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Desert crust microorganisms, their environment, and human health

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ABSTRACT

This article reviews current knowledge on cyanobacteria, the dominant primary producers, and other microorganisms in arid desert environments. These microorganisms have developed an array of adaptations to hot, arid climates with intense UV radiation, extreme diurnal temperature fluctuations, and high soil salinity. Crust microorganisms positively contribute to their harsh ecosystems, by preventing evapotranspiration, fixing nitrogen, and blocking solar radiation. In doing so, desert crust prevents soil erosion and facilitates the establishment of plant species. However, like aquatic cyanobacteria, desert cyanobacteria have the potential to produce toxins linked to human and animal illness. Furthermore, the impact of terrestrial cyanobacterial toxins on human health in desert regions is poorly understood. A largely ignored, but potentially important human exposure route for cyanotoxins in desert environments is through the inhalation of desert crusts during dust storms and anthropogenic activity. Future work in this field should include the characterization of toxins produced in desert regions as well as the presence of toxins in clinical and environmental materials.

1. Introduction to desert environments

Arid desert land occupies as much as 33% of the global terrestrial surface, much of which surrounds the equator. The Sahara desert alone occupies the same square acreage as the United States. Arid climates are defined by the significant absence of rainfall. Within this climate zone are three generally accepted subcategories: hyper-arid regions, which receive less than 100 mm annual rainfall, arid regions, which receive 100–300 mm annual rainfall and sub-arid regions, which can receive up to 800 mm annual rainfall. Of these three subcategories, arid is the most common, occupying 14.6% of the world's land area (FOA Forest, 1989).

While rainfall averages are useful in generalizing the arid climate, there are also vast exceptions in drought/rainfall cycles. The Atacama Desert in Chile suffered a 400-year drought, interrupted in 1971 by a torrential downpour. The Atacama, one of the driest deserts in the world, is considered the physiological dryness limit for life (Davila et al., 2008). What little precipitation does occur in such harsh environments is not always available to the plant and animal life. Long drought seasons create hard crusts on desert soil, resulting in runoff, characterized by flood channels and wadis. Physical, inorganic crusts have been extensively investigated because of their negative impact on arid agricultural land. What little moisture does remain in the soil undergoes excessive evapotranspiration. Deserts bordering coastal lands derive most of their moisture from moist onshore breezes. This moisture evaporates from the soil leaving behind high concentrations of NaCl.

Wind also affects the ecosystem of desert areas, where strong air currents in desert regions cause wind erosion and the phenomena of moving dunes (Wiggs et al., 1995, 2001). The scarce plant distribution in deserts provides little protection from wind-soil erosion forces. In addition to uprooting and sometimes covering pioneering plants, wind-driven soil transport reduces the nutrient content of soils. In New Mexico, aeolian transport of soil was shown to reduce organic carbon and nitrogen in the ground by 25% (Junran et al., 2007). This was attributed to the fact that most photosynthetic and nitrogen fixation occurs in the top few millimeters of soil (Garcia-Pichel and Belnap, 2001). This erosion and hampered nutrient availability makes colonization all but impossible for most species of flora and fauna.

Diel temperature fluctuations in arid environments also present a unique hurdle for pioneering organisms to overcome. Extremely high daytime temperatures can cause lethal desiccation in plant

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species. After dusk, near or below freezing temperatures can freeze and lyse plant cells. Hot deserts typically experience diel temperature ranges from 0 °C to 37 °C, while cold deserts such as those in Greenland, can fluctuate from as little as 0 °C to 4 °C. The Hopq Desert in China experiences minimum temperatures below −30 °C and high temperatures above 40 °C (Wang et al., 2013).

2. Prokaryotic organisms in desert environments

2.1. Hypolithic

Hypolithic bacterial communities have been studied less extensively than the photosynthetic cyanobacterial ones, which dominate this ecosystem. The abiotic factors that determine the composition and activity of hypolithic bacterial communities are available liquid water derived from rainfall and fog as well as salinity (Azua-Bustos et al., 2011; Pointing et al., 2009; Warren-Rhodes et al., 2006). Studies performed in the Atacama desert, Chile, show that both soil and hypolithic heterotrophs are positively correlated to soil moisture from rainfall and thus more abundant in wetter sites along a 11,500 m^2 precipitation gradient (Navarro-González et al., 2003; Warren-Rhodes et al., 2006). Based on 16S rRNA-sequence diversity analysis, hypolithic communities unlike soil communities, were comprised primarily of Acidobacteria, alpha, beta and gamma sub-classes of the Proteobacteria and were co-extracted with cyanobacterial colonizers.

Stomeo et al. (2013) working with samples collected in the Namib desert, spanning the Atlantic coasts of Angola, Namibia and South Africa, showed that rainfall-moisture has a different effect on both soil and hypolithic communities than fog-moisture. A higher number of Operational Taxonomic Units (OTU) derived from terminal restriction length polymorphisms (T-RFLP) of the 16S rRNA gene were observed in hypolithic communities of rainfall-dominated sites than those from fog-dominated sites. In contrast, soil communities were not influenced by the climate as they had a similar number of OTUs in both regimes. Also, the genetic fingerprints derived from soil communities revealed greater overall variation than those derived from the hypolithic communities. Makhalanyane et al. (2013) concluded that the noted variations suggest soil and hypolithic communities do not develop in isolation from one another but have cross recruitment.

2.2. Desert crusts

Obligate heterotrophic bacterial communities are important components of the consortium of organisms that make up the desert crusts. Their colonization on the crust is subsequent to the pioneering cyanobacteria who are the dominant primary producers contributing to nitrogen and carbon fixation. Investigation of the spatial patterns of heterotrophic bacterial communities at the micro-scale revealed a crust maturity-dependent distribution (Evans and Johansen, 1999). In pioneering desert crusts in the Colorado Plateau, communities were most abundant in the immediate sub-surface (1–2 mm), whereas in the more well-developed pigmented crusts the highest abundance was observed on the surface (0–1 mm) (Garcia-Pichel et al., 2003). Other studies performed at the centimeter to kilometer scale failed to observe such vertical stratification of the heterotrophic communities, yet the range of total viable counts are comparable and decline with depth (3.1×10^2–3.6×10^7 CFU/g of soil) (Bolton et al., 1993; Kuske et al., 2002; Skujinš, 1984).

The soil texture of desert crusts is also a determining factor in the total number of microorganisms they can support. The lowest numbers are found in exposed or compacted crusts and un-crusted soil followed by silt-surface crusts. Clay crusts support the highest numbers of bacteria owing to their ability to hold more moisture and organic matter within the pore space where microbial life exists (Gallardo and Schlesinger, 1995; Garcia-Pichel et al., 2003; Saxton and Rawls, 2006; Skujinš, 1984).

Phylogenetic analyses using culture-independent methods indicate that the majority of 16S rRNA sequences amplified from desert crust soils belong to cyanobacteria. In cases where crust samples originate from hyper-arid sites, they constitute up to 80% of the total sequenced community (Abed et al., 2010; Zaady et al., 2010). The bacterial populations uniformly belong to the phyla of Bacteroidetes, Proteobacteria, Deinococcus-Thermus and Gemmatimonadetes with the exception of the delta-Proteobacterial Myxobacteria only found in desert crust samples from Oman, and the phylum Actinobacteria detected only in the Sonoran desert and Colorado Plateau (Gundlapally and Garcia-Pichel, 2006; Nagy et al., 2005).

3. Prokaryotic organisms in dust storms originating from desert environments

Microbes attached to mineral dust or other airborne particles are transported over long distances (Griffin, 2007). Whitman et al. (1998) demonstrated that as many as 10^9 bacterial cells may be contained in one gram of desert dust, yet the abiotic factors that influence their population numbers, diversity and distribution are still not well understood. In general, concentrations of airborne microbes are higher during dust events, as compared to background conditions, and bacterial populations outweigh those of fungi (Choi et al., 1997; Griffin et al., 2001, 2003; Kellogg et al., 2004; Prospero et al., 2005).

Survival of microorganisms in the atmosphere is dependent on the same abiotic factors as their survival in desert environments, namely, the ability to withstand desiccation, extreme temperature fluctuations, oxygen and nutrient limitation and exposure to UV radiation (Alan and Harrison, 2004; Imshenetsky et al., 1978). According to the available literature, the best predictors of both the total number of bacteria and culturable bacteria in the atmosphere are air temperature and wind speed (Bovallius et al., 1978; Harrison et al., 2005; Mouli et al., 2005). Estimates of total bacterial concentrations in the atmosphere are the lowest in the desert ecosystem (1.6×10^2–3.8×10^4 CFU/m^3) and comparable to those of the sea air (Burrows et al., 2009; Lighthart and Shaffer, 1994).

Dust identified bacteria are phylogenetically affiliated with a plethora of genera belonging to the phyla of Gram-positive Firmicutes and Actinobacteria and the Gram-negative Proteobacteria. The majority of the bacteria isolated from African dust events over the Caribbean were Gram-positive spore-formers belonging to the genera *Bacillus* and *Microbacterium* (Griffin et al., 2001, 2003; Prospero et al., 2005). Perfumo and Marchant (2010) isolated thermophilic species of *Geobacillus* from African desert dust over Turkey and Greece and Hua et al. (2007) isolated halotolerant strains of *Staphylococcus* and *Bacillus* and of the Gram-negative *Halomonas* from Asian desert dust events in Japan. Finally, Leski et al. (2011) detected the presence of potential human pathogens in airborne samples collected from locations in Iraq and Kuwait by using a newly-designed high-density resequencing microarray. Genera identified include the Gram-positive *Mycobacterium*, *Clostridium* and *Bacillus* and the Gram-negative intracellular parasites *Brucella* and *Coxiella*.

4. Cyanobacteria desert adaptations

Cyanobacteria are so well adapted to the extremes of living conditions that they have been suggested for pioneering life on Mars (Friedmann and Ocampo-Friedmann, 1995). Indeed, fossils