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Substrate utilization patterns of desert soil microbial communities in response to xeric and mesic conditions

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ABSTRACT

The Negev Desert is characterized by low soil moisture and organic matter content and an unpredictable rainfall amount, dispersion, and intensity. Water and nutrient availability are, therefore, the major limiting factors of biological activity in arid and semi-arid ecosystems. Plants have developed different ecophysiological adaptations in order to cope with the harsh conditions in this xeric environment, e.g., excretion of salt (*Reaumuria negevensis*) and chemical compounds (*Artemisia sieberi*) through the leaves. Microorganisms constitute a major part of these ecosystems' total biomass, and are diverse members of the soil food web, being primarily responsible for breaking down complex organic compounds, which are then recycled. They are also known to be very sensitive to abiotic changes and can time their activity to the environmental conditions.

Soil samples were collected monthly from a 0 to 10 cm depth, under the canopies of *A. sieberi, Noaea mucronata*, and *R. negevensis*. Samples collected from inter-shrub spaces served as control. CO_2 evolution, microbial biomass, microbial functional diversity, and the physiological profile of the community, were determined by MicroResp™ analysis. A significant difference was found between the two dry periods in most of the examined parameters. The values of water, organic matter content, and total soluble nitrogen were higher in soil samples collected in the vicinity of *R. negevensis* than in samples collected in the vicinity of *N. mucronata*, *A. sieberi*, and the open area. A similar trend was found in CO_2 evolution, microbial biomass, and H' values, in which soil samples collected beneath the canopies of *N. mucronata* and *R. negevensis* and from open area had higher values during the wet periods (which were characterized by a mesic environment) and in samples collected beneath the *A. sieberi* in the wet 2006 and dry 2007 periods.

1. Introduction

The abundance and activities of a soil microbial community play an important beneficial role in nutrient acquisition for primary producers. It is known that the abundance and activities of soil microorganisms are determined by various environmental factors, such as soil type, temperature, moisture availability, organic matter, etc. (Buyanovsky et al., 1982; Coleman, 1985; Wardle, 1992; Sarig and Steinberger, 1993; Sarig et al., 1999; Katterer and Andren, 2001; Whitford, 2002). The different components of soil biota in desert ecosystems, which are characterized by low soil moisture content and unpredictability in water amount, frequency, and time (Evenari et al., 1982; Whitford, 2002), are found to respond to the above environmental triggers. The Negev Desert is known as such a xeric environment, where rainfall timing is predictable (November–March) while amount, dispersion, and intensity are unpredictable. However, the lack of moisture for the remaining period was augmented by dew formation as an additional source of moisture (210 days, mainly in autumn) triggering soil biological activity (West and Skujins, 1978a; Garner and Steinberger, 1989). In addition, soil organic matter is known to be relatively low in these ecosystems ($\sim 100\ g\ m^{-2}$) due to low nutrient availability (Noy-Meir, 1973, 1974; West and Skujins, 1978b). According to Buyanovsky et al. (1982), Coleman (1985), Beare et al. (1992) and Sarig and Steinberger (1993), the interaction between moisture and organic availability is one of the major features determining soil biotic functions in arid and semi-arid ecosystems. Therefore, the capability of soil biota to fulfill their biological role and function is greater near perennial shrubs, under whose canopies a more favorable environment exists compared to the open, between-shrub space (Sarig and Steinberger, 1993).

Nonetheless, in order to overcome the extreme environment, plant and soil biota have evolved diverse ecophysiological abilities suitable to the alteration in the abiotic conditions in time and space

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(Sarig and Steinberger, 1993). These ecophysiological adaptations, which include salt (*Reaumuria negevensis*) and chemical (*Artemisia sieberi*) compound excretion beneath the plant canopy, provide an allelopathic environment in addition to organic matter and soil moisture.

The microbial community is considered one of the main parts of the soil biota and plays an important role in the nutrient cycle and availability. It is sensitive to abiotic changes (Mills and Wasser, 1980; Kennedy and Smith, 1995), soil quality, and plant cover (Pankhurst et al., 1995), and is, therefore, considered to be one of the most important biological indicators of stress in terrestrial ecosystems. Sarig and Steinberger (1994) have demonstrated that microorganisms in desert soils can cope with a higher salt concentration and can utilize 'windows of activity' that may be ephemeral in space and time, thus being able to accomplish their biological functions (Evenari, 1981; Whitford, 2002; Shamir and Steinberger, 2007).

According to Steinberger and Whitford (1983), Coleman (1994), Sarig et al. (1994), Whitford (2002), and Loranger-Merciris et al. (2006), the shrub canopy helps protect the area under the plant against high radiation and decreases wind velocity which, together, contribute to improved water balance and increased litter and seed accumulation below the canopy. The plants also contribute organic components to the microbial communities in the soil by shedding some of their parts, such as roots, leaves, stems, and branches. Ronn et al. (2002), Smalla et al. (2001), Chen et al. (2003), and Shamir and Steinberger (2007) have elucidated the importance of the shrub canopy to soil organic matter above- and below-ground, contributing to the soil quality and being able to affect the bacteria/fungi ratio, composition, and development. According to Bolton et al. (1994), most of the carbon in the soil separated from the plant root. The different root exudates and the composition of the root cell components are influenced by the plant diversity (Marschner et al., 2001). The variety of organic compounds released by plants has been postulated to be one of the key factors affecting the diversity of microorganisms in the rhizosphere of different plant species (Bowen and Rovira, 1991; Bolton et al., 1994; Grayston et al., 1998; Marschner et al., 2001). Despite the important role of the bacterial community in the semi-arid ecosystem, little is known about the relationship between the plant xeric environment and soil microbial functional diversity (Broughton and Gross, 2000; Loranger-Merciris et al., 2006; Patra et al., 2008).

Many previous studies on biodiversity included studies on microorganism cultures, followed by new molecular techniques such as 16S rRNA sequence analysis, DNA melting profiles, and many others. However, these techniques failed to afford any indication of the functional diversity of soil microbial communities. Traditional methods that were used to identify microbial diversity, such as cultivating soil extractions on selective growth media, were found to face similar difficulties due to the fact that only some of the total bacteria (less than 1%) grow on conventional media (Kell et al., 1998; Ronn et al., 2002). According to Grayston et al. (1998), the analysis of functional diversity, associated with C utilization, is of greater significance in ecological studies compared to taxonomic analysis (Zak et al., 1994; Degens et al., 2000; Emmerling et al., 2002; Berg and Steinberger, 2008).

In desert systems, perennial shrubs have evolved a range of ecophysiological adaptations in order to cope with the xeric environment. Thus, each plant rhizosphere establishes 'entity islands', a key factor governing the microbial community.

Our objective was to determine the level of microbial activity and the metabolic diversity of soil microbial communities in relation to wet and dry periods (which reflect mesic and xeric environments, respectively) and shrub ecophysiological adaptation in a Negev Desert ecosystem. The hypothesis to be tested was that microbial communities under the canopy of different shrubs will be determined by ecophysiological adaptation, such as excretion of salt (*R. negevensis*) and chemical compounds (*A. sieberi*) via the leaves. The influence on the microbial communities will be measured by microbial biomass, CO_2 evolution and. functional diversity.

2. Materials and methods

The study site was located in the northern Negev Desert at the M. Evenari Runoff Research Farm (34°46′E/30°47′N), Avdat, Israel. The area consists of loess plain rocky slopes with shallow, saline, gray, lithogenic, calcareous soils. The soil at the study site is an alkaline (pH 7.8), deep, fine-textured loessial sierozem, with small amounts of organic carbon (0.47%) and large amounts of carbonate (40%). The climate is Mediterranean, with mild, rainy winters (5–14 °C in January) and hot summers (18–32 °C in June). The multiannual evaporation rate is 2615.3 mm. The rainy period usually begins in October and ends in late April, with most of the rainfall occurring as scattered showers between December and February. The multiannual mean rainfall is 90 mm and fluctuates between 34 mm in a drought year to 187 mm in an extremely rainy year. The multiannual mean amount of dew at this location contributes an amount of water equal to 35 mm of rainfall. Dewfall occurs during approximately 210 nights, mainly in late summer and autumn. The perennial vegetation is dominated by desert–shrub associations, in which the most common species are *R. negevensis*, *A. sieberi*, and *N. mucronata* (Evenari et al., 1982).

The study was conducted over a period of 25 months, between November 2005 and October 2007. We divided this period into four clearly identified periods: two wet (rainy) periods and two dry periods (Fig. 1). The first wet period lasted from November 2005 to April 2006, and was followed by a dry period from May to October 2006. The second wet period lasted from November 2006 to April 2007, followed by a dry period from May to October 2007.

Four soil samples from below each of the different canopies of *R. negevensis, A. sieberi*, and *N. mucronata*, and from the control-open inter-shrub space, were collected during the above-mentioned period of 25 months (total number of samples $= 4 \times 4 \times 25$) from the vicinity of the rhizosphere (0–10 cm depth). Each soil sample was placed in an individual plastic bag and stored in a cool insulated box until arrival at the laboratory. At the laboratory, the soil samples were stored at 4 °C after sieving through a 2-mm mesh in order to remove stones, roots, and other organic debris.

The shrubs used for the study are known to be very common and to have different ecophysiological adaptations. *R. negevensis* is known as a salt bush that passes salt from its ramified root system to the leaves. When these leaves are shed to the soil surface, 'islands of salinity' are created under the plant canopies (Flowers et al., 1977; Sarig and Steinberger, 1994). The salt has a hygroscopic effect on the water absorption ability (Evenari, 1981), and thus a relatively higher moisture level and prolonged biotic activity are expected. *A. sieberi* is known to excrete chemical compounds (allelopathic adaptation) that act as germination inhibitors for other plants in their surroundings (Friedman, 1995). These two mechanisms cause inhibition of other plants, including annuals, from growing in their surroundings (Friedman, 1995). *N. mucronata* is not known to have any effect on either annual or perennial germination, and was used as a control plant.

3. The collected soil samples were subjected to the following analyses

(1) *Soil moisture and organic matter determination* – gravimetric determination of soil water content was carried out by drying