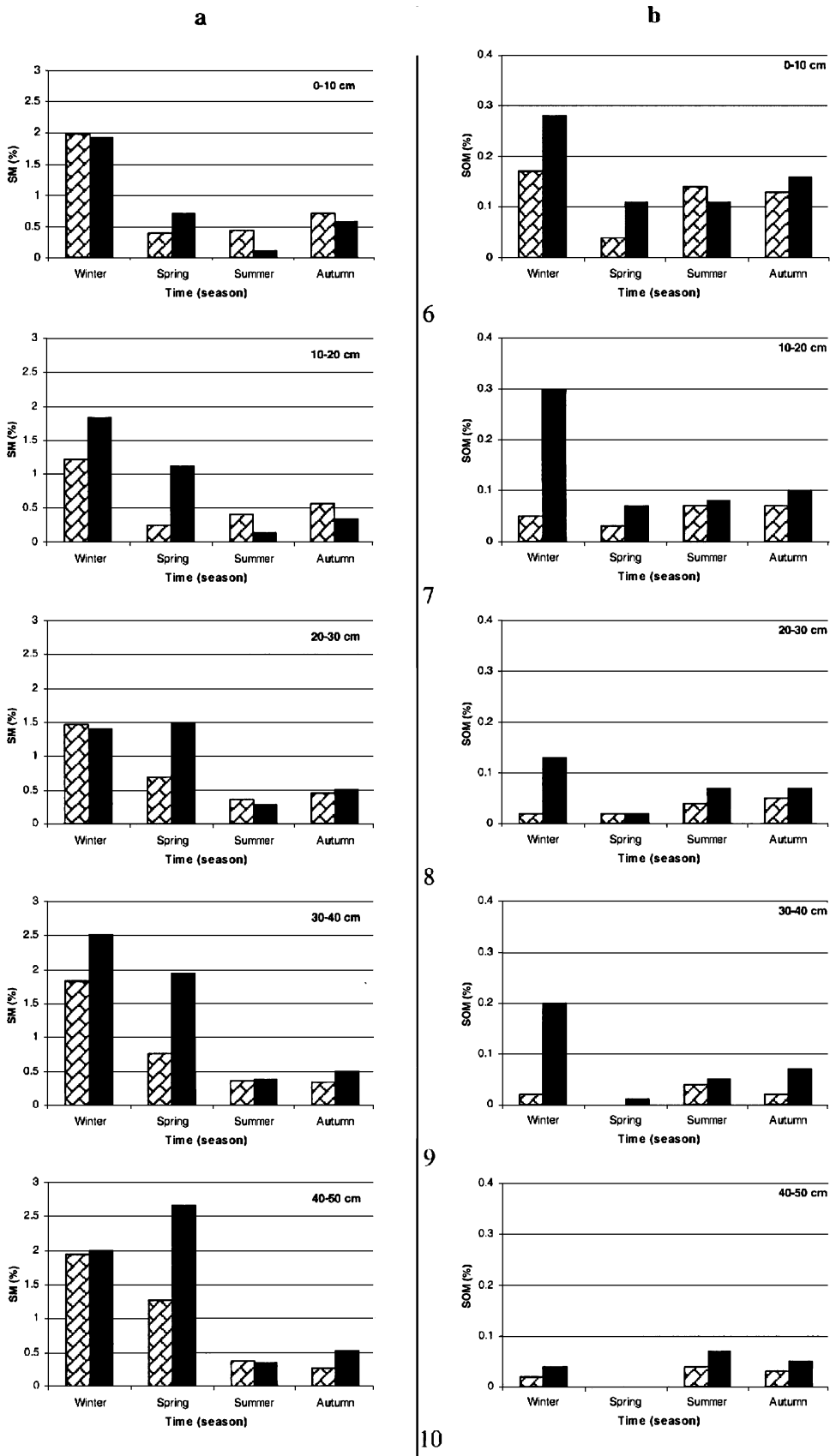
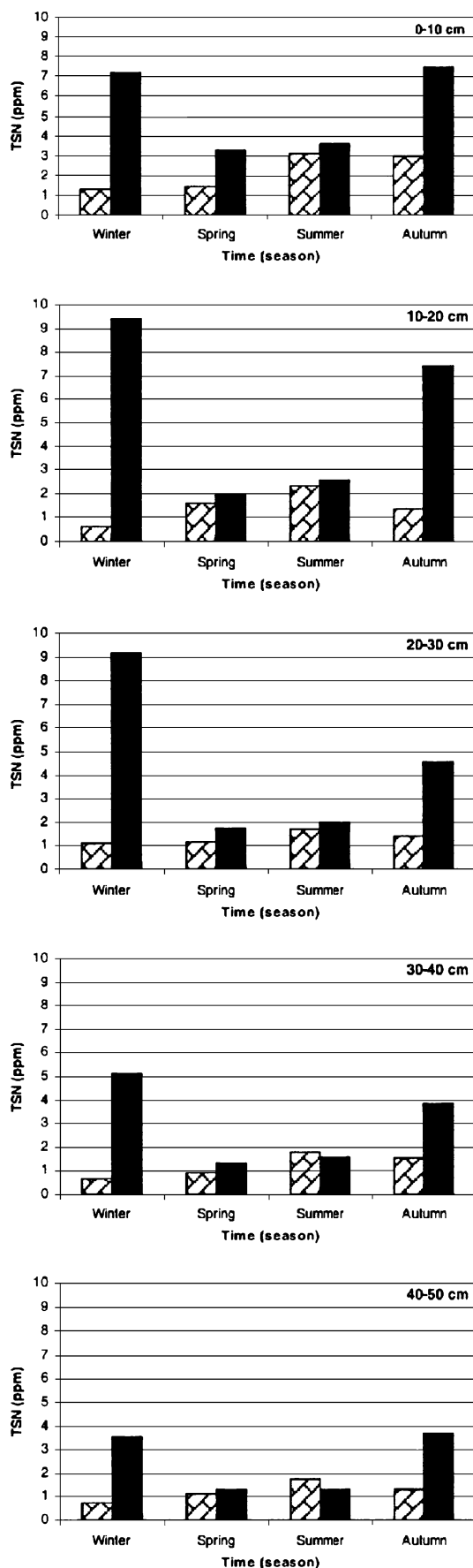


Figure 1. (a) Seasonal variations in soil moisture (SM) content and (b) soil organic matter (SOM) during the research period (February 2003–January 2004), control; *T. aphylla* ($n = 4$).



bacterial and fungal contributions can be calculated by the following equation:

$$\% \text{PROKARYOTES} = (1 - 3) / 1 - 4 \times 100$$

$$\% \text{EUKARYOTES} = (1 - 2) / 1 - 4 \times 100$$

The mixture added to the soil samples was therefore prepared as follows: (1) control = 67 mg talcum powder + 33 mg glucose; (2) bacterial population = 57 mg talcum powder + 33 mg glucose + 10 mg streptomycin; (3) fungal population = 47 mg talcum powder + 33 mg glucose + 20 mg cyclohexamide; and (4) total effect = 37 mg talcum powder + 33 mg glucose + 10 mg streptomycin + 20 mg cyclohexamide. The mixture was added homogeneously to the soil samples and used for IRGA analysis.

The soil microbial biomass C obtained by SIR was transformed to $\mu\text{g C g}^{-1}$ according to the method described by Kaiser *et al.* [12], in which $\text{SIR } C_{\text{mic}} (\mu\text{g g}^{-1} \text{ soil})$ was $\mu\text{g CO}_2 \text{ g}^{-1} \text{ soil h}^{-1} \times 40.04 + 3.75$ [3]. Bacterial and fungal contributions to the total MB were determined based on the relative percentages of each component, by using the selective inhibitors.

All calculations were performed according to the procedure described by Anderson and Domsch [3]. Data were subjected to statistical analysis of variance (ANOVA). Differences with $p < 0.05$ were considered statistically significant.

Results

Soil Moisture. Soil moisture in the samples collected at the control sites and under plants exhibited similar trends. Maximal soil moisture values (1.6% and 1.95%) were obtained in winter (February) in the control and beneath the plants, respectively, whereas the minimal values, 0.6% and 0.25%, were obtained in summer (July) from samples collected in the control and beneath the plants, respectively (Fig. 1a).

A significant difference was observed between seasons ($p < 0.0001$) and between depths ($p < 0.05$) at both sampling sites. Moreover, the wettest soil layer at both sites was the deepest (40–50 cm). In the control samples, the driest soil layer was at a depth of 10–20 cm, and in the vicinity of the plant it was at a depth of 0–10 cm.

Organic Matter. The highest SOM content was obtained in the samples collected beneath the plant, with a mean of 0.3% SOM in winter (February) in the 10- to 20-cm depth soil layer. This value is more than 1.5 times higher than the highest SOM value in the control soil

◀ **Figure 2.** Seasonal variations in total soluble nitrogen (TSN) during the research period (February 2003–January 2004), ▨: control; ■: *T. aphylla* ($n = 4$).

samples, which reached a maximum of 0.17% SOM in winter in the upper (0–10 cm) soil layer (Fig. 1b).

Generally, soil samples taken in the vicinity of the plant were richer in organic matter content than the parallel control samples. We found the same trend of decreasing SOM from the soil surface toward the deepest soil layer for both types of sampling locations. Significant differences ($p < 0.0001$) in SOM content were found between seasons, between sampling locations, and between depths.

SOM in the control samples fluctuated between 0% in spring at depths of 30–40 cm and 40–50 cm, and 0.17% in winter at a depth of 0–10 cm. A significant difference ($p < 0.05$) was observed between spring and the other three seasons within the control soil samples. Moreover, in the control soil samples, a significant difference ($p < 0.05$) was found between the 0- to 10-cm depth and all four deeper soil layers. Within soil samples that were collected beneath the plant, a significant difference ($p < 0.05$) was obtained between the first two depths (0–10 and 10–20 cm) and the three other soil layers.

Total Soluble Nitrogen. TSN values show a different trend between the two sampling sites. A seasonal effect was observed in the control soil samples, with high TSN values: summer > autumn > spring > winter. In the soil samples beneath the plant, the trend is different: winter > autumn > summer > spring. The highest value under the plant (6.6 ppm) was three times higher than the highest value in the control samples (2.14 ppm) (Fig. 2).

A significant difference ($p < 0.0001$) was observed in the control samples between seasons, and between the soil surface (0–10 cm) and the other four soil layers, whereas beneath the plant, a significant difference ($p < 0.05$) was observed between seasons with no significant differences ($p > 0.05$) between depths.

Microbial Biomass. The MB value reached a maximal value of $89.8 \mu\text{g C g soil}^{-1}$ in the soil under the plant and $57.3 \mu\text{g C g soil}^{-1}$ in the control samples. A significant difference ($p < 0.0001$) in MB was found independent of sampling time. No significant difference ($p > 0.05$) in MB was found along the vertical profiles in the control samples (Fig. 3A); however, a significant difference ($p < 0.05$) between the soil surface (0–10 cm) and the deepest layer (40–50 cm) was found. Maximal values throughout the seasons were found in autumn at both sampling sites, whereas the minimal values in winter for the control samples and in summer for samples in the plant vicinity were 32.6 and $31.1 \mu\text{g C g soil}^{-1}$, respectively.

The bacterial and fungal biomass (Figs. 4 and 5) was found to be significantly affected by time ($p < 0.0001$),

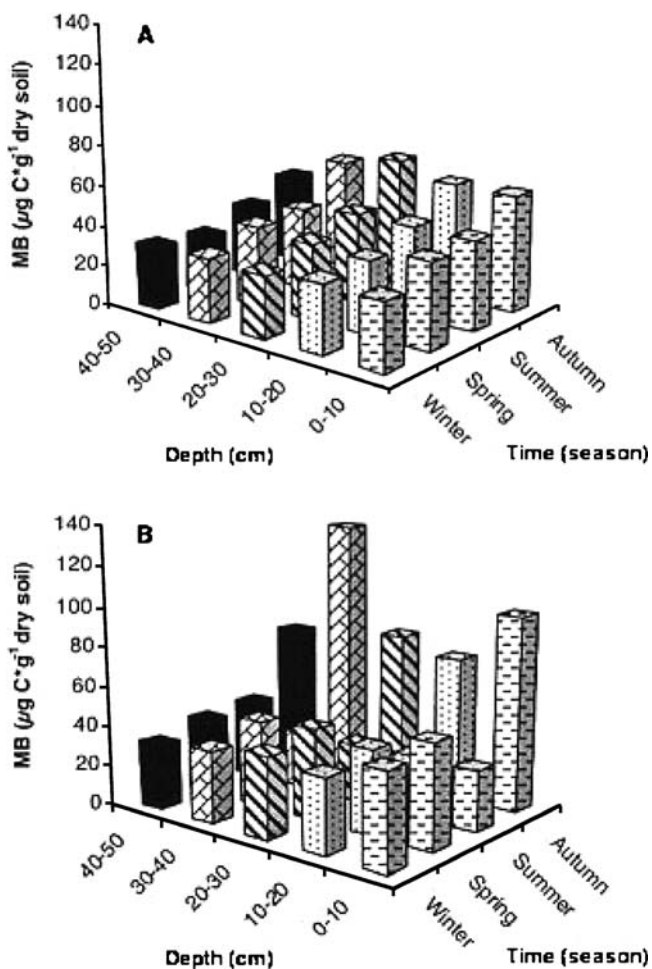


Figure 3. Seasonal variations in total microbial biomass (MB) during the research period (February 2003–January 2004). (A: control; B: vicinity of *T. aphylla*; $n = 4$.)

with no significant differences ($p > 0.05$) along the vertical scale at both sites.

The highest fungal biomass ($31.3 \mu\text{g C g soil}^{-1}$) was found in the vicinity of the plant in autumn (Fig. 4). In these soil samples, a significant difference ($p < 0.05$) was found between autumn and the other three seasons. In the control samples, an opposite trend was found, with significant differences ($p < 0.05$) between autumn and summer and between winter and spring.

A significant ($p < 0.05$) seasonal effect of bacterial biomass was obtained with a high biomass in autumn > spring > winter and summer (Fig. 5).

Soil Respiration and the Metabolic Quotient Index
Soil respiration values in the control samples were found to fluctuate between $0.89 \mu\text{g CO}_2\text{-C (g soil h)}^{-1}$ in spring and reaching $1.46 \mu\text{g CO}_2\text{-C (g soil h)}^{-1}$ in summer, whereas in the vicinity of the plant they were 0.5 and $2.47 \mu\text{g CO}_2\text{-C (g soil h)}^{-1}$ in winter and autumn, respectively.

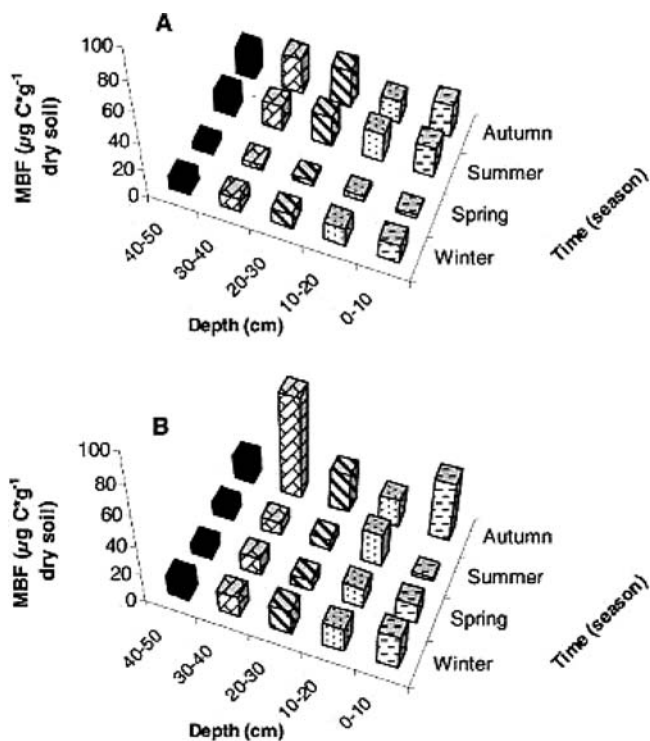


Figure 4. Seasonal variations in fungal microbial biomass (FMB) during the research period (February 2003–January 2004). (A: control; B: vicinity of *T. aphylla*; $n = 4$).

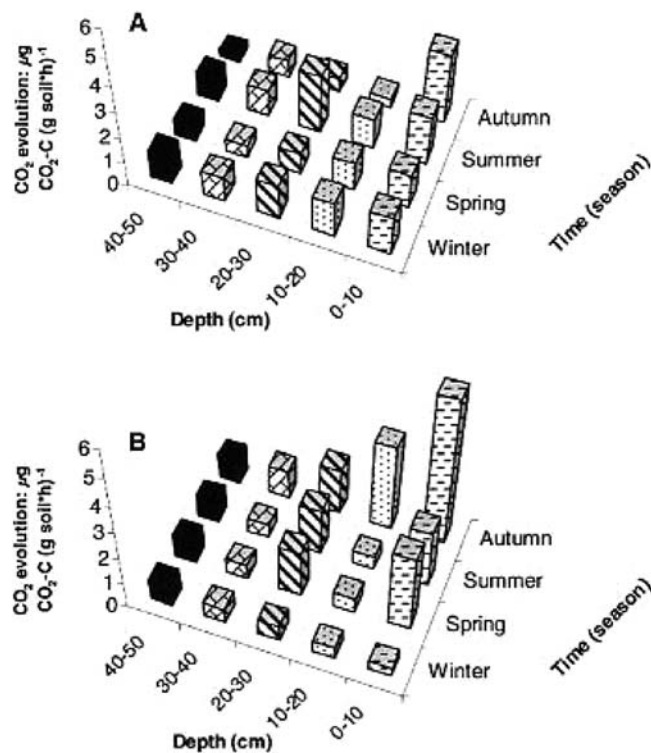


Figure 6. Seasonal variations in CO₂ evolution during the research period (February 2003–January 2004). (A: control; B: vicinity of *T. aphylla*; $n = 4$).

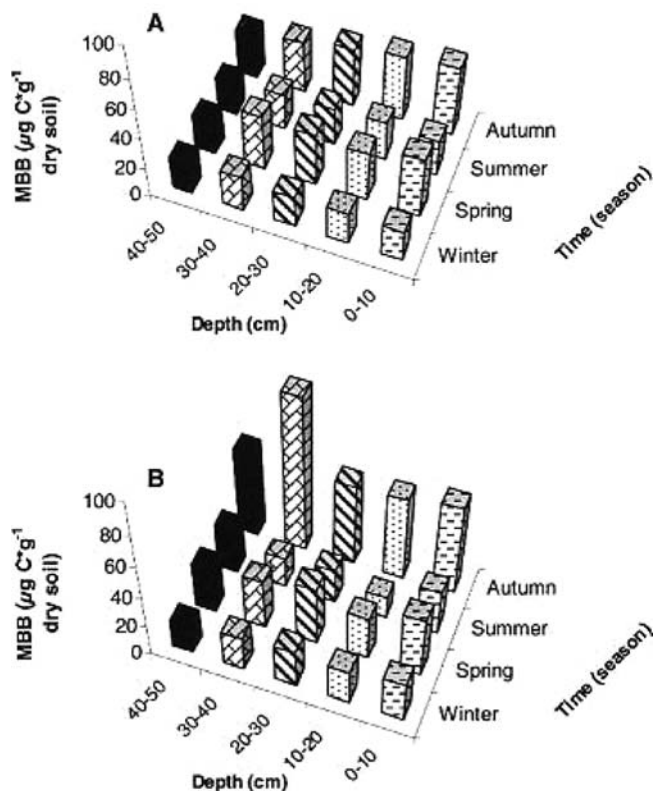


Figure 5. Seasonal variations in bacterial microbial biomass (BMB) during the research period (February 2003–January 2004). (A: control; B: vicinity of *T. aphylla*; $n = 4$).

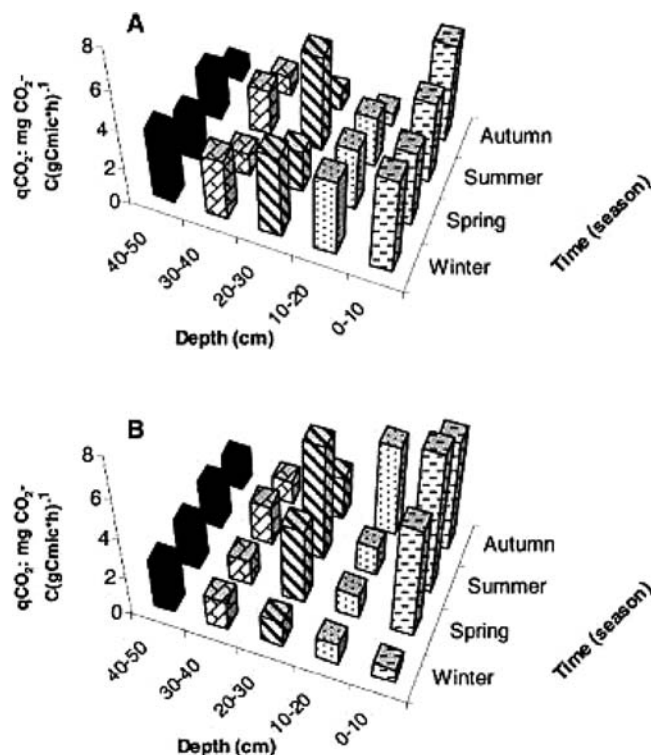


Figure 7. Seasonal variations in the qCO₂ index during the research period (February 2003–January 2004). (A: control; B: vicinity of *T. aphylla*; $n = 4$).

A significant difference ($p < 0.05$) was found in soil respiration within depths (Fig. 6a) in the control soil samples, with no significant differences ($p > 0.05$) between the four seasons. In contradistinction, CO₂ evolution in soil samples collected in the vicinity of the plant exhibited a significant difference ($p < 0.05$) between depths as well as between seasons (Fig. 6b).

The lowest metabolic quotient (qCO₂) values at either sampling location were found at the 30- to 40-cm depth. These values were 2.03 mg CO₂-C (g C_{mic} h)⁻¹ for the control samples and 1.49 mg CO₂-C (g C_{mic} h)⁻¹ for samples from the vicinity of the plants. qCO₂ index changes were found to be significantly affected ($p < 0.05$) by temporal spatial sampling (Fig. 7). For the control samples, there were significant differences ($p < 0.05$) between the 0- to 10-cm layer and all the other depths.

Discussion

The soil microorganism population plays an important and necessary role in all ecosystems. Abiotic conditions such as soil moisture, air and soil temperatures, salinity, nutrients, and radiation have been found to have a great temporal and spatial distribution effect on soil microorganisms [27]. Currently, there is a lack of knowledge on how these abiotic parameters affect soil microbiota, especially in desert systems. Clark [5] and Krasilnikov [13] showed that bacterial quantity is much higher in the rhizosphere than in bare soil.

In the desert systems, each type of population has a short activity period, which is affected by suitable climatic conditions and dormant periods. Existence during a dormant period is based on the activity–period products. Wetting of desert soil by rainfall events causes a very high response in microbial activity and leads to a significant increase in the inner soil MB.

SOM consisting of animal and plant residues acts as an energy source for all soil populations. The highest accumulation of organic matter was found at the soil surface, and was moved to deeper soil layers by water infiltration and soil biota activity [24].

Because the MB percentage is directly influenced by environmental parameters, it is a very efficient index for analyzing the decrease in soil quality [18, 25]. Based on Odum's theory [15, 16], Anderson and Domsch [4] defined the qCO₂ metabolic index as a gauge to disturbances in ecological systems. The qCO₂ index decreases during succession and recuperation after disturbance.

The qCO₂ index is an important ecosystem index contributing to the understanding of the SOM recycling rate [17]. In the samples collected in the vicinity of the plant at different soil layers, no significant differences ($p > 0.05$) in qCO₂ were found, whereas in the control soil

samples, significant difference ($p < 0.05$) was obtained with depth, i.e., samples from the 0- to 10-cm depth exhibited significantly higher values ($p < 0.05$) than those from the deepest soil layer (40–50 cm). In the bare soil, most of the biological activity was observed up to the 40-cm depth. On the other hand, in soil samples collected in the vicinity of the plant, biological activity at the deeper soil layers was observed, which may yield a vertical similarity in CO₂ evolution. Therefore, we did not observe any significant difference related to the contribution of the samples collected in the plant vicinity.

TSN values, both in the control samples and in samples collected in the plant vicinity, exhibited a similar pattern, i.e., they were significantly ($p < 0.0001$) affected by sampling period. However, in the deepest layer (40–50 cm) in the vicinity of the plant, the TSN value (2.4 ppm) was twice as high as in the control sample (1.2 ppm) taken at the same depth. These results are supported by data obtained by Sarig *et al.* [21] and He *et al.* [10] in their studies on desert shrubs in the Negev highlands.

Because the soil microbial population plays a key role in many inner soil processes, we measured MB and estimated soil microbial activity rate. Low values of MB indicate stabilization of the abiotic conditions. For the samples taken in the vicinity of the plant and the control soil samples, there was a significant difference ($p < 0.05$) in bacterial and fungal biomass throughout the seasons, whereas for the samples in the vicinity of the plant, there was no significant difference ($p > 0.05$) between the different soil layers. For the control samples, we observed a significant difference ($p < 0.05$) between bacterial biomass at the deepest (40–50 cm) soil layer (23.7 µg C g soil⁻¹) and the bacterial biomass at all other depths.

In conclusion, our results show that soil microbial activity in sandy desert soil reacts rapidly to the temporal and vertically spatial changes in abiotic conditions. These changes strongly elucidate the differences between total soil MB in the surface and deeper depth as well as between sampling locations. The difference between the bacterial and fungal biomass ratio is also elucidated.

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