CellPress

Opinion

The Mineralosphere Concept: Mineralogical Control of the Distribution and Function of Mineral-associated Bacterial Communities

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Soil is composed of a mosaic of different rocks and minerals, usually considered as an inert substrata for microbial colonization. However, recent findings suggest that minerals, in soils and elsewhere, favour the development of specific microbial communities according to their mineralogy, nutritive content, and weatherability. Based upon recent studies, we highlight how bacterial communities are distributed on the surface of, and in close proximity to, minerals. We also consider the potential role of the mineral-associated bacterial communities in mineral weathering and nutrient cycling in soils, with a specific focus on nutrient-poor and acidic forest ecosystems. We propose to define this microbial habitat as the mineralosphere, where key drivers of the microbial communities are the physicochemical properties of the minerals.

Trends

Rocks and minerals vary in their chemical composition, weatherability, and distribution.

Rocks and minerals support the development of life and especially of complex bacterial communities, capable of weathering minerals.

Is colonization of rocks and minerals by bacteria a random or a controlled process?

Several studies suggest that physicochemical properties of minerals and rocks determine mineral colonization by bacteria, supporting the definition of the mineralosphere concept.

Parallels can be made between the rhizosphere effect on bacterial communities and the mineralosphere effect proposed here.

Rocks and Minerals: Support of Life

Earth conditions allow the continuous genesis of igneous, metamorphic, and sedimentary **rocks** (see Glossary). Such processes continue to shape landscapes, generating new rock material as a result of tectonics, sedimentation of organic and inorganic particles, or conversely, rock erosion over geological timescales. Our planet can therefore be considered as a mosaic of different rocks and minerals (Figure 1), subjected to various degrees of environmental pressure and characterized by different physicochemical characteristics. Minerals are also differentiated according to their weatherability. Indeed, certain classes of mineral are easily weathered in acidic conditions, while others are recalcitrant [1]. Due to their nutritive content and their variable dissolution rates, mineral surfaces can be considered as reactive interfaces where nutritive cations are potentially accessible to the biosphere.

Whatever their location and their physical and chemical form, minerals play a central role in our environment. Regardless of their location and origins, from atmospheric dust, aquatic, terrestrial, deep-biosphere minerals, or even human teeth, all mineral and rock environments have the potential for microbial colonization. Rocks and minerals serve as physical supports for the attachment of microorganisms (bacteria, fungi) and plants, and as nutritive reserves participating in nutrient cycling, soil fertility, and water quality. From an evolutionary perspective, microbial

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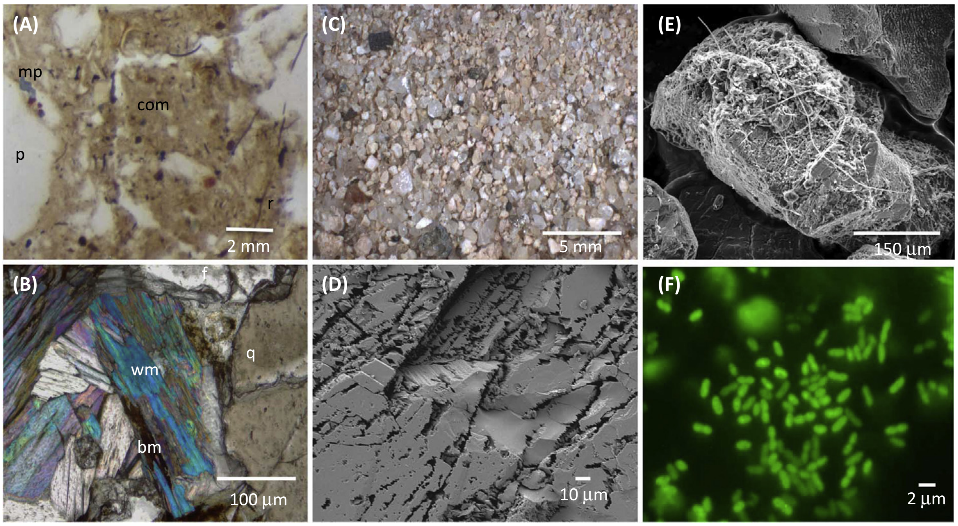

Figure 1. Mosaic of Environments and Microbial Colonization. (A) Thin-layer section of soil surfaces imaged with a stereomicroscope. This panel presents the soil heterogeneity, with tree roots (r), pores (p), mineral particles (mp), clays and organic matter (com). (B) A granite particle (q, quartz; wm, white mica; bm, black micas; f, feldspaths). The particle was imaged using a polarizing microscope. (C) Granitic saprolite showing the different mineral particles present (quartz, micas, and feldspaths) and the variability of size and colour, imaged with a stereomicroscope. (D) An apatite particle imaged with a scanning electron microscope. This presents the different cracks and fissures, which can be used as habitat by microorganisms. (E) Apatite particles imaged after several years of incubation in soil conditions (mesh bag approach). The apatite particles appeared covered by a complex organomineral biofilm containing fungal hyphae and bacteria. (F) Bacterial cells on biotite surfaces imaged by epifluorescence microscopy. Bacteria colonize mineral surfaces where they can establish complex biofilms. Such biofilms have been observed *in situ* on the surface of various stone monuments and aquifer minerals [38], experimentally using pure-culture-based experiments [39], but rarely *in situ* on soil minerals. However, panel E of this figure clearly shows a complex organomineral structure on the surface of the apatite particles. Interestingly, Certini *et al.* [35] reported the presence of complex mats on mineral surfaces such as sandstone rocks.

habitation of minerals seems to be an ancient strategy [2–4]. Interestingly, life on Earth itself may have originated within a mineral habitat [5]. Analyses of microbial interactions in the critical zone have revealed the exceptional abilities of microorganisms, both prokaryotes and eukaryotes, to successfully colonize and interact with a diverse array of rocks and minerals [6–21].

Do these minerals drive the establishment and development of specific microorganisms adapted to colonize such environments? Or conversely, are these minerals merely inert supports for microbial opportunists? Answering this question is of major importance because nutrient-poor, rocky mineral environments represent one of the main sources of nutritive cations for ecosystem functioning. One way to answer this question is to determine whether mineral colonization is a random process, or controlled by environmental conditions (extrinsic factors) and/or mineral characteristics (intrinsic factors). In this opinion paper, we argue that minerals represent specific microbial habitats, the intrinsic characteristics of which control microbial community establishment. We propose to call such mineral-influenced habitats the 'mineralosphere' [22]. We have chosen to focus on heterotrophic bacterial communities, the role of which in mineral weathering remains poorly understood compared to fungal communities. Analysing mainly *in situ* examples from aquatic and terrestrial environments, we will consider the extrinsic and intrinsic factors which make minerals suitable habitats for microbial colonization. We will also discuss the links between mineral chemistry and weatherabililty, together with the composition, diversity, and functional potentials of the mineral-inhabiting bacterial communities. A more thorough understanding of the factors driving mineral colonization by bacteria will allow enhanced appreciation of the potential roles of bacteria in mineral weathering, soil formation, and nutrient cycling.