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Spatial abundance of microbial nitrogen-transforming genes and inorganic nitrogen in biocrusts along a transect of an arid sand dune in the Negev Desert

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Nitrogen (N) is considered to be the second most limiting factor after water for biomass production in arid and semiarid ecosystems. Biological soil crusts (BSCs) play an important role as N providers, especially in sand dunes. In this study, we looked at the levels of inorganic N forms and the abundance of N-cycle-associated genes in five well-defined BSCs along a transect of a sand dune in the Negev Desert. Four of the crusts are cyanobacterial crusts (with crust A occupying the interdune and the south-facing slope, and the remaining crusts, B, C, D occupying the north-facing slope) and one moss-dominated crusts (E), inhabiting the interface between the north-facing footslope and the interdune, where it benefits from additional water supply by subsurface flow and runoff. Although all crusts contained comparable numbers of the *nifH* gene (a marker for N_2 fixation), the accumulation of inorganic N forms followed the order A ≈ B < C ≈ D < E, with crust E characterized by exceptionally high levels of ammonium and nitrite. All crusts were dominated by bacterial ammonia oxidizers, while significant numbers of archaeal ammonia oxidizers were detected only in crust E. Likewise, the highest numbers of *Nitrobacter* spp. (nitrite oxidizers) were detected in crust E. All crusts were dominated by *nirK*-type denitrifiers over *nirS* ones. The accumulation of nitrite in crust E suggested a significant inhibition of nitrite oxidation, possibly due to oxygen limitation following subsurface flow. It is suggested that temporal disparity between aerobic and anaerobic conditions results in partial nitrification and the accumulation of ammonia and nitrite in crust E, being also responsible for the higher emission of nitrous oxide. Our findings show a close link between the abiotic conditions, crust type and N dynamics, thus highlighting the importance of small-scale hydrological processes in the N cycle of arid lands.

1. Introduction

After water, nitrogen (N) is the second most limiting factor for biomass production in arid regions (West, 1991). The sparse vegetation and plant–bacteria associations in desert ecosystems that may contribute to the N stock have drawn attention to a variety of possible N contributors, particularly to the microbial communities, which form the biological soil crusts (BSC) that cover large portions of arid lands (Büdel, 2001).

Among the BSC microbial communities, cyanobacterial species play an important role in N_2 fixation (Evans and Lange, 2001). Their role is especially important in sand, which does not support a large population of N_2-fixing nodulated plants (Garcia-Moya and McKell, 1970), since its texture creates aerated microenvironments that inhibit successful symbiosis (Wolf and Rohrs, 2001). Indeed, sandy areas may be extensively covered by BSC, which in addition to its role in stabilizing the sandy surface (Jia et al., 2012) and affecting the hydrology of the ecosystem through runoff generation (Kidron, 1999), can play an important role in N supply and transformations.

Many aspects of N dynamics have been reported from arid land crusts. Most of the research was carried out in the northwestern United States deserts where aspects, such as N_2 fixation (Johnson et al., 2005; Strauss et al., 2012), N_2-fixing microorganisms (Yeager et al., 2007), ammonia oxidation activity (Johnson et al.,

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2005; Strauss et al., 2012), ammonia-oxidizers community (Marusenko et al., 2013) and denitrification (Peterjohn and Schlesinger, 1991; Johnson et al., 2007), were investigated. Yet, examination of the N dynamics in sand dunes was mainly reported from temperate or subhumid regions. For example, high accumulations of NO_3^-–N and NO_2^-–N in coastal sand dunes in England and in crusted surfaces in the northern USA have been reported (Skiba and Wainwright, 1984; Smith et al., 2004). In an inland sand dune in Germany, the levels of inorganic N forms and the abundance of genes involved in N transformations were found to be dependent on the developmental stage of the BSC (Brankatsch et al., 2013). Intense leaching in these high-precipitation regions was seen as responsible for the low levels of NO_3^-–N in developed crusts despite the high numbers of ammonia-oxidizing archaea (AOA) that were detected. The activity and community structure of the N-transforming microorganisms (such as the relative amount of ammonia-oxidizing bacteria, AOB and the AOA) and thus the N dynamics were inevitably impacted by the low pH levels ($\approx$5) of these subhumid sand dunes.

Contrary to the low pH that characterizes subhumid dunes, arid dunes and soil are characterized by a neutral to alkaline pH (Brady, 1984), and leaching is minimal due to low precipitation rates. Furthermore, water scarcity, combined with dune morphology, was previously reported to affect crust properties in the Negev Desert. With dune morphology affecting hydrological processes, such as subsurface flow and evaporation, variable wetness duration was found to characterize different sections of the dune, which, in turn, accounts for a distinct crust type of different biomass and species composition (Kidron et al., 2009, 2010). Consequently, we hypothesize that both N-transforming microorganisms, total inorganic N and N forms, may be linked to the crust habitat, which determines, in turn, the crust type in the sand dune.

Toward this end, we examined the levels of inorganic N forms and the abundance of marker genes for N_2 fixation, nitrification and denitrification in different BSC types, covering the Hallamish Dune Field in the Negev Desert. These processes produce mobile inorganic N forms that are available for assimilation (biomass production), leaching, and emission to the atmosphere, thus affecting all other trophic levels and, subsequently, the productivity and stability of the dune field.

2. Materials and methods

2.1. Study site and crust description

The research was conducted at the Nizzana Research Site (NRS) within the Hallamish Dune Field, western Negev Desert, Israel (34°23′E, 30°56′N), which has been subjected to extensive geomorphological and hydrological research. Long-term mean annual precipitation is 95 mm (November–April). Mean annual temperature is 20 °C; it is 26.5 °C during the hottest month of July and 11.8 °C during the coldest month of January (Rosenan and Gilad, 1985). Annual potential evaporation is ~2600 mm (Evenari, 1981). The dune field comprises west-east-trending, 15–20 m-high longitudinal dunes. While having non-crusted and mobile crests, most of the mid-dunes and the entire bottom dunes are covered by BSCs. BSCs also cover the 50–200 m wide areas in between the dunes (interdunes).

At the NRS, five types of crusts were defined and mapped on the sandy surfaces of the dunes (Kidron et al., 2010). Four of the crusts are cyanobacterial (crusts A–D), and one is moss-dominated (crust E). Whereas crust A extends over the sandy interdunes and the south-facing footslopes, crusts B-D are confined to the north-facing slope. On the stabilized dunes, crust B extends over the upper slope, crust C at the upper-mid slope, and crust D at the midslope. Crust E occupies the interface between the footslope and the interdune (see schematic drawing in Table 1). Being at the interface, this habitat also receives runoff, which enriches crust E with fines i.e., silt and clay (Kidron, 2001).

The crusts show a gradual increase in thickness, water-holding capacity, organic matter, and fine content from crust A to E. An increase in heterotrophic bacteria (Yu et al., 2012) and fungi (Grishkan and Kidron, 2013) from crusts A to E is also exhibited along the same transect. Main crust characteristics are shown in Table 2.

2.2. Crust sampling

Four pairs of plots, 4 × 4 m each, were demarcated in each crust type (crusts A–E) along a 30 m-transect (Table 1). Within each plot, a pair of subplots, 20 × 20 cm each, was randomly chosen. Twenty-four samples, 1.2 cm-diameter and 1 cm-thick each, were randomly taken from one pair of subplots (six from each subplot) for chlorophyll determination. The crusts from the other pair of subplots were scalped, brought to the laboratory and stored at room temperature (~25 °C) under dark conditions 2–3 days until processing. Given the fact that many processes of N dynamics take place at the soil-atmosphere interface and that the crusts differ in their thickness (by up to one order of magnitude), all calculations (except for the pH and EC) were carried out on a surface area basis (square meter or square centimeter) rather than on soil weight. We believed that in this way, the vertical distribution of the microorganisms (especially prominent in the thickest crust, crust E) would not blur the results, given the low contribution that microorganisms below the photic zone (of 2–3 mm; see Garcia-Pichel and Bebout, 1996) may have in crust E if the calculation had been made on a mass basis.

Table 1
Location and transect of crust types. Arrow in drawing indicates subsurface flow.

Crust	Location
A	The most xeric crust. Covers the interdune and the south-facing slopes
B	Covers the upper gently north-facing slope
C	Covers the mid-upper section of the north facing slope
D	Covers the steep north-facing midslope
E	Covers the interface between the north-facing footslope and the interdune