

## Seasonal Effect of Geomorphological Chronosequence Features on Soil Biota Dynamics

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### ABSTRACT

Numerous studies have been devoted to the physical-chemical weathering processes leading to the creation of unique soil formations having their own history that induce soil-biotic diversity. However, the extent to which unique geomorphic formations influence soil biotic seasonal variation is not clear. Our aim was to define seasonal variations of soil biota in soils of different-aged terraces of the Makhtesh Ramon anticline erosional cirque in southern Israel. The strong effect of Makhtesh Ramon (Ramon crater) erosional fluvial terrace age initiated by climatic changes during the Late Pleistocene-Early Holocene period on seasonal variations in both soil properties and the abundance and composition of soil biota were demonstrated. However, age dependence was not constant and values for observed soil properties and microbial activity were negligible between younger and older terraces for certain seasons, while free-living nematodes along with bacterial-feeding group were strongly dependent on the geomorphic features of the ages throughout the study period.

*Key Words:* geomorphic formation, Makhtesh Ramon, microbial biomass, nematode community, trophic group

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Traditional soil-formation theory indicates that soil develops progressively under the influence of environmental-state factors, until it is in equilibrium with the prevailing environmental condition. Furthermore, Walker and Syers (1976) and Hugget (1998) concluded that soil chronosequences are still among the most important and powerful tools for pedological investigations, based on the multidirectional-change theory, including estimation of geomorphic-feature ages in a hyperarid environment (Amit *et al.*, 1996).

Five erosional cirques of different sizes are located in the central part of the Negev Desert, with Makhtesh Ramon being one of the largest (Plakht, 2003). Makhtesh (Hebrew for crater) Ramon exhibits numerous geological features: a large variety of rock types, with superb assemblages of macro- and microfossils from the Triassic (about 220 million years ago) up to the upper Cretaceous (about 70 million years ago) (Mazor, 1992). Makhtesh Ramon is located in southern Israel in the Negev Desert area. Structurally, the area is an anticline with a central eroded valley, mostly drained by a single river, Nahal Ramon. The evolution of the present exposure of Makhtesh Ramon is the result of post-Eocene erosion and structural modification (Nativ and Mazor, 1987). According to Plakht (1995), the physico-chemical weathering in this crater resulted in the formation of soil horizons on the truncated surfaces of bedrocks with different compositions. The first stage of the lowering of base level began with erosional activity associated with deformation along the Dead Sea-Arava Rift Valley (Zilberman, 1991; Ben-David, 1993; Ben-David *et al.*, 2002). The lower landforms are younger because of the higher topographic position of Makhtesh Ramon in relation to its base level in the Dead Sea basin. An interrupted incision of the Makhtesh Ramon drainage system has occurred since the Pliocene. During the Pleistocene, Makhtesh

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Ramon was situated high, relative to its drainage base level (Ben-David *et al.*, 1992). This resulted in the preservation of stepped fluvial terraces, the lowest of which is the youngest (Plakht, 1996).

Seven terraces that were dated by the radio-thermo-luminescent (RTL) method, with ages from 10 to 500 ka, were found in the Makhtesh Ramon crater and described by Plakht (2000). Previous investigations (Yeates, 1982; Pen-Mouratov *et al.*, 2004a) showed that the abundance and composition of soil organisms are related and affected by the physical and chemical characteristics of soil in a different part of world. In our recent study, Shukurov *et al.* (2005) studied the influence of the age of erosional fluvial terraces of Makhtesh Ramon (crater) on soil chemical and biological properties. Significant effects of erosion age of terraces on soil properties (soil moisture, organic carbon, soil salinity, and electrical conductivity) and on soil biota (microorganisms and soil free-living nematodes) were exhibited at the end of the rainy season. Following the above-mentioned study, we asked whether seasonal changes in the Makhtesh Ramon of unevenly aged terraces affect soil biotic fluctuations. Our next aim was, therefore, to define seasonal variations in the soil microbial community and soil free-living nematode populations in different-aged terraces of the anticline erosional cirque, Makhtesh Ramon. The following terraces were observed seasonally during 2003–2005 for this purpose: i) the alluvium of a terrace of 48–60 ka age (Terrace I) is composed mainly of pebbles in the sandy matrix of Makhtesh Ramon, which sometimes contains buried gypsic paleosol; ii) the alluvium of a terrace of 101–150 ka age (Terrace II) in Makhtesh Ramon is composed mainly of interbedded pebbles and sandy-loamy layers, alternating with horizons of buried calcic paleosol containing carbonate nodules; iii) coarse gravel dominates the composition of the alluvium of a terrace of 205–240 ka age (Terrace III) in Makhtesh Ramon; and iv) a terrace of 375–443 ka age (Terrace IV) is the highest in Makhtesh Ramon, consisting mainly of a well-rounded conglomerate interbedded with layers of well-cemented carbonate sand.

## MATERIALS AND METHODS

Makhtesh Ramon crater is 40 km long, about 9 km wide, and 400 m deep, with altitudes varying from 1020 m on the western rim to 420 m above sea level in the east (Nativ and Mazor, 1987). The area is characterized by an arid to extremely arid climate. Mean multi-annual rainfall is 85 mm at the northern rim of the Makhtesh and 56 mm at the bottom, most of it coming from the west and northwest (Nativ and Mazor, 1987). Mean annual temperature is 17–19 °C (Plakht, 2003). Soil thickness does not exceed 20–30 cm. Due to arid climatic conditions, the processes of physical weathering prevail and the physically weathered material contains no material finer than 30 µm (Gale and Hoare, 1991). Vegetation cover is scarce and confined mainly to the stream channels. Trees are rare, and only two species, *Tamarix nilotica* and *Acacia raddiana*, are represented (Ward and Olsvig-Whittaker, 1993).

Soil samples ( $n = 320$ ) were taken from the 0–10-cm layer of each of the four erosion terraces. Five individual replicates of the soil samples were randomly collected from every site in the early hours seasonally during 2003–2005. Every soil sample consisted of five pseudo-replicates. Soil samples were collected at a distance above 15 m from any plants in the open area of the four terraces (I–IV).

Each soil sample (1 kg weight) was collected and placed in an individual plastic bag, which was then sealed. The samples were kept in insulated boxes for transport to the laboratory, where they were kept at 4 °C until biological and chemical analyses were performed. Before laboratory analysis, the soil samples were sieved through a 2-mm mesh sieve in order to remove organic remains.

All collected samples of different types of soil formations were subjected to the following analyses: i) Soil moisture was determined gravimetrically (105 °C, 48 h). ii) Organic matter was determined by oxidization with dichromate in the presence of H<sub>2</sub>SO<sub>4</sub>, without application of external heat (Rowell, 1994). iii) Total soluble nitrogen (TSN) in soil was determined automatically (Kroon, 1993) with a Skalar Autoanalyzer System (SFAS, 1995). iv) Soil microbial biomass ( $C_{mic}$ ) was determined using a chloroform fumigation incubation (CFI) assay, according to Jenkinson and Powlson (1976). Five-gram soil samples were adjusted to 40% water-holding capacity and fumigated in a CHCl<sub>3</sub>-saturated atmosphere in a desiccator for 24 h. The fumigated and corresponding non-fumigated (control) samples were then

transferred to 0.5-L glass jars and incubated for 10 days at 25 °C in the dark. CO<sub>2</sub> concentration was measured in the head space of the glass jars using a gas chromatograph (GC), and C<sub>mic</sub> was calculated as:

$$C_{mic} = [(CO_2-C \text{ from fumigated soil}) - (CO_2-C \text{ from control sample})] / kc$$

where *kc* is the fraction of MB that is mineralized to CO<sub>2</sub>-C, and a *kc* of 0.41 was used, as proposed by Anderson and Domsch (1993). v) Microbial respiration (MR) was evaluated by determining CO<sub>2</sub> using a Shimadzu C-R6A gas chromatograph (Sparling and West, 1990). Similar to the soil microbial biomass analysis, the samples for CO<sub>2</sub> respiration analysis were incubated for 10 days at 25 °C in the dark. And vi) nematode communities were extracted from 100 g soil samples using the Baermann funnel procedure (Cairns, 1960). The recovered organisms were counted and preserved in formalin (Steinberger and Sarig, 1993), and identified according to trophic level using a compound microscope.

The metabolic quotient (*q*CO<sub>2</sub>) was calculated as the ratio between CO<sub>2</sub> production and microbial biomass (Anderson and Domsch, 1990). The *q*CO<sub>2</sub> is a specific parameter for evaluating the effects of environmental conditions on the soil microbial biomass. The microbial quotient, known as substrate availability, was determined as the percentage of C<sub>mic</sub>/C<sub>org</sub> (microbial biomass C/organic C) ratio (Insam and Haselwandter, 1989; Hofman *et al.*, 2003).

Characteristics of nematode communities were described by means of indexes: i) absolute abundance of individuals 100 g<sup>-1</sup> dry soil; and ii) abundance of omnivore-predators (OP), plant-parasites (PP), fungal-feeding (FF) and bacterial-feeding (BF) nematodes (trophic structure) (Steinberger and Loboda, 1991; Pen-Mouratov *et al.*, 2003, 2004a, b).

All data obtained were subjected to statistical analysis of variance using the SAS statistical software package (ANOVA, Tukey's test, and Pearson correlation coefficient) and were used to evaluate differences between separate means. In addition, the data were tested by computing redundancy discriminate analysis (RDA) (ter Braak and Smilauer, 2002) in order to evaluate differences between separate means. Differences with *P* < 0.05 were considered statistically significant.

## RESULTS

### *Soil properties*

Soil moisture (SM) ranged between 16 and 66 g kg<sup>-1</sup>, increasing during the wet (autumn-winter) period (Table I). Moreover, soil moisture values were not different between terraces during the wet period but were different during the dry (spring-summer) period (Tables I and II). In the younger terraces (Terraces I and II), mean soil moisture ranged between 26 and 66 g kg<sup>-1</sup> and was not significantly different from the older terraces (Terraces III and IV), where the mean values ranged between 16 and 54 g kg<sup>-1</sup> (Table I). However, significant differences were found between the younger and the older terraces during the wet period (Table I). In spring, SM was found to decrease gradually from the young Terrace II (age of 101 ka) to the older terraces (Terraces III and IV) and were not different from Terrace I (48 ka). In summer, SM exhibited greater differences between the young and old terraces, with variations from 22 to 23 g kg<sup>-1</sup> in younger terraces and from 16 to 18 g kg<sup>-1</sup> in older terraces (Table I).

Soil organic matter ranged between 0.05% and 0.2%. Similar to SM, it increased during the wet (autumn-winter) period (Table I). Moreover, OM values exhibited no differences between terraces in autumn (Tables I and II). During the following three seasons, the OM was minimal (0.05%–0.09%) in the oldest terrace (Table I).

Total soluble nitrogen showed seasonal dependence, increasing in winter, and ranged between 27.7 and 79.9 mg kg<sup>-1</sup> during the study period (Tables I and II). TSN exhibited a relatively low mean value of 27.7–51.4 mg kg<sup>-1</sup> for the oldest terrace (Terrace IV) and was significantly different from all other terraces during the winter-spring-summer periods (Table I).

TABLE I

Soil properties from different terraces of Makhtesh Ramon crater

Terrace	Soil property <sup>a)</sup>		
	SM	OM	TSN
	g kg <sup>-1</sup>	%	mg kg <sup>-1</sup>
		<i>Autumn</i>	
I	41a <sup>b)</sup>	0.15a	43.6ba
II	66a	0.18a	46.8ba
III	46a	0.18a	49.9a
IV	45a	0.09a	34.1b
		<i>Winter</i>	
I	48a	0.20a	79.9a
II	53a	0.20a	75.3a
III	54a	0.20a	67.4a
IV	42a	0.09b	51.4b
		<i>Spring</i>	
I	31ba	0.07ba	45.3a
II	35a	0.08a	41.9b
III	26b	0.10a	41.2b
IV	2.6b	0.05b	33.4c
		<i>Summer</i>	
I	22a	0.11a	39.7a
II	23a	0.11a	39.6a
III	18b	0.14a	36.4a
IV	16b	0.08b	27.7b

<sup>a)</sup>SM = soil moisture; OM = organic matter; TSN = total soluble nitrogen.<sup>b)</sup>Values with the same letter(s) are not significantly different ( $P < 0.05$ ) between terraces.

TABLE II

Univariate analysis of variance (ANOVA) for soil properties, soil microbial activity, and nematode trophic structure in different terraces of Makhtesh Ramon crater during different seasons of the year

Index <sup>a)</sup>	Autumn		Winter		Spring		Summer	
	<i>F</i> -test	<i>P</i> value	<i>F</i> -test	<i>P</i> value	<i>F</i> -test	<i>P</i> value	<i>F</i> -test	<i>P</i> value
Soil property								
SM	0.99	NS <sup>b)</sup>	1.1	NS	2.86	0.05	3.04	0.04
OM	0.72	NS	2.78	0.04	4.92	0.006	6.17	0.001
TSN	2.31	NS	4.97	0.003	18.62	0.0001	16.15	0.0001
Soil microbial activity								
MB	0.54	NS	3.04	0.03	1.31	NS	7.36	0.0007
MR	0.28	NS	1.94	NS	0.05	NS	0.34	NS
$qCO_2$	2.39	NS	1.35	NS	2.2	NS	2.77	0.05
$C_{mic}/C_{org}$	1.4	NS	2.25	NS	0.64	NS	6.92	0.001
Nematode trophic structure								
TN	8.96	0.0001	7.32	0.0001	14.59	0.0001	7.46	0.0003
BF	7.88	0.0002	8.85	0.0001	16.68	0.0001	6.2	0.001
FF	1	NS	0.56	NS	2.19	NS	1.03	NS
PP	1	NS	NF <sup>c)</sup>	NF	NF	NF	1.62	NS
OP	0.91	NS	1.36	NS	NF	NF	1.01	NS

<sup>a)</sup>SM = soil moisture; OM = organic matter; TSN = total soluble nitrogen; MB = microbial biomass; MR = microbial respiration;  $qCO_2$  = metabolic quotient;  $C_{mic}/C_{org}$  = microbial biomass C/organic C; TN = total number of nematodes; BF = bacterial-feeding; FF = fungal-feeding; PP = plant-parasites; OP = omnivore-predators.<sup>b)</sup>Not significant.<sup>c)</sup>No individual nematode found.

*Microbial biomass and microbial respiration*

Soil microbial biomass (MB) ranged between 11.4 and 81.3 mg  $C_{mic} g^{-1}$  soil and was significantly different between terraces only in winter ( $P < 0.03$ ) and in summer ( $P < 0.0007$ ). In winter, MB exhibited significant differences between younger (Terraces I and II) and older (Terraces III and IV) terraces, reaching a maximum value of 39.6  $\mu g C_{mic} g^{-1}$  soil in young terrace II and minimum 9.8  $\mu g C_{mic} g^{-1}$  soil in the oldest terrace (Terrace IV). In summer, MB reached a maximum value of 81.3  $\mu g C_{mic} g^{-1}$  soil in the youngest terrace (Terrace I) while no significant differences were found between the other terraces (Fig. 1, Table II).

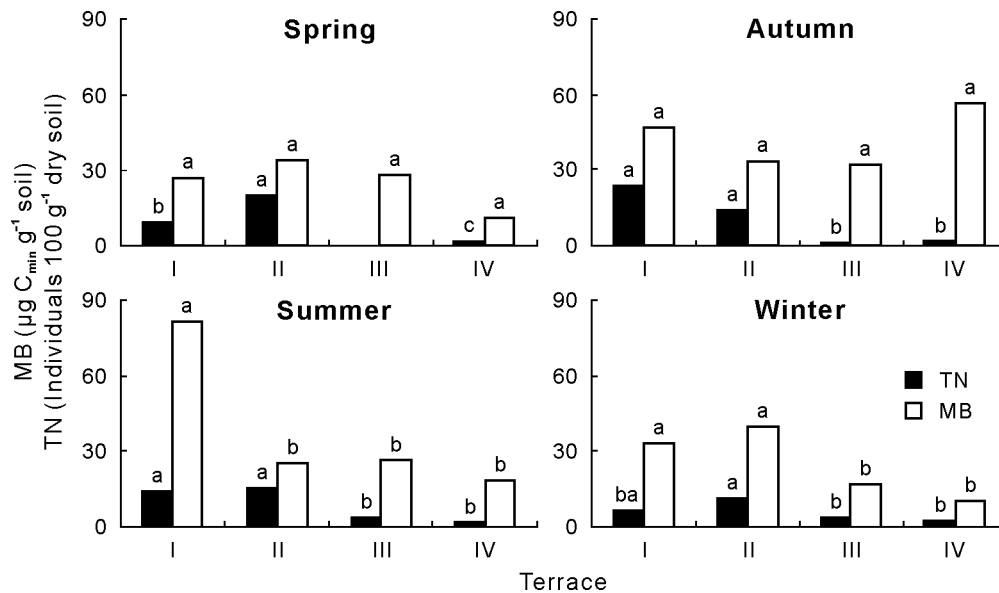


Fig. 1 Seasonal variations in the soil microbial biomass (MB) and total number of nematodes (TN) in soil samples taken from the different terraces of the Makhtesh Ramon erosion cirque. Bars with the same letter(s) are not significantly different ( $P < 0.05$ ) between terraces.

Microbial respiration (MR) values ranged between 16.0 and 33.2  $\mu g CO_2-C g^{-1} soil h^{-1}$  and were not significantly different between terraces during the study period (Table II). MR exhibited seasonal dependence ( $P < 0.0001$ ), reaching the highest mean values in autumn (31.32  $\mu g CO_2-C g^{-1} soil h^{-1}$ ) and the lowest in spring (16.25  $\mu g CO_2-C g^{-1} soil h^{-1}$ ).

The  $qCO_2$  ranged between 0.46 and 7.0  $mg CO_2-C g^{-1} C_{mic} h^{-1}$ , exhibiting seasonal dependence ( $P < 0.05$ ), decreasing from autumn to summer. However,  $qCO_2$  was significantly different between the observed terraces only in summer ( $P < 0.05$ ), reaching the maximum mean value (2.05  $mg CO_2-C g^{-1} C_{mic} h^{-1}$ ) in the oldest terrace (Terrace IV) and minimum mean value (0.46  $mg CO_2-C g^{-1} C_{mic} h^{-1}$ ) in the youngest terrace (Terrace I).

The  $C_{mic}/C_{org}$  showed a relatively similar pattern to that of the  $qCO_2$  (Table II).  $C_{mic}/C_{org}$  ranged between 1.1% and 9.4%, with values significantly different between seasons ( $P < 0.002$ ).  $C_{mic}/C_{org}$  was similar to the  $qCO_2$  and exhibited differences between terraces only in summer, reaching a maximum value (6.34%) in the youngest terrace (Terrace I). It was not significantly different between the other observed terraces.

A negative correlation was found between terrace age and soil properties with SM in spring-summer, with OM in winter and in summer, and with TSN in winter and spring (Table III). MB was found to be negatively correlated with terrace age in winter and summer and with SM in autumn. MB was found to be positively correlated with SM in winter, with OM in spring and with TSN in autumn-winter

(Table III). The  $q\text{CO}_2$  of the soil microbial community exhibited positive correlation with terrace age, SM, and OM in summer, autumn, and spring, respectively, and negative correlations with TSN in summer.  $C_{\text{mic}}/C_{\text{org}}$  exhibited negative correlation with terrace age and SM in summer and autumn, respectively, and positive correlation with SM and TSN in winter and autumn, respectively (Table III).

TABLE III

Correlation coefficients between observed indices<sup>a)</sup> and soil properties<sup>b)</sup> during four seasons of the year

Index	Autumn					Spring				
	Age	SM	OM	TSN	$q\text{CO}_2$	Age	SM	OM	TSN	$q\text{CO}_2$
Age							-0.32*			-0.76***
MB		-0.50***		0.45**				0.42*		
$q\text{CO}_2$		0.78***						0.55**		
$C_{\text{mic}}/C_{\text{org}}$		-0.41**		0.34*						
TN	-0.50***					-0.43**				
Trophic structure										
BF	0.47***	-0.24*				-0.37*				
FF										0.57**
PP										
OP										

Index	Winter					Summer				
	Age	SM	OM	TSN	$q\text{CO}_2$	Age	SM	OM	TSN	$q\text{CO}_2$
Age			-0.19**	-0.29***			-0.34**	-0.29*		
MB	-0.26**	0.23*		0.28**		-0.49**				
$q\text{CO}_2$						0.44**			-0.47**	
$C_{\text{mic}}/C_{\text{org}}$		0.23*				-0.40*				
TN	-0.24**					-0.47***			0.35**	
Trophic structure										
BF	-0.25***					-0.43***			0.26*	
FF										
PP							0.52***		0.26*	
OP				0.16*	0.38***					

\*, \*\*, \*\*\*Significant at  $P < 0.05$ ,  $0.01$ , and  $0.001$ , respectively.

<sup>a)</sup>MB = microbial biomass;  $q\text{CO}_2$  = metabolic quotient;  $C_{\text{mic}}/C_{\text{org}}$  = microbial biomass C/organic C; TN = total number of nematodes ( $100 \text{ g}^{-1}$  dry soil); BF = bacterial-feeding; FF = fungal-feeding; PP = plant-parasites; OP = omnivore-predators.

<sup>b)</sup>Age = age of terraces; SM = soil moisture; OM = organic matter; TSN = total soluble nitrogen.

### *Nematode communities*

The mean total number of nematodes (TN) in the soil samples taken from the different terraces ranged from 1 to 24 individuals  $100 \text{ g}^{-1}$  dry soil, indicating significant differences between younger and older terraces during all study periods, reaching a maximum in autumn and a minimum in winter (Fig. 1, Table II). The mean TN values were significantly different between younger (Terraces I and II) and older (Terraces III and IV) terraces during all seasons (Fig. 1). TN exhibited negative correlation with terrace age during all seasons and positive correlation with TSN in summer (Table III).

### *Nematode trophic groups*

The bacterial-feeders (BF) exhibited a similar trend to that of the total nematodes, while the other trophic groups had different patterns of density in the observed soil formations (Fig. 2). The BF was the most abundant trophic group, with *Wilsonema* as the most dominant taxon, and showed significant differences between younger (Terraces I and II) and older (Terraces III and IV) terraces during all seasons except winter. In winter, BF abundance was significantly higher only in the young Terrace II, with no differences being observed for the other terraces (Fig. 2).

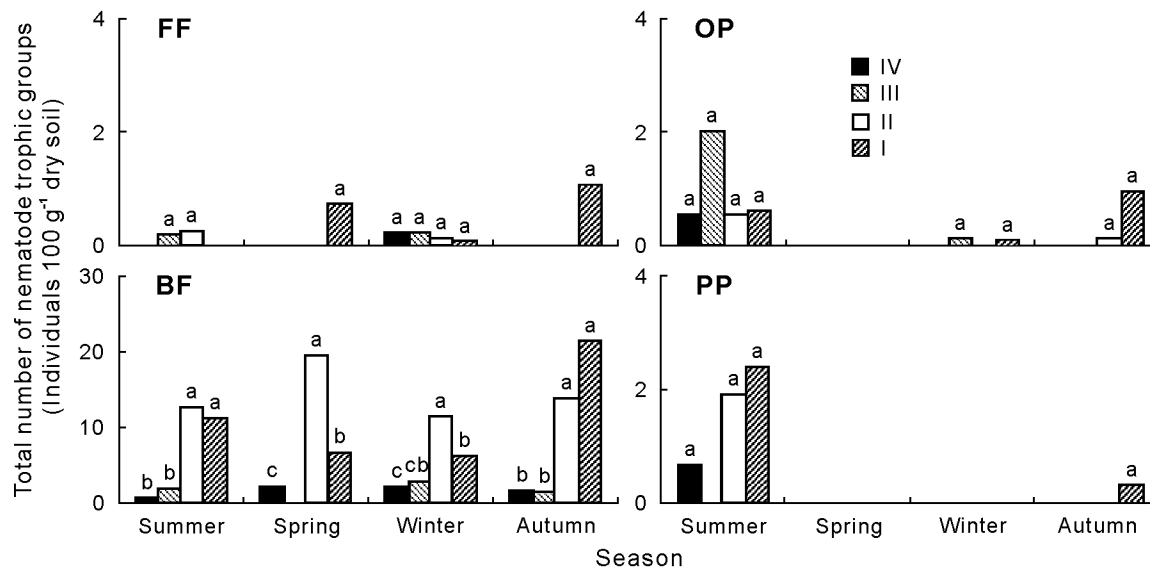


Fig. 2 Seasonal variations in the nematode trophic groups in soil samples taken from the different terraces of the Makhtesh Ramon erosion cirque. I, II, III and IV stand for Terraces I, II, III and IV, respectively. BF = bacterial-feeding; FF = fungal-feeding; PP = plant-parasites; OP = omnivore-predators. Bars with the same letter(s) are not significantly different ( $P < 0.05$ ) between terraces.

Unlike the total number of nematodes and the bacterial-feeding trophic group, FF and OP values were not different between the observed terraces during the study period (Table II, Fig. 2). The FF trophic group ranged between 0 and 1 individual per 100 g dry soil and exhibited no differences between seasons. The fungal-feeding group was represented by *Ditylenchus* genera. The OP trophic group, with *Mesodorylaimus* as the most dominant genus, ranged between 0 and 2 individuals per 100 g dry soil and reached maximum values in summer, with no differences between other seasons (Fig. 2).

The PP feeding group, represented by *Xiphinema* genera, ranged between 0 and 2 individuals per 100 g dry soil and showed no statistical differences between terraces during the observed seasons (Fig. 2, Table II). However, the data obtained during the study period demonstrated that the total number of PP nematodes was higher in the younger terraces than in the older terraces ( $P < 0.02$ ) during the summer season. The OP feeding group was found to show a similar trend to the PP, reaching maximum values in summer, however, a more significant appearance was obtained in autumn, with no significant differences between them (Fig. 2, Table III).

BF, similar to TN, showed negative correlation with terrace age during all seasons and positive correlation with TSN in summer (Table III). Moreover, BF exhibited negative correlation with SM in autumn (Table III). FF exhibited positive correlation with the  $qCO_2$  of the soil microbial community in spring (Table III). PP was positively correlated with SM and TSN in summer (Table III). OP showed positive correlation with TSN and  $qCO_2$  in winter (Table III).

Multivariate analysis of the soil properties, microbial biomass, and nematode communities showed clear discrimination relative to the observed terraces during the different seasons (Fig. 3). TN, BF, and PP values were higher in the younger (Terraces I and II) than in the older terraces (Terraces III and IV) during all seasons (Fig. 3). Microbial biomass values as well as values of other trophic groups of nematodes varied between terraces during the observed seasons (Fig. 3).

DISCUSSION

Previous studies found both linear and non-linear correlations between soil properties and time. The results of the present investigation are in agreement with previous studies and showed seasonal

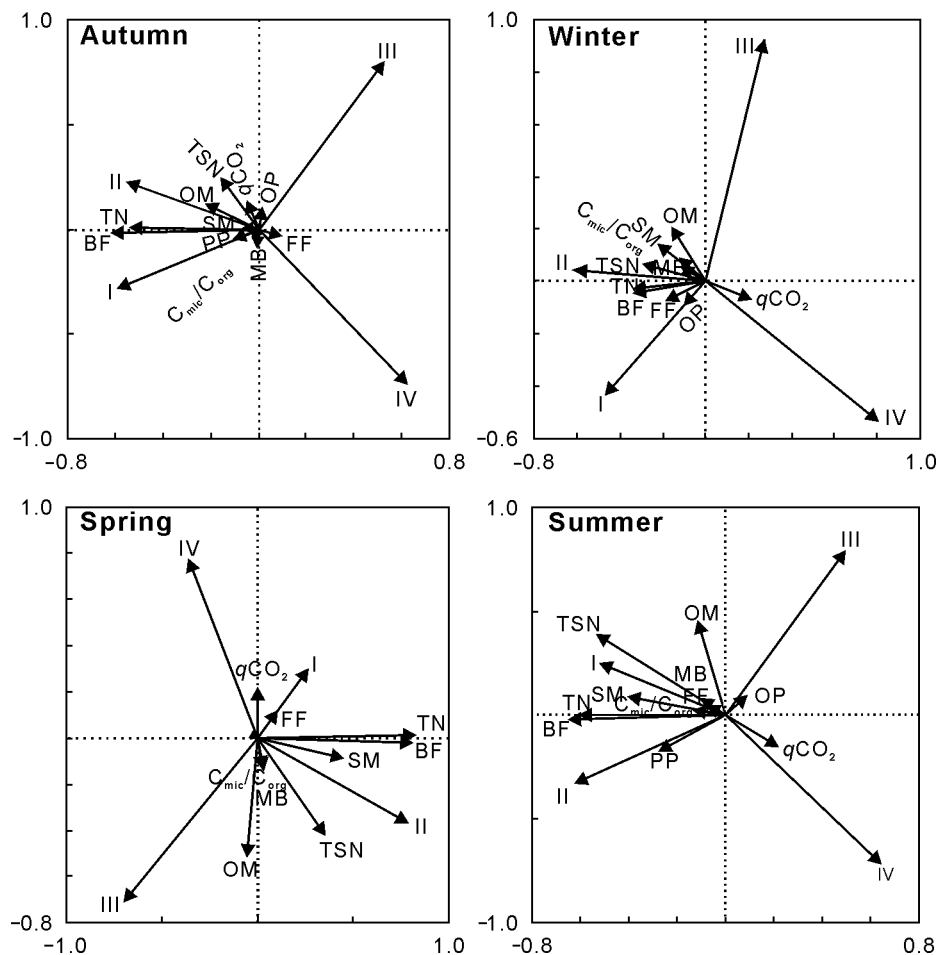


Fig. 3 Redundancy analysis of soil biota seasonal variations with reference to soil properties in soil samples taken from the different terraces of the Makhtesh Ramon erosion cirque. I, II, III and IV stand for Terraces I, II, III and IV, respectively. MB = microbial biomass; TN = total number of nematodes; BF = bacterial-feeding; FF = fungal-feeding; PP = plant-parasites; OP = omnivore-predators; SM = soil moisture; OM = organic matter; TSN = total soluble nitrogen;  $qCO_2$  = metabolic quotient; and  $C_{mic}/C_{org}$  = microbial biomass C/organic C.

changes in the observed soil properties. The sum total of soil properties obtained during the study period decreased in the oldest terrace and exhibited dependence on the age of geomorphic features. In spite of the above mentioned discovery, age dependence was not constant, and differences between the observed soil properties were negligible between terraces for certain seasons of the year. The soil moisture values were the most variable, followed by organic matter and then by total soluble nitrogen.

Many studies (*e.g.*, Neher *et al.*, 2005; Williamson *et al.*, 2005) published in the last decades have emphasized that the abundance and species of soil organisms are dependent on the type and physical characteristics of the soil, where a change in soil microbial parameters and soil free-living nematodes afford an early warning of decreasing soil quality (Kandeler *et al.*, 1999; Yeates *et al.*, 1999).

Our recent investigation in the same study area (Pen-Mouratov *et al.*, 2008) demonstrated that the severe erosion initiated by climatic changes during the Late Pleistocene-Early Holocene periods had significant consequences on the abundance and composition of soil communities. In addition, the data obtained in the current study are coincident with previous conclusions about greater biological activity of soils in lower and younger terraces than in higher and older terraces (Shukurov *et al.*, 2005). However, in contrast to the above-mentioned investigation that concluded that there was a strong dependence of microbial and nematode population activity on terrace age, the present investigation shows seasonal



variations of the observed soil biota. Therefore, contrary to soil free-living nematode communities that demonstrated a tight correlation with the age of geomorphic features during all seasons, the soil microbial biomass was dependent on the age of the geomorphic features only in unfavorable periods (winter and summer). Moreover, the  $q\text{CO}_2$  ecophysiological index, which reflects environmental stress in soil microbial populations (Anderson and Domsch, 1993), indicated seasonal variation in the suitability of environments with the most unfavorable conditions for microorganisms in the older terraces (Terraces III and IV) in summer and in winter, in Terraces II and IV in autumn, and in Terraces I and IV in spring. However, the omnivore-predator nematodes belonging to a K-life-strategy (persisters, sensitive to disturbance) were positively correlated with the ecophysiological index (in winter), which indicated differences in the requirements for environmental quality of omnivore-predator nematodes and soil microorganisms.

The bacterial-feeding nematodes belong to the r-life-strategy group (colonizers, tolerant to environmental disturbance) and were the most numerous in all soil formations (55%–95%), reaching significantly higher values in the younger terraces during all seasons. The total number of nematodes belonging to other trophic groups was not large and not significantly different from the observed geomorphic features during all seasons.

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