Journal of Arid Environments 163 (2019) 50–58

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Abiotic and plant gender effects on the structure and function of soil microbial communities associated with *Acanthosicyos horridus* (Nara) in the Namibian sand-dune desert ecosystem

Chen Sherman[a], Eugene Marais[b], Gillian Maggs-Kölling[c], Jonathan Adams[d], Yosef Steinberger[a,*]

[a] The Mina & Everard Goodman Faculty of Life Sciences, Bar-Ilan University, Ramat-Gan, 5290002, Israel
[b] Department of Entomology, National Museum of Namibia, Windhoek, Namibia
[c] Gobabeb Research and Training Centre, Namibia
[d] Division of Agrifood and Environment, School of Water, Energy and Environment, Cranfield Soil and Agrifood Institute, Cranfield University Bedfordshire, UK

ARTICLE INFO

Keywords:
Namibia Desert
Microbial community
Nara
Sand dune

ABSTRACT

In a xeric environment, plant ecophysiological adaptation helps determine soil microbial-community structure beneath plant canopies. We compared the plant-associated microbiota of the dioecious perennial plant *Acanthosicyos horridus* (Nara) in the Namib Desert in relation to soil parameters, climate, and plant gender. Abiotic soil attributes (soil moisture, total organic matter, salinity) and plant gender were among the main factors correlating with soil microbial-community biomass, basal respiration, and substrate-induced respiration rates. These varied between an extremely arid Far East (FE) site and a less arid site in the sandy, saline delta ecosystem. *A. horridus* gender was correlated with soil microbiome composition and activity, and varied between the relatively humid and more xeric environments. This study highlighted the apparent role of plant dimorphism in determining soil biotic composition and diversity in a desert ecosystem; however, the cause of the relationship between plant gender and microbial community remains uncertain. Possible explanations include gender-related variation in the plant itself, a link to certain abiotic soil conditions that incidentally influence plant gender, or a combination of both. This is the first example of gender-related differences in microbiota reported in a plant from an arid environment, and only the second example from the plant world in general.

1. Introduction

The coastal desert of Nambia is characterized not only by its extreme aridity but also by strong onshore winds, rainlessness, fog, dew, and relatively low temperature, as well as its extensive dune fields. In this xeric, low-primary-productivity and unpredictable environment, perennial shrubs, such as *A. horridus*, a dioecious plant, are a keystone species, with the female plant providing food for wildlife and the local bushmen in the area. This totally leafless plant produces a fruit (melon) that is strongly aromatic, being easily detected by the surrounding wildlife.

The plant community in deserts is known to be closely linked to the soil microbial community, with the plant providing shelter (e.g., decreased radiation and temperature) and energy (in the form of organic matter), and with the microbial community playing a fundamental role in soil biogeochemical processes, providing a wide range of nutrients (Lehman et al., 2015; Buyer et al., 2016; Singh et al., 2016). It is known that the desert soil microbial community is affected by plant species composition and soil chemical characteristics, such as soil moisture, organic matter, etc. (Sarig and Steinberger, 1993; Bhatnagar and Bhatnagar, 2005; Wardle, 2006).

Soil microorganisms in terrestrial xeric ecosystems are known to play an important role in soil organic turnover (Coleman, 1985; Adl, 2003; Oren and Steinberger, 2008). Since they are involved in numerous key processes, such as decomposition, mineralization, soil stabilization, etc. (Coleman, 1985; Coleman and Crossley, 1996; Sherman et al., 2014), the huge range of soil organic-matter composition presents a challenge to microbial communities and their ability to metabolize the different organic sources (Garcia-Pausas and Paterson, 2011). The structure of organic matter in a xeric ecosystem is modified by high radiation and extreme fluctuation in temperature and moisture level, causing its chemical breakdown and physical attrition, which increases its surface area and accelerates decomposition processes in desert systems (Sherman et al., 2012), supporting a diverse microbial community. Ladygina and Hedlund (2010), Whitford (2002), Vishnevetsky and Steinberger (1997), and Sherman and Steinberger (2012) demonstrated

* Corresponding author.
E-mail address: Yosef.steinberger@biu.ac.il (Y. Steinberger).

https://doi.org/10.1016/j.jaridenv.2019.01.009
Received 4 July 2018; Received in revised form 10 December 2018; Accepted 9 January 2019
Available online 22 January 2019
0140-1963/

the relationship between the composition and diversity of the microbial community and plant-cover composition and diversity. Moreover, Zak et al. (2003), working in the Chihuhuan Desert, emphasized the presence of a strong relationship between soil microbial biomass and plant diversity, while the Wardle et al. (1999) and Kielak et al. (2008) debate on the relationship between plant communities and soil microbial functional diversity remains unsettled.

Assessment of soil microbiota functionality based on its ability to undertake a range of metabolic activities has become widely used (Chapman et al., 2007). Due to its versatility and simplicity, metabolic diversity has been used to study the soil biota of a range of different environments, including rehabilitated mines, tropical forests, arable deserts, and sandy soils (Ginzburg and Steinberger, 2006; Banning et al., 2012; Yu and Steinberger, 2012a).

The Namib Desert is known for its extreme arid habitats (Ward et al., 1983), with unpredictable rainfall. Fog, dew, and atmospheric moisture are among the most reliable water sources (Henschel and Seely, 2008). In addition to high evapotranspiration and high radiation, the Namibian Desert is one of the largest sandy deserts in the world (Laity, 2008). In such an environment, vegetation patchiness might control soil heterogeneity (Gombeer et al., 2015), with microsites under individual perennial plants becoming enriched with soil nutrients and organic matter from above-as well as below-ground sources (e.g., roots). In such microsites, moisture availability prolongs soil biotic activity (Garner and Steinberger, 1989). According to Ohya et al. (2017), dioecious plants are more precocious in reproduction than monoecious plants in such extreme habitats.

Little is known about the sandy soil microbial community in the Namib, and the potential role of plant cover as facilitator of abiotic- and biotic-component conditions and the interactions between the two. The objective of the present study was to compare the effect of *Acanthosicyos horridus* (Nara melon) plant cover in two different environments at different points on a 150 km climate gradient across the Namib, on a soil microbial community physiological profile (CLPP) and on functional diversity. We hypothesized that soil moisture, organic matter, pH availability, on a spatial scale, and plant sexual gender (Zilber-Rosenberg and Rosenberg, 2008; Lau and Lennon, 2012) would change the microbial community physiological profile. We were curious in a general way about the influence of such a fundamental characteristic as plant gender. In this arid environment, where plants grow isolated from one another in the landscape, there is the possibility that traits such as gender can show themselves. There has, so far, been only one published study that found an influence of plant gender on plant-associated microbiome, and this was on the above-ground parts of dioecious strawberry plants (*Fragaria*) grown in pots in a mesic environment (Wei and Ashman, 2018). To our knowledge, gender effects on microbiome have never been found in a plant growing in the wild, in an arid environment, or in the soil bulk surrounding the roots.

2. Materials and methods

2.1. Study site

The hyperarid Namib Desert is one of the world's oldest deserts that, according to Prestel et al. (2008) and Jacobson et al. (2015), is a classical detritus-driven ecosystem. The daily temperature on the sand surface ranges between 15 and 55 °C, sometimes reaching 70 °C (Seely and Louw, 1980). The mean multi-annual rainfall in the area is 14.1 mm, with a minimum that can reach 4.9 and a maximum of 23.5 mm rainfall. In addition, there is an input of annual fog equal to 69.2 mm, and it is thought that a similar amount is contributed by dew formation (Norgaard and Dacke, 2010). The total annual precipitation days are a mean of 59, ranging between 45 and 138 days (GRTC First Order Meteorological Station).

The plant cover of the Namib Desert is composed of several ephemeral plant species, such as *Sporobolus robustus* and *Eragrostis spinose*, riverine perennial grasses found along river banks, and the dominant trees are *Acacia erioloba* (giraffe thorn), *Acacia albida* (ana tree), and *Salvadora persica* (mustard tree). The dune slopes are covered with sparsely vegetated grasses, such as *Stipagrosti sabulicola* and *Stipagrosti gonostachys*, which can also be found between the *Arthararua leubnitziae* (pencil plant), *Zygophyllum stapfii*, and *Acnathosicyos horridus* (Nara melon) dunes (Louw and Seely, 1982).

One of the most abundant plants in the area is the perennial cucurbit *Acanthosicyos horridus*, which is scattered across the landscape, totally leafless, attains a height of about 1.5 m, and has deep roots able to reach underground water. Male and female plants occur in different clumps, with the female plants having spiny fruits occurring in February and April. These fruits are eaten by animals and collected by the local human population as an important food source (Berry, 2003).

2.2. Soil sampling and processing

All soil samples were collected in the early morning hours in order to avoid the heating and drying of early-morning dew formation. The samples were collected at each one of the three sites: **a**) from the upper 0–10 cm layer (n = 4), beneath the *A. horridus* male plant; **b**) beneath the *A. horridus* female plant (n = 4); and **c**) interspaces between plants, at a minimum distance of 40 m – as control (n = 4). Each soil sample consisted of a pool of four randomly selected soil samples beneath the same shrub (e.g., north, east, south and west directions) representing one replicate. At the open space, the control samples each replicated also comprised a pool of four samplings. The samples were collected beneath the shrub canopy by using a 7 cm diameter soil core at two stations in April 2015. The first station, Kuiseb Delta, was located on the green belt on the sand dunes 3 km from the shore of the Atlantic Ocean. The mean amount of rainfall at this station was up to 99 mm per year, with a variability of 80%, latitude 23°06.968′, longitude 14°28.640', and 26 m above sea level (asl). The second station, [Far East (FE) sand dunes] was located 150 km in a southeast direction from the ocean, with an average rainfall ranging between 200 and 300 mm, with variability of 60%, latitude 23°40.315′, longitude 15°39.251′, and 872 m asl. Each soil sample was placed in an individual plastic bag and kept in an air-tight cooler in order to prevent heating during transport to the laboratory.

2.3. Physicochemical and biological analysis of soil samples

Soil moisture (SM) content was determined gravimetrically by drying soil samples for 72 h at 105 °C (Black, 1965).

Organic matter (OM) content was determined by igniting samples at 360 °C for 8 h.

Soil pH was determined with a pH electrode in the filtered supernatant, a mixture containing 20 g soil and 40 ml distilled water (DW), followed by shaking for 10 min (160 rpm) and incubation overnight at room temperature.

Conductivity was determined by measuring electrical conductivity in a soil-water suspension (soil:double distilled water = 2:5) using an autoranging EC/temp meter (TH2400, EI-Hamma).

Water-holding capacity (WHC): In order to determine soil water-holding capacity (WHC), 100 g soil samples were flooded with tap water in a bottom-perforated vessel for 5 min. The WHC was inferred from the amount of residual water remaining following infiltration of gravitation water.

Soil bulk density (BD) was determined by the ratio of the weight of dry **soil** (M_{solids}) divided by the total **soil** volume (V_{soil}).

Carbon and nitrogen were determined by using the modified Kjeldahl method, ISO 11261:1995 (E) N mg/kg.

Microbial biomass (a metabolically active microbial community) ***and CO_2 evolution*** were detected using the MicroResp™ plate method (Campbell et al., 2003; Oren and Steinberger, 2008). 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: before the plates were placed on the deep wells containing the soil samples (time 0), and after 1 h (time 1). During that time, the plates were incubated in the dark at 27 °C (Sherman and Steinberger, 2012). The result for each well was calculated and compared to the 16th well, which contained the same soil sample and water, measuring the basal respiration with no carbon source at all. Glucose was added to determine microbial biomass according to the substrate-induced respiration method (Anderson and Domsch, 1978).

Metabolic quotient (qCO_2) was determined by calculating the ratio between basal respiration and microbial biomass. It is used to determine the ecophysiological status of soil microorganisms (Anderson and Domsch, 1993).

Shannon–Wiener index (H') - Analysis of community functional diversity of soil microbial communities. Shannon diversity indices were based on equation H = Σ piln(pi), where pi is the relative use of substrate i in a sampling plot for microbial diversity assessment of C substrates used (Derry et al., 1999).

Community-level physiological profile (CLPP) was detected using the MicroResp™ plate (Campbell et al., 2003). Fifteen different carbon sources of carbohydrates, carboxylic acids, amino acids, and aromatic carboxylic acids (Table 1) were added to whole soil samples in deep well plates (0.07 g in each well). 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 ground (0.2 mm size) soil samples (time 0), and after 1 h of microbial respiration (which colonized the soil) (time 1). During that time, the plates were incubated in the dark at 27 °C.

2.4. Data analysis

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

In addition, redundancy analysis (RDA) was used to correlate environmental factors, such as sampling location and sites, with soil abiotic parameters and biotic variables, by using the CANOCO, version 5 (ter Braak and Smilauer, 2002). The Monte Carlo permutation (499) test was used to calculate the significance of any given relationship established between the environmental factors and the measured soil parameters (ter Braak, 1995). RDA analysis produced graphic illustrations, with arrows relating the environmental factors to their corresponding measured parameters. Arrows pointing in similar directions indicate a positive correlation, while arrows pointing in opposite directions indicate a negative one. The longer the arrow, the greater the significance of the relationship.

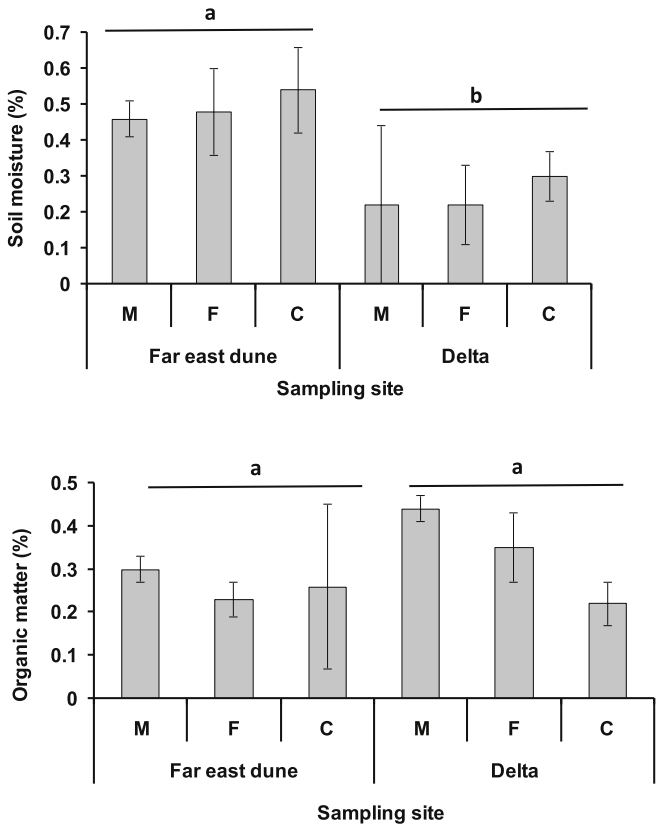

Fig. 1. Changes in mean values of soil moisture (%) and organic matter (± SD) in soil samples collected at two different sand-dune sites (Far East and Delta) in the vicinity of male (M) and female (F) *Acanthosis horridus* plants, and in the open space acting as control (C). Bars with different superscripts indicate significant differences ($p < 0.05$).

3. Results

3.1. Soil physicochemical analysis

Soil moisture levels measured in samples collected at the two different sites and the three locations are presented in Fig. 1. The soil moisture levels recorded in the male, female, and control samples at each of the sampling sites ranged between 0.46 and 0.54% and between 0.22 and 0.30% for the FE dune and Delta sites, respectively. A significant ($P < 0.05$) difference in soil moisture levels between the two sites was detected, with the moisture level in the FE site being significantly higher than in the Delta site. Soil moisture was found to be significantly ($p = 0.0013$) affected by sampling site only (Table 1; Fig. 1).

Soil organic content was found to be significantly affected ($P < 0.05$) by plant gender. In the vicinity of the male plant, the values were significantly higher in comparison with the soil samples collected in the vicinity of the female plant (Fig. 1). Moreover, the total organic

Table 1
Fifteen different carbon sources of carbohydrates, carboxylic acids, amino acids, and aromatic carboxylic acids used for Community-level physiological profile (CLPP) determination.

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 HCl g-Amino butyric acid	D-Galactose	Oxalic acid
	L-Lysine	D-Glucose	
	N-Acetyl-glucosamine	Trehalose	

Table 2
Univariate analysis of variance (ANOVA) for properties and microbial activity at sites, habitat, and the interactions between them of soil samples collected in the vicinity of *Acanthosis horridus* plants.

	Site		Habitat		Site × Habitat	
	F-test	*p-value*	*F-test*	*p-value*	*F-test*	*p-value*
SM	17.27	0.0013	0.65	NS	0.01	NS
WHC	2.91	NS	16.55	0.0004	6.73	0.011
Bulk density	1.74	NS	35.76	< 0.0001	16.66	0.0003
OM	3.1	NS	3.12	NS	1.99	NS
N	0.95	NS	26.26	< 0.0001	0.21	NS
C/N	5.26	0.0407	16.34	0.0004	3.73	NS
CO2 evol.	0	NS	4.41	0.0367	0.48	NS
MB	0.02	NS	5.17	0.024	0.48	NS
qCO2	0.2	NS	1.24	NS	5.57	0.0195
H'	1.91	NS	0.48	NS	0.34	NS
Aromatic acids	10.53	0.007	0.78	NS	0.52	NS
Amino acids	7.49	0.0181	0.34	NS	0.23	NS
Carbohydrates	1.47	NS	2.07	NS	1.03	NS
Carboxylic acids	20	0.0008	0.2	NS	0.3	NS
CLPP	17.07	0.0014	0.3	NS	0.1	NS

SM - soil moisture; WHC— water - holding capacity; OM - organic matte.
N - nitrogen; C/N - carbon/nitrogen ration; MB - microbial biomass.
H - functional diversity.

matter in the control samples was significantly ($P < 0.05$) lower in comparison with the other samples only at the Delta sampling site. Overall, no significant difference between the sampling sites, location, and the interaction between them was found (Table 2).

Each site and location overlies calcareous bedrock, conferring pH values in the alkaline range (7.6–9.5), with a mean value of 8.4, with no significant difference between the site and locations (Table 2). However, the interplay between site and habitat was found to significantly ($p < 0.0003$) affect the pH values.

Conductivity was found to be significantly ($p < 0.0001$) higher in the soil samples collected in the vicinity of plants, reaching a maximum value of 2845 mS/m, while in the control samples at the same location, the values were found to be three-fold lower, ranging between 423 and 708 mS/m (Table 3). At the FE site, the conductivity values in the vicinity of *A. horridus* were found to be 300-fold lower in comparison to Delta site, ranging between 3.4 and 8.7 mS/m, while at the control sampling site, the values ranged between 1.0 and 1.2 mS/m, which was about 600-fold lower than the control sample at the Delta site (Table 3). Based on the above data, we can clearly see that conductivity was significantly affected by sampling site, which significantly ($p < 0.001$) decreased the values toward the inland FE location (Table 3).

Water-holding capacity (WHC) and bulk density variables were found to be significantly affected by habitat and the interaction between site and habitat [($F = 16.55$; $p < 0.0004$) and ($F = 6.73$; $p < 0.011$), respectively] (Table 2). The values for WHC ranged between 0.23 and 0.27%, while the bulk density (BD) values ranged between 1.37 and 154 g cm^3 (g· ml^{-1}) (Table 2). Moreover, WHC was found to be correlated with BD, N, C/N ratio, and microbial-community values (Table 4). The BD was found to show an opposite trend – the above variables decreased significantly with the increase in BD (Table 2).

Organic C was found to be very low (below 1.0%), reaching a maximal mean value of 0.091%, with minimal values below 0.001% at the control sampling sites. The total nitrogen values obtained were significantly ($p < 0.05$) higher (193 ± 26.15 ppm) in the samples collected in the vicinity of male-gender plants at the Delta site, decreasing to values of 146 ⁺3.05 ppm in the vicinity of female plants, and 78.3 ± 4.04 ppm in the control open-space samples (Table 3). A similar trend was obtained at the FE sampling site, with values of 191 ± 64.2, 123 ± 9.53, and 64.33 ± 8.38 ppm in the vicinity of male-gender plants, female-gender plants, and control samples, respectively (Table 3).

Based on the above values, the C/N calculated ratio was found to be very low, ranging between 0.0004 and 0.000008, with a significant ($p < 0.05$) difference between the two sites (Table 3).

Soil microbial processes – CO_2 evolution (Fig. 2) in the soil samples collected in the vicinity of the male-gender plants at both sites exhibited generally higher values in comparison with the female and control samples. The values obtained were found to be generally low, ranging between 0.01 and 0.05 μg CO_2—C g dry $soil^{-1}$ h^{-1}; however, they were significantly ($p < 0.0367$) affected by habitat (Table 1).

Microbial biomass exhibited a similar pattern to CO_2 evolution (Fig. 2), with relatively high values in samples collected in the vicinity of male-gender plants, 2.51 and 2.94 μg C·g dry soil $^{-1}$ for the FE and Delta sites, respectively. In samples collected in the vicinity of female-gender plants and control samples at the two sites, no significant difference was obtained between the two (values ranging between 1.62 and 1.92 μg C·g dry soil $^{-1}$, respectively). Microbial biomass was found to be significantly different by habitat only ($F = 5.17$; $p < 0.024$) and not by site or by the interaction between the habitat and site (Table 2).

The metabolic quotient (qCO_2), which is used to measure the ecophysiological status of soil microorganisms, indicated no significant differences between the sampling sites (Fig. 3). However, at the FE site, higher qCO_2 ratios were found in both samples taken from the male-gender plants and the control samples (16.5 and 16.20 μg CO_2—C g^{-1} biomass-C h^{-1}, respectively). At the Delta site, the highest qCO_2 was observed in the samples collected in the vicinity of the female-gender plants (17.70 μg CO_2—C g^{-1} biomass-C h^{-1}). The qCO_2 was found to be significantly ($F = 5.57$, $p = 0.0195$) affected by site and habitat interaction (Table 2).

Substrate utilization – The relative utilization of the tested substrates at the two sites and the three locations by the soil microbial community in soil samples are presented in Fig. 4. Therefore, by supplying different substrate sources, we facilitate the utilization of the four main groups, i.e., carboxylic acids, aromatic acids, carbohydrates, and amino acids (Fig. 4; Table 4). The CLPP of the microbial community, which was found to be significantly ($p < 0.0014$) affected by sampling site, was at the FE sand-dune site, where the utilization values reached a maximum value of 14 μg C·g^{-1} dry soil h^{-1}. The values obtained at the Delta site were two-fold higher, i.e., over 30 μg C*g^{-1}

Table 3
Mean (+SD) values of the different soil properties obtained in samples collected in the vicinity of the *Acanthosis horridus* male (M) and female (F) plants and from the control (C) open space, at the Far East and Delta sites.

		Bulk density (g.cm-3 (g.ml-1))	Water holding capacity (%)	Organic matter (%)	N (ppm)	C/N (*10-3)		Conductivity	
Far east	M	1.37 ± 0.04	0.27 ± 0.02	0.3 ± 0.03	191 ± 64.2^{a}	4 ± 0.02^{a}	b	6.08 ± 2.38^{a}	b
	F	1.41 ± 0.03	0.27 ± 0.01	0.23 ± 0.04	123 ± 9.53^{ab}	1 ± 2^{ab}		4.39 ± 0.84^{a}	
	C	1.42 ± 0.03	0.26 ± 0.01	0.26 ± 0.19	64.33 ± 8.38^{b}	0.1 ± 0.00173^{b}		1.04 ± 0.10^{b}	
Delta	M	1.32 ± 0.03^{c}	0.29 ± 0.02^{a}	0.44 ± 0.03^{a}	193 ± 26.15^{a}	4 ± 1^{a}	a	2298 ± 182.4^{a}	a
	F	1.38 ± 0.02^{b}	0.26 ± 0.01^{b}	0.35 ± 0.08^{a}	146.6 ± 3.05^{b}	5 ± 1^{a}		2049.3 ± 565.8^{a}	
	C	1.54 ± 0.03^{a}	0.23 ± 0.01^{c}	0.22 ± 0.05^{b}	78.3 ± 4.04^{c}	0.001 ± 0^{b}		602 ± 117.8^{b}	

Bulk density (g.cm-3 (g.ml-1)); Water holding capacity (%) – WHC; Conductivity (mS/m); M – male; F – female; C - control.

Table 4
Mean (+SD) values of the microbial community substrate utilization obtained in the vicinity of *Acanthosis horridus* male (M) and female (F) plants and the control (C) open space, at the Far East and Delta sites.

		Arom acid	Carboxylic acid			Carbohydrates					Amino groups				
		OH	Citric	Malic	Oxalic	Fruct	Galact	Gluc	Arab	Trehal	GABA	Alanine	Cysteine	Lysine	NAGA
Far east	M	1.0180	3.5686	3.5459	1.8962	0.0035	0.0032	0.0101	0.0016	0.0384	0.0138	0.0253	3.7508	0.0147	0.0560
	F	0.5389	3.7095	4.0464	1.5350	0.0163	0.0181	0.0101	0.0048	0.0078	0.0115	0.0145	2.3937	0.0150	0.0600
	C	0.8428	3.7401	3.5489	2.0943	0.0062	0.0012	0.0075	0.0075	0.0010	0.0087	0.0175	2.6274	0.0186	0.0484
Delta	M	2.5814	6.7496	8.4080	7.0221	0.0664	0.0304	0.0256	0.0234	0.0846	0.0210	0.0415	5.2018	0.0202	0.1145
	F	2.1723	5.9347	7.2944	5.4940	0.0120	0.0168	0.0322	0.0046	0.0061	0.0225	0.0240	4.8813	0.0241	0.0890
	C	1.5737	4.6633	7.4500	6.4541	0.0131	0.0091	0.0005	0.0075	0.0085	0.0137	0.0454	5.2826	0.0685	0.2181

M – male; F – female; C – control; Arom – Aromatic acid; OH - 3,4-OHbenzoic acid; Citric – Citric acid; Malic – Malic acid; Oxalic – Oxalic acid; Fruct - D-Fructose; Galac - D-Galactose; Gluc - D-Glucose; Arab - L-Arabinose; Trehal – Trehalose; Alanine - L-Alanine; Cysteine - L-Cysteine HCl; Lysine - L-Lysine.

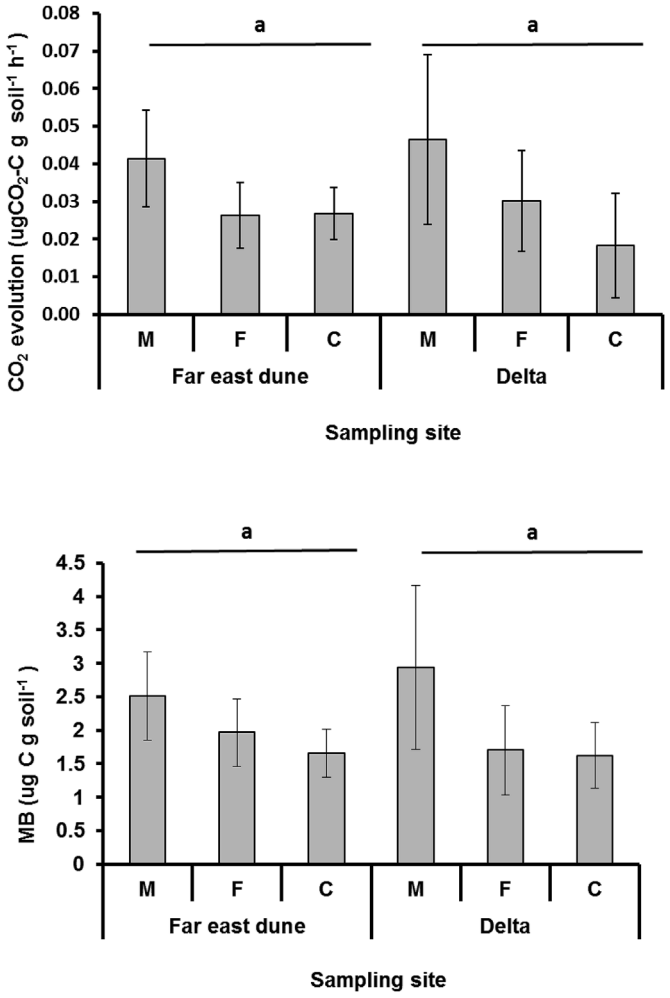

Fig. 2. Changes in mean values (± SD) of CO_2 evolution and microbial biomass (MB) in soil samples collected at two different sand-dune sites (Far East and Delta) in the vicinity of male (M) and female (F) *Acanthosis horridus* plants, and in the open space acting as control (C). Letters signify Duncan's multiple range test groupings (n = 4). Mean values that are not followed by the same letter differ significantly from one another ($p < 0.05$).

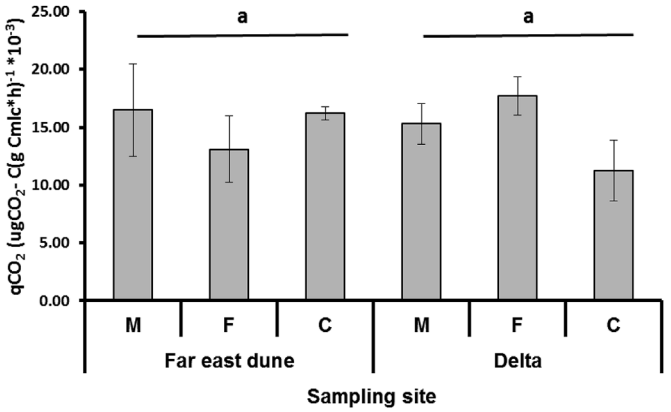

Fig. 3. Changes in mean values (± SD) of qCO_2 in soil samples collected at two different sand-dune sites (Far East and Delta) in the vicinity of male (M) and female (F) *Acanthosis horridus* plants, and in the open space acting as control (C). Letters signify Duncan's multiple range test groupings (n = 4). Mean values that are not followed by the same letter differ significantly from one another ($p < 0.05$).

dry soil h^{-1}.

The main significant ($p < 0.05$) difference in substrate utilization was in the carboxylic acid, which increased 3–5 fold from the FE to the Delta sampling sites. For the other three substrates, i.e., aromatic acids, amino acids, and carbohydrates, there was a minimum two-fold increase that was also significant ($p < 0.05$) (Fig. 4; Table 5). The amino acids, as well as carboxylic acid substrate utilization, were significantly correlated ($p < 0.05$) with SM, while the aromatic acid was found to be significantly ($p < 0.05$) correlated with SM, OM, and C/N ratio. Carbohydrate substrate utilization was found to be significantly ($p < 0.05$) related with WHC, N, microbial respiration, and microbial biomass (Table 5). The influence of the environmental parameters on the substrate utilization of different carbons are presented in Table 5. The sampling site was found to significantly affect the substrate utilization of three out of four carbon substrates (Table 2).

The interplay of site and habitat was found to affect the utilization of all substrates except D-fructose, D-galactose, L-arabinose, and trehalose – all belonging to the carbohydrate group. In addition, L-lysine and NAGA from the amino groups were found to be similarly utilized at both sampling sites.

Substrate utilization rates of 3,4-OH-benzoic acid, D-fructose, D-galactose, trehalose, GABA, L-alanine, and L-cysteine in soil samples collected beneath the native male-gender plants of *A. horridus* were higher in comparison with those samples collected in the vicinity of the female-gender plants (Table 4).

Microbial functional diversity (H) was not affected by either site, habitat, or the interaction between the two (Table 1). However, it was significantly ($p < 0.01$) correlated with the substrate utilization of amino, aromatic, and carboxylic acids, and CLPP, as presented in Table 5.

3.2. Relative contributions of environmental factors to taxonomical composition

The use of RDA, which emphasizes the relationship between

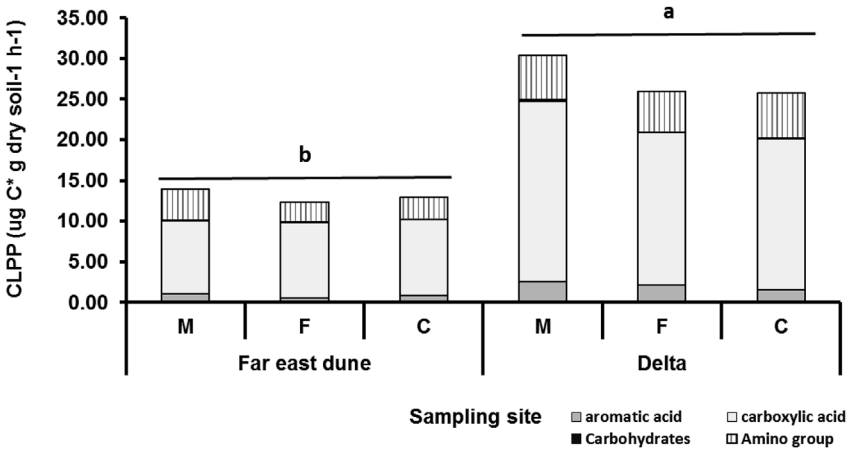

Fig. 4. CLPP (%) utilization in soil samples collected at two different sand-dune sites (Far East and Delta) in the vicinity of male (M) and female (F) *Acanthosis horridus* plants, and in the open space acting as control (C). Letters signify Duncan's multiple range test groupings (n = 4). Mean values that are not followed by the same letter differ significantly from one another ($p < 0.05$).

environmental factors, soil abiotic parameters, and biotic components, showed clear discrimination relative to the different sites and sampling location (male gender, female gender, and control) (Fig. 5). The two extreme environmental conditions, as represented by the Delta and FE sites, were found to greatly elucidate the effect on each of the variables. Moreover, the CLPP, together with the substrate utilization of carboxylic, amino, aromatic, and carbohydrate acids, was greatly affected by the Delta sampling site and male gender. The female-gender plants had little effect compared with the male-gender plants. Fig. 5 elucidates the dissimilarity between the study sites and plant-gender effect.

RDA showed that the total variation is 24.50, with the explanatory variables accounting for 46% of the total variation in the data. RDA showed that the first two axes explained 43.29% by Axis 1 and 2.37% by Axis 2 of the variation in the community composition, yielding a cumulative variation of 89.66% (Fig. 5).

4. Discussion

The aim of this study was to investigate the influence of the *A. horridus* plant and its gender in determining soil microbial community density, CO_2 evolution, and biomass in the plant vicinity. A unique aspect of the present study is that it focused on how these effects varied between two very different sites, one near the Delta and the second in the far-eastern part of Namibia Desert. Comparison was made between the two sites and three sampling locations, with samples collected in the vicinity of the male and female *A. horridus* plants and in the open spaces of the control site at a distance from the plants, in an attempt to characterize the effects of plant presence, plant gender, gender and climate.

Loreau (2010) and Allan et al. (2013) showed that change in biological diversity is affected by ecosystem characteristics and function. Such a process is mainly affected by plant diversity in the ecosystem. In this context, plant diversity plays a key role in soil characteristics and functions, determining nitrogen content, carbon sequestration, and soil biotic-community density and diversity (Hooper and Vitousek, 1998; Lange et al., 2014; El Moujahid et al., 2017). Perennial plant diversity was very low in the study area. The most common perennial plant was *A. horridus* itself, this being the only plant cover that determines below-ground sources, such as organic matter and soil moisture, as well as microbial-community components and activity. Soil organic matter is determined by root litter rhizo-distribution and litter input. Our study showed not only a significant effect of the presence of the plant in general (compared to bare areas, but also a significant effect on soil organic matter content in the vicinity of the plant as affected by plant gender, i.e., soil organic matter content was higher in samples collected beneath the male-gender plant compared with the female-gender plant. Such an effect is of interest in that plant gender affects the energy sources and supply to the soil ecosystem in this instance.

The overall soil physicochemical parameters obtained in the present study (e.g., established for climatic, geographic orientation, soil moisture, conductivity, water-holding capacity, and total nitrogen), were found to be similar to results presented by Oren and Steinberger (2008) and Lange et al. (2014). The soil microbial community in a desert ecosystem is influenced by a range of environmental variables, e.g., soil texture, extreme dryness, the mosaic patterns of organic matter, moisture availability, and perennial vegetation cover (Ronca et al., 2015). Ravit et al. (2006), in their study, showed that lower organic carbon in soil can be attributed to faster decomposition of organic matter, which, in turn, reduces microbial biomass in long term in arable soils, and this turnover is even faster in xeric environments.

One of the cumulative triggers of soil microbial-population activity is the interplay between moisture availability and salinity, which have an opposite parallel route and are unpredictable in time and space due to rainfall distribution and proximity to the ocean – saline water source. Our results were found to be similar to those of Sarig and Steinberger (1993, 1994), who found higher microbial biomass under saline conditions both in natural systems and in irrigation-treated systems in the Negev Desert, thus elucidating the contribution of *A. horridus* in elevating salinity contents in both the Delta and FE sites proportionally.

A similar trend was found for soil respiration and microbial biomass at both sites: they decreased with the decrease in salinity found to be correlated with the values of soil salinity in samples collected in the vicinity of male gender > female gender > control (Sardinha et al., 2003; Tripathi et al., 2006). This trend indicates that a less stressful environment (Anderson and Domsch, 1990) reduces the difference between sampling site and location. The results obtained in the current study support the findings of Sarig and Steinberger (1993, 1994), and contribute to a broader understanding of the interplay between site and habitat soil water availability and salinity occurring on a large scale.

In the present study, an evaluation was carried out of gender effect as a cumulative trigger for microbial population activity in 'fertile islands' in the vicinity of *A. horridus* shrubs and in exposed interspace areas. The sampling enabled us to display the difference in gender ecophysiological behavior of *A. horridus*, as well as the effect of salinity between the two extreme sites, on microbial CO_2 evolution and microbial biomass. The dissimilarity resulted in CO_2 evolution and in microbial biomass in both below-canopy and open-control habitats, thus elucidating the importance of the efficiency of substrate utilization parameters as a facilitator in decreasing the pressure of abiotic factors.

In the MicroResp system, we used different carbon sources to produce a metabolic profile of the microbial community. A statistically significant difference in microbial community substrate utilization preference, ranging between 65 and 75% substrate utilization at both sites, was toward carboxylic acid, similar to the findings of Qin et al. (2017) working on forest and agroecosystems. The order by which substrates were utilized by soil organisms was different compared with

Table 5
Pearson's correlation coefficients between the variables of the data obtained from the whole study. Asterisks indicate significant correlation at probability levels of 0.05(*), 0.01(**) and 0.0001 (***); NS, not significant (SM – soil moisture, WHC – water-holding capacity; BD – bulk density; OM – organic matter; N – soil nitrogen content; C/N – carbon nitrogen ratio; Resp – microbial CO_2 evolution; MB – microbial biomass; H' – functional diversity).

	SM	WHC	BD	OM	N	C/N	Resp	MB	qCO2	*H'*	Amino acids	Aromatic acids	Carbohydrates	Carboxylic acids	CLPP
SM	-	NS	NS	NS	NS	NS	NS	NS	NS	NS	− 0.482*	− 0.577*	NS	− 0.593**	− 0.589*
WHC		-	- 0.894***	NS	0.665**	0.502*	0.699**	0.636**	0.488*	NS	NS	NS	0.508 *	NS	NS
BD			-	− 0.606**	− 0.710**	− 0.607**	− 0.632**	− 0.521*	− 0.563*	NS	NS	NS	NS	NS	NS
OM				-	0.548*	0.53801*	NS	NS	NS	NS	NS	0.556 *	NS	NS	NS
N					-	0.704**	0.670**	NS	NS	NS	NS	NS	0.604 **	NS	NS
C/N						-	NS	NS	NS	NS	NS	0.481 *	NS	NS	NS
Resp							-	0.916***	0.588*	NS	NS	NS	0.738 **	NS	NS
MB								-	NS	NS	NS	NS	0.734 **	NS	NS
qCO2									-	NS	NS	NS	NS	NS	NS
H'										-	0.748 **	0.772 **	NS	0.67 **	0.722 **
Amino acids											-	0.814 ***	NS	0.851 ***	0.908 ***
Aromatic acids												-	0.489 *	0.868 ***	0.903 ***
Carbohydrates													-	NS	NS
Carboxylic acids														-	0.99 ***

Soil moisture – SM; Water-holding capacity – WHC; Bulk density – BD; Organic matter – OM; N – nitrogen; Carbon nitrogen ratio – C/N; Conductivity – Cond; CO_2 evolution – Resp; Microbial biomass – MB; Functional diversity – H'; Amino acid – Amino; Arom – Aromatic acid; Carbohydrates – Carboh; Carboxylic acid – Carbox.

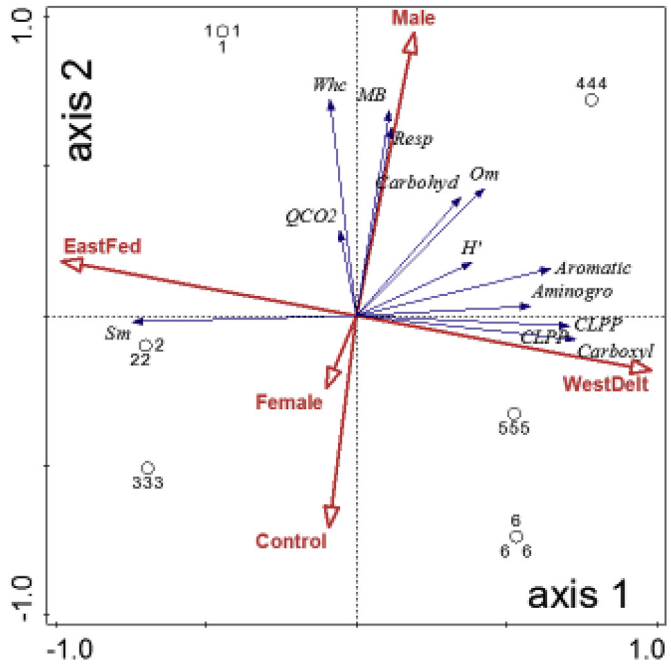

Fig. 5. Redundancy analysis (RDA) linking between the sampling sites, locations, microbial communities and substrate utilization for soil samples collected at two different sand-dune sites (Far East – EastFed and Delta –West Delt) in the vicinity of male and female *Acanthosis horridus* plants, and in the open spaces, acting as control. The lengths of the arrows represent the contribution of each component to the variation of the sample. The angle between two arrows is a measure of the correlation between the two variables (small angle means strong correlation). (Sm – soil moisture; Om – organic matter; Whc – water-holding capacity; Resp – CO_2 evolution; MB – microbial biomass; QCO_2 – metabolic quotient; CLPP – community-level physiological profile; H' – functional diversity; Carboxyl – carboxylic acid; Aminogro – amino acids; Aromatic – aromatic acids; Carbohyd – carbohydrates.

that mentioned in the above two studies, with amino-acid and aromatic-acid groups, together with carboxylic acid, found to cover over 99% of the substrate utilization. In the present study, as well as in other studies conducted on xeric or environmentally stressful systems (Sherman and Steinberger, 2012; Yu and Steinberger, 2012a, b; Saul-Tcherkas et al., 2013; Martirosyan and Steinberger, 2014; Wang et al., 2014), the total amount of carboxylic-acid utilization was found to increase. The only way to justify such an increase in carboxylic acid is that the microbial community, during short-term activity in such an extreme environment, will invest in the establishment of a bacterial fatty acid pool, as proposed by Christian et al. (2007). This fatty acid pool will supply the amino acid group to the microbial community during any unpredictable period of activity, in response to abiotic environmental variables, thus triggering activity. According to Klimek et al. (2016), the use of carboxylic acids is more effective in respiring other added C substrates, in particular amino acids. In many cases, microbial catabolic diversity in the whole-soil samples may be important for determining the rates of ecosystem functions, particularly in non-stable environmental conditions (McGuire and Treseder, 2010), where in our case, no significant differences by either site, habitat, or the interaction between the two were found. Furthermore, the results obtained by RDA analysis emphasized the strong relationship between the carboxylic acid and its increased consumption as a C source at the Delta site, which may be a result of higher exudation by plant roots due to extreme abiotic soil conditions. At such a stage, the microbial community will change from a "reserve" form to a "pulse" stage, as defined by Noy-Meir (1973), and during this stage, the fatty acid pools will supply the amino-acid and carbohydrate groups to the microbial community, which will accelerate them to fulfill their biological functions

during the short periods of 'window of activity". We assume that the low carbohydrate utilization was due to very low levels of organic matter in the sand dunes detected, having an impact on below-ground microflora density and diversity (Neilson et al., 2012).

Tognetti (2012), in his paper entitled "Adaptation to climate change of dioecious plants: Does gender balance matter", continues the debate on Charles Darwin's theory of gender dimorphism. In his theoretical model dealing with the relationship between the male and female ratio, Tognetti found that a decrease in precipitation, increase in temperature, intensifying habitat fragmentation, and decreasing resource acquisition, each results in an increase in the M/F ratio. All studies so far have mainly focused on above-ground processes, without taking into consideration the effect of dioecious plants on below-ground biota. In our present study, the effect of gender dioecy in the *A. horridus* plant was found to be correlated with soil biota activity, moving from a relatively humid to a more xeric environment. Moreover, this study highlighted various avenues for future studies, such as: (a) the soil microbial diversity -plant gender relationship; and (b) the role of plant dimorphism in determining soil biota composition and diversity in a desert ecosystem. It seems likely that the low species diversity of this system allowed the peculiarities of the biology of the dominant plant species to dominate the soil system and acts as a source of spatial heterogeneity. It would be interesting to explore whether such effects often occur in arid systems, whether related to gender, litter chemistry, or other traits.

Declaration of interests

None.

Acknowledgements

We thank Ms. Sharon Victor for her useful comments.

Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.jaridenv.2019.01.009.

References

Adl, S.M., 2003. The Ecology of Soil Decomposition. CABI Publishing, Wallingford.
Allan, E., Weisser, W.W., Fischer, M., Schulze, E.D., Weigelt, A., Roscher, C., Baade, J., Barnard, R.L., Bessler, H., Buchmann, N., Ebeling, A., Eisenhauer, N., Engels, C., Fergus, A.J.F., Gleixner, G., Gubsch, M., Halle, S., Klein, A.M., Kertscher, I., Kuu, A., Lange, M., Le Roux, X., Meyer, S.T., Migunova, V.D., Milcu, A., Niklaus, P.A., Oelmann, Y., Pasalic, E., Petermann, J.S., Poly, F., Rottstock, T., Sabais, A.C.W., Scherber, C., Scherer-Lorenzen, M., Scheu, S., Steinbeiss, S., Schwichtenberg, G., Temperton, V., Tscharntke, T., Voigt, W., Wilcke, W., Wirth, C., Schmid, B., 2013. A comparison of the strength of biodiversity effects across multiple functions. Oecologia 173, 223–237.
Anderson, J.P.E., Domsch, K.H., 1978. Physiological method for quantitative measurement of microbial biomass in soils. Soil Biol. Biochem. 10, 215–221.
Anderson, T.H., Domsch, K.H., 1990. Application of ecophysiological quotients (qCO_2 and qD) on microbial biomasses from soils of different cropping histories. Soil Biol. Biochem. 22, 251–255.
Anderson, T.H., Domsch, K.H., 1993. The metabolic quotient for CO_2 (qCO_2) as a specific activity parameter to assess the effects of environmental conditions, such as pH, on the microbial biomass of forest soils. Soil Biol. Biochem. 25, 393–395.
Banning, N.C., Lalor, B.M., Cookson, W.R., Grigg, A.H., Murphy, D.V., 2012. Analysis of soil microbial community level physiological profiles in native and post-mining rehabilitation forest: which substrates discriminate? Appl. Soil Ecol. 56, 27–34.
Berry, C., 2003. Aspects of phenology and condition of inland and coastal !Nara plants in the Namib-Naukluft Park, Namibia. Dinteria 28, 1–18.
Bhatnagar, A., Bhatnagar, M., 2005. Microbial activity in desert ecosystems. Curr. Sci. 89, 91–100.
Black, C.A., 1965. Methods of Soil Analysis: Part 1. Physical and Mineralogical Properties, Including Statistics of Measurement and Sampling. American Society of Agronomy, Madison, WI.
Buyer, J.S., Schmidt-Kuntzel, A., Nghikembua, M., Maul, J.E., L, M, 2016. Soil microbial communities following bush removal in a Namibian savanna. Soil 2, 101–110.
Campbell, C.D., Chapman, S.J., Cameron, C.M., Davidson, M.S., Potts, J.M., 2003. A rapid microtiter plate method to measure carbon dioxide evolved from carbon substrate amendments so as to determine the physiological profiles of soil microbial communities by using whole soil. Appl. Environ. Microbiol. 69, 3593–3599.
Chapman, S.J., Campbell, C.D., Artz, R.R.E., 2007. Assessing CLPPs using MicroReSp (TM) - a comparison with biolog and multi-SIR. J. Soils Sediments 7, 406–410.
Christian, B.W., Lind, O.T., 2007. Multiple carbon substrate utilization by bacteria at the sediment-water interface: seasonal patterns in a stratified eutrophic reservoir. Hydrobiologia 586, 43–56.
Coleman, D.C., 1985. Through a ped darkly: an ecological assessment of root-soil-microbial-faunal interactions. In: Fitter, A.H., Atkinson, D., Read, D.J., Usher, M.B. (Eds.), Ecological Interactions in Soil. Blackwell Scientific Publications, Cambridge, U.K., pp. 1–21.
Coleman, D.C., Crossley, D.A., 1996. Fundamentals of Soil Ecology. Academic Press, London.
Derry, A.M., Staddon, W.J., Kevan, P.G., Trevors, J.T., 1999. Functional diversity and community structure of micro-organisms in three arctic soils as determined by sole-carbon-source-utilization. Biodivers. Conserv. 8, 205–221.
El Moujahid, L., Le Roux, X., Michalet, S., Bellvert, F., Weigelt, A., Poly, F., 2017. Effect of plant diversity on the diversity of soil organic compounds. PLoS One 12, e0170494.
Garcia-Pausas, J., Paterson, E., 2011. Microbial community abundance and structure are determinants of soil organic matter mineralisation in the presence of labile carbon. Soil Biol. Biochem. 43, 1705–1713.
Garner, W., Steinberger, Y., 1989. A proposed mechanism for the formation of 'Fertile Island' in the desert ecosystem. J. Arid Environ. 16, 257–262.
Ginzburg, O., Steinberger, Y., 2006. The effect of harvester ant (Messor spp.) nest activity on soil microbial biomass and functional diversity in a desert system. In: The 34th Annual Israel Society for Ecology and Environmental Quality Sciences Conference, 26-27 June 2006, Haifa, Israel.
Gombeer, S., Ramond, J.B., Eckardt, F.D., Seely, M., Cowan, D.A., 2015. The influence of surface soil physicochemistry on the edaphic bacterial communities in contrasting terrain types of the Central Namib Desert. Geobiology 13, 494–505.
Henschel, J.R., Seely, M.K., 2008. Ecophysiology of atmospheric moisture in the Namib Desert. Atmos. Res. 87, 362–368.
Hooper, D.U., Vitousek, P.M., 1998. Effects of plant composition and diversity on nutrient cycling. Ecol. Monogr. 68, 121–149.
Jacobson, K., Evans, S., Jacobson, P., 2015. Below-ground and surface decomposition in the Namib Sand Sea. In: FOGLIFE Second Annual Colloquium, June 15-19, 2015. Gobabeb Research and Training Center, Namibia.
Kielak, A., Pijl, A.S., van Veen, J.A., Kowalchuk, G.A., 2008. Differences in vegetation composition and plant species identity lead to only minor changes in soil-borne microbial communities in a former arable field. FEMS Microbiol. Ecol. 63, 372–382.
Klimek, B., Chodak, M., Jazwa, M., Solak, A., Tarasek, A., Niklinska, M., 2016. The relationship between soil bacteria substrate utilisation patterns and the vegetation structure in temperate forests. Eur. J. For. Res. 135, 179–189.
Ladygina, N., Hedlund, K., 2010. Plant species influence microbial diversity and carbon allocation in the rhizosphere. Soil Biol. Biochem. 42, 162–168.
Laity, J.L., 2008. Deserts and Desert Environments. Wiley-Blackwell Publications, USA.
Lange, M., Habekost, M., Eisenhauer, N., Roscher, C., Bessler, H., Engels, C., Oelmann, Y., Scheu, S., Wilcke, W., Schulze, E.D., Gleixner, G., 2014. Biotic and abiotic properties mediating plant diversity effects on soil microbial communities in an experimental grassland. PLoS One 9, e96182.
Lau, J.A., Lennon, J.T., 2012. Rapid responses of soil microorganisms improve plant fitness in novel environments. Proc. Natl. Acad. Sci. U.S.A. 109, 14058–14062.
Lehman, R.M., Cambardella, C.A., Stott, D.E., Acosta-Martinez, V., Manter, D.K., Buyer, J.S., Maul, J.E., Smith, J.L., Collins, H.P., Halvorson, J.J., Kremer, R.J., Lundgren, J.G., Ducey, T.F., Jin, V.L., Karlen, D.L., 2015. Understanding and enhancing soil biological health: the solution for reversing soil degradation. Sustainability 7, 988–1027.
Loreau, M., 2010. Linking biodiversity and ecosystems: towards a unifying ecological theory. Phil. Trans. Biol. Sci. 365, 49–60.
Louw, G.N., Seely, M.K., 1982. Ecology of Desert Organisms. Longman Group Ltd., London and New York.
Martirosyan, V., Steinberger, Y., 2014. Microbial functional diversity in the phyllosphere and laimosphere of different desert plants. J. Arid Environ. 107, 26–33.
McGuire, K.L., Treseder, K.K., 2010. Microbial communities and their relevance for ecosystem models: decomposition as a case study. Soil Biol. Biochem. 42, 529–535.
Neilson, J.W., Quade, J., Ortiz, M., Nelson, W.M., Legatzki, A., Tian, F., LaComb, M., Betancourt, J.L., Wing, R.A., Soderlund, C.A., Maier, R.M., 2012. Life at the hyperarid margin: novel bacterial diversity in arid soils of the Atacama Desert, Chile. Extremophiles 16, 553–566.
Norgaard, T., Dacke, M., 2010. Fog-basking behaviour and water collection efficiency in Namib Desert Darkling beetles. Front. Zool. 7, 23.
Noy-Meir, I., 1973. Desert ecosystems: environment and producers. Annu. Rev. Ecol. Systemat. 4, 25–51.
Ohya, I., Nanami, S., Itoh, A., 2017. Dioecious plants are more precocious than cosexual plants: a comparative study of relative sizes at the onset of sexual reproduction in woody species. Ecol. Evol. 7, 5660–5668.
Oren, A., Steinberger, Y., 2008. Catabolic profiles of soil fungal communities along a geographic climatic gradient in Israel. Soil Biol. Biochem. 40, 2578–2587.
Prestel, E., Salamitou, S., Dubow, M.S., 2008. An examination of the bacteriophages and bacteria of the Namib Desert. J. Microbiol. 46, 364–372.
Qin, X., Wei, C., Li, J., Chen, Y., Chen, H.S., Zheng, Y., Nong, Y., Liao, C., Chen, X., Luo, Y., Lu, J., Zeng, Z., Wei, J., 2017. Changes in soil microbial community structure and functional diversity in the rhizosphere surrounding tea and soybean. J. Agric. Sci. 12, 1–13.
Ravit, B., Ehenfeld, J.G., Haggblom, M.M., 2006. Effects of vegetation on root-associated microbial communities: a comparison of disturbed versus undisturbed estuarine sediments. Soil Biol. Biochem. 38, 2359–2371.

Ronca, S., Ramond, J.-B., Jones, B.E., Seely, M., Cowan, D.A., 2015. Namib Desert/interdune transects exhibit habitat-specific edaphic bacterial communities. Front. Microbiol. 6, 845.
Sardinha, M.T., Muller, H., Schmeisky, R., Joergensen, G., 2003. Microbial performance in soils along a salinity gradient under acidic conditions. Appl. Soil Ecol. 23, 237–244.
Sarig, S., Steinberger, Y., 1993. Immediate effect of wetting event on microbial biomass and carbohydrate production mediated aggregation in desert soil. Geoderma 56, 599–607.
Sarig, S., Steinberger, Y., 1994. Microbial biomass response to seasonal fluctuation in soil salinity under the canopy of desert halophytes. Soil Biol. Biochem. 26, 1405–1408.
Saul-Tcherkas, V., Unc, A., Steinberger, Y., 2013. Soil microbial diversity in the vicinity of desert shrubs. Microb. Ecol. 65, 689–699.
Seely, M.K., Louw, G.N., 1980. First approximation of the effects of rainfall on the ecology and energetics of a Namib Desert dune ecosystem. J. Arid Environ. 3, 25–54.
Sherman, C., Grishkan, I., Barness, G., Steinberger, Y., 2014. Fungal community - plant litter decomposition relationships along a climate gradient. Pedosphere 24, 437–449.
Sherman, C., Steinberger, Y., 2012. Microbial functional diversity associated with plant litter decomposition along a climatic gradient. Microb. Ecol. 64, 399–415.
Sherman, C., Sternberg, M., Steinberger, Y., 2012. Effects of climate change on soil respiration and carbon processing in Mediterranean and semi-arid regions: an experimental approach. Eur. J. Soil Biol. 52, 48–58.
Singh, K., Trivedi, P., Singh, G., Singh, B., Patra, D.D., 2016. Effect of different leaf litters on carbon, nitrogen and microbial activities of sodic soils. Land Degrad. Dev. 27, 1215–1226.
ter Braak, C.J.F., 1995. Non-linear methods for multivariate statistical calibration and their use in palaeoecology: a comparison of inverse (k-nearest neighbours, partial least squares and weighted averaging partial least squares) and classical approaches. Chemometr. Intell. Lab. Syst. 28, 165–180.
ter Braak, C.J.F., Smilauer, P., 2002. CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (Version 4.5). Biometrics, Wageningen and Ceske Budejovice, Microcomputer Power (Ithaca NY, USA). pp. 500.
Tognetti, R., 2012. Adaptation to climate change of dioecious plants: does gender balance matter? Tree Physiol. 32, 1321–1324.
Tripathi, S., Kumari, S., Chakraborty, A., Gupta, A., Chaprabarti, K., Bandyapadhay, B.K., 2006. Microbial biomass and its activities in salt-affected coastal soils. Biol. Fertil. Soils 42, 273–277.
Vishnevetsky, S., Steinberger, Y., 1997. Bacterial and fungal dynamics and their contribution to microbial biomass in desert soil. J. Arid Environ. 37, 83–90.
Wang, L., Chen, Z., Shang, H., Wang, J., Zhang, P.Y., 2014. Impact of simulated acid rain on soil microbial community function in Masson pine seedlings. Electron. J. Biotechnol. 17, 199–203.
Ward, J.D., Seely, M.K., Lancaster, N., 1983. On the antiquity of the Namib. South Afr. J. Sci. 79, 175–183.
Wardle, D.A., 2006. The influence of biotic interactions on soil biodiversity. Ecol. Lett. 9, 870–886.
Wardle, D.A., Bonner, K.I., Barker, G.M., Yeates, G.W., Nicholson, K.S., Bardgett, R.D., Watson, R.N., Ghani, A., 1999. Plant removals in perennial grassland: vegetation dynamics, decomposers, soil biodiversity, and ecosystem properties. Ecol. Monogr. 69, 535–568.
Wei, N., Ashman, T.L., 2018. The Effects of Host Species and Sexual Dimorphism Differ Among Root, Leaf and Flower Microbiomes of Wild Strawberries in Situ Scientific Reports 8. , 5195.
Whitford, W.G., 2002. Ecology of Desert Systems. Academic Press, New York, London.
Yu, J., Steinberger, Y., 2012a. Soil microbial metabolic profiles in two geomorphological units in a semistable sand-dune ecosystem. Soil Biol. Biochem. 45, 71–78.
Yu, J., Steinberger, Y., 2012b. Vertical distribution of soil microbial biomass and its association with shrubs from the Negev Desert. J. Arid Environ. 78, 110–118.
Zak, D.R., Holmes, W.E., White, D.C., Peacock, A.D., Tilman, D., 2003. Plant diversity, soil microbial communities, and ecosystem function: are there any links? Ecology 84, 2042–2050.
Zilber-Rosenberg, I., Rosenberg, E., 2008. Role of microorganisms in the evolution of animals and plants: the hologenome theory of evolution. FEMS Microbiol. Rev. 32, 723–735.