

Plant-associated microbiomes in arid lands: diversity, ecology and biotechnological potential

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Abstract

Background Aridification is a worldwide serious threat directly affecting agriculture and crop production. In arid and desert areas, it has been found that microbial diversity is huge, built of microorganisms able to cope with the environmental harsh conditions by developing adaptation strategies. Plants growing in arid lands or regions facing prolonged abiotic stresses such as water limitation and salt accumulation have also developed specific physiological and molecular stress responses allowing them to thrive under normally unfavorable conditions.

Scope Under such extreme selection pressures, special root-associated bacterial assemblages, endowed with

capabilities of plant growth promotion (PGP) and extremophile traits, are selected by the plants. In this review, we provide a general overview on the microbial diversity in arid lands and deserts versus specific microbial assemblages associated with plants. The ecological drivers that shape this diversity, how plant-associated microbiomes are selected, and their biotechnological potential are discussed.

Conclusions Selection and recruitment of the plant associated bacterial assemblages is mediated by the combination of the bio-pedo-agroclimatic conditions and the plant species or varieties. Diversity and functional redundancy of these associated PGPR makes them very active in supporting plant improvement, health and resistance to drought, salt and related stresses. Implementing proper biotechnological applications of the arid and desert-adapted PGPR constitute the challenge to be raised.

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Introduction

Arid areas cover nearly 47 % of Earth's land surface. Such extended regions are characterized by various harsh environmental conditions mainly soil deficiency in water and nutrients, high salinity and acidity, low precipitation, high temperatures and UV irradiation (Whitford 2002). All the organisms thriving in these

extreme environmental conditions, including plants and bacteria, adopt complex survival strategies to alleviate abiotic stresses. In desert environments, microorganisms are the first colonizers (Mapelli et al. 2012; Borin et al. 2010). They possess special adaptation mechanisms, partly related to their ability of expressing and regulating only those genes required to survive and respond appropriately to the physical and chemical composition of these particular habitats (Bohnert et al. 1995; Begley et al. 2002; Boor 2006; Colica et al. 2014). They are able to create stable associations with higher organisms like fungi, lichens and mosses to form the so-called biological soil crusts (BSC) which have a crucial performance in stabilizing soil against erosion and in the restoration of deserts soils (de-Bashan et al. 2010; Bashan et al. 2012; Xu et al. 2013). BSCs can also be favourable niches for the germination of plant seeds.

Microorganism colonization and services in extreme environments are essential for the plant establishment. While microorganisms favour the availability of water and nutrients for the plant, in return plant root system supply carbon sources for growth, representing a stable survival niche (Neilands 1995; Graham and Vance 2000; Richardson et al. 2009). In the plant root system, the rhizosphere, the first millimetres of soil surrounding plant root surface, is a thin dynamic layer of high activity and metabolism. Plant rhizosphere represents a suitable survival niche to microorganisms where nutrients are more available. In this compartment, bacteria are the most abundant microorganisms and since they are mostly providing useful services to support root and plant growth they are commonly defined as Plant Growth Promoting Rhizobacteria (PGPR). PGPR exert beneficial effects on the growth of the host plant via direct and indirect mechanisms. They directly promote the plant growth by increasing the availability of nutrients, for instance by fixing atmospheric nitrogen (Graham and Vance 2000; Richardson et al. 2009), solubilizing inorganic phosphate and producing siderophores that increase the availability of mineral nutrients such as iron (Neilands 1995; Richardson 2001). PGPR contribute to the modulation of plant hormone balance through the synthesis of hormone-like molecules, mainly auxins, cytokinins and gibberellins (Costacurta and Vanderleyden 1995; Spaepen et al. 2007). Indirect mechanisms include the prevention of attacks of plant pathogens through the synthesis of antibiotics or antifungal compounds and through competition for nutrients (Van Loon et al. 1997; McCully 2005; Couillerot et al. 2009; Saharan and Nehra 2011). On their

side, plants noticeably contribute to the selection of PGPR by releasing root exudates, which generate a positive selection pressure and increase competitiveness among bacteria in root colonization (Shukla et al. 2013). A fraction of PGPR can also enter in root interior tissues, the so called endosphere, establishing the endophytic populations' community (Hallmann et al. 1997; Zinniel et al. 2002; Compant et al. 2005; Cankar et al. 2005; Danhorn and Fuqua 2007; Dias et al. 2009; Rhoden et al. 2015). Plants harbor endophytic bacteria that colonize a variety of internal plant tissues namely shoot, seeds and root tissues (Rosenblueth and Martínez-Romero 2006). In this context, Ulrich et al. (2008) identified *Paenibacillus*, *Methylobacterium* and *Stenotrophomonas* endophytes in the shoot tips and zygotic embryos of Norway spruce (*Picea abies*). In other studies, the endophytic bacteria *Methylobacterium extorquens*, *Pseudomonas synxantha*, *mycobacterium sp.* and *Rhodotorula minuta* were isolated from shoot tips of callus cultures of Scots pines (*Pinus sylvestris* L.) (Laukkanen et al. 2000; Pirttila et al. 2000). Besides, different bacterial genera have been identified within the endophytic community of potato (*Solanum tuberosum*) root tissues, for instance *Rheinheimera*, *Dyadobacter*, *Devosia*, *Pedobacter* and *Pseudoxanthomonas* (Manter et al. 2010). In *Mammillaria fraileana* seeds, endophytic bacteria distributed underneath the membrane covering the embryo and in the vascular tissue have been detected in addition to a large population of endophytic bacteria that have been isolated from stems and roots (Lopez et al. 2011). For instance, *Bacillus megaterium*, *Pseudomonas putida* and *Enterobacter sakazakii* have been isolated from the vascular cylinder, while *Azotobacter vinelandii* has been isolated from the root cortex.

This symbiotic association can be established without harming the plant (Lopez et al. 2011). Hence, several endophytes are of great importance given the beneficial effects that they offer to their host plants. Some endophytes are endowed with promoting growth potential (Dias et al. 2009; Bae et al. 2009; Lopez et al. 2011; Etesami et al. 2014) and biocontrol activities against phytopathogens (Melnick et al. 2013; Falcão et al. 2014). These particular characteristics lead them to be employed in several biotechnological applications. Thanks to their secondary metabolites, endophytes are employed as medicinal remedies (Strobel 2007; Qin et al. 2011) and as a tool for phytoremediation of organic contaminants giving their ability to degrade xenobiotics (Lodewyckx et al. 2002; Kuiper et al. 2004; Germaine

et al. 2006; Doty 2008). They also play an important role in soil fertility and improvement of sustainable production of non-food crops for biomass and biofuel production (Ryan et al. 2008).

In stressful conditions mimicking arid and desert environments, it has been shown that biotic resistance of *Quercus pubescens* to insect pest infestation is not affected by warming and drought stresses. Leaf palatability is rather influenced by the variability of trichome density implicated in such induced adaptation (Backhaus et al. 2014). Similarly, in salt stressed plants, adaptation implies a complex regulation machinery involving Ethylene Responsive Factor (ERF) (Klay et al. 2014). There is an increasing body of literature showing that arid soils may favour the selection of bacteria capable of providing suitable services to alleviate plant drought stress (Marasco et al. 2012; Marasco et al. 2013a; Shelef et al. 2013) suggesting that this adaptation may be manifesting in the bacterial assemblages.

Another important factor affecting the functioning of the root systems in arid soils is the multiple symbiotic interactions such as those that may occur between different life domains. An interesting case is the mutualistic tripartite symbiotic interaction established between the desert plant *Salsola inermis* with the beetle *Conorhynchus pistor* and its symbiotic bacterium *Klebsiella pneumonia* (Shelef et al. 2013). The bacterial symbiont inhabiting the gut of the plant-hosted beetle larvae, provide nitrogen to the beetle and the plant hosts. On its side, the host plant protects the beetle from predators and parasites with its roots and provides organic matter to the animal and to its symbiont. This example shows that symbiotic cooperation is capable to improve the growth sustainability of the partners under the harsh conditions of the desert. In addition, plant genotype was shown to have a direct effect in shaping the rhizosphere associated microbial communities (Haney et al. 2015).

Plants surviving in arid ecosystems can sustain specific root associated PGPR communities that are selected by the environmental factors peculiar of the different locations (Marasco et al. 2013a; Ferjani et al. 2015; Mapelli et al. 2013). Plant and cultivar type as well as nutrients richness of the soil, are pivotal factors for PGPR recruitment (Zhang et al. 2014; Latour et al. 1996). This selection gives rise to diverse PGPR communities with common capabilities for improving plant functionalities under the harsh conditions determined by drought and saline stresses in arid environments.

Within this context, several studies have explored this unique root-soil interface and assessed its biodiversity in arid lands, with particular interest for i) understanding PGPR activities involved in plant growth promotion and protection, ii) assessing the importance of the PGPR ecological-niche and diversity, and iii) exploiting PGPR to improve agricultural sustainability. In the following sections we discuss these aspects in the light of the recent literature.

Microbial diversity associated to plants growing in arid lands and deserts

Arid regions are characterized by low rainfall and substantial unvegetated areas, which offer a typical ecosystem with patchwork-shaped microbial assemblages (Pointing and Belnap 2012; Nagy et al. 2005). In the recent years, several surveys have been focused on the complexity of the microbial diversity associated to soils in these extreme ecosystems. Despite the different geographic location of arid lands and deserts across the world, the bacterial communities of lithic substrates were dominated by *Cyanobacteria* (DiRuggiero et al. 2013). In addition, *Proteobacteria*, *Firmicutes*, *Actinobacteria* and *Bacteroidetes* are the main phyla generally detected in these soils. In the Taklamakan desert, the largest mobile desert in Asia (China), fifteen phyla were obtained but the most abundant were *Proteobacteria* (25.10 %), *Firmicutes* (24.8 %), *Bacteroidetes* (22.7 %) and *Actinobacteria* (8.9 %), respectively (An et al. 2013). In another Asian desert, the Gobi desert, 13 phyla were observed confirming the dominance of *Firmicutes* (69.9 %), *Proteobacteria* (12.2 %) and *Bacteroidetes* (8.2 %) (An et al. 2013).

The Sonoran and Mohave deserts in North America present BSCs bacterial communities dominated by *Cyanobacteria* and a few proportion of bacteria related to *Acidobacteria*, *Actinobacteria*, *Bacteroidetes*, *Proteobacteria*, *Chloroflexi* and *Deinococcus* phyla. The bacterial communities in the Atacama Desert, the oldest and driest desert located in South America, showed the dominance of *Actinobacteria* and *Chloroflexi* with a low abundance of *Acidobacteria* and *Proteobacteria* (Neilson et al. 2012). These data have been confirmed also by the characterization of the bacterial community in the Tataouine Desert, a part of the world largest Sahara Desert in South Tunisia (Chanal et al. 2006). The common diversity traits

observed in the bacterial communities of different deserts may be attributed to the largely common harsh environmental conditions of all these deserts, which are however affected by microbial cell inputs determined by the circulation of the airborne dust associated to sand storms (Nagy et al. 2005).

Despite the presence of similar bacterial community in arid lands and deserts, plants are able to shape and select specific root-associated bacterial communities that include bacteria capable to cope with the abiotic stress of these ecosystems (Table 1, Fig. 1).

Several studies confirmed that the so called rhizosphere effect holds as well in desert ecosystems. 16S rRNA gene sequences produced by PCR-DGGE analysis of the bacterial community associated with the roots of *Larrea tridentate* located in the Mohave Desert of southern California, revealed a predominance of *Proteobacteria* (*Bradyrhizobiaceae*, *Rhodospirillaceae*, *Pseudomonadaceae*, *Aurantimonadaceae*, *Enterobacteriaceae*, *Xanthomonadaceae*, and *Alcaligenaceae*), *Bacteroidetes* (*Chitinophagaceae* and *Flexibacteraceae*), *Firmicutes* (*Bacillaceae*), and *Actinobacteria* (*Micrococcaceae*) (Jorquera et al. 2012). In arid, yet cultivated soils in Egypt, the bacterial communities associated to the rhizosphere of pepper and medical plants were prevalently colonized by *Firmicutes* and *Proteobacteria*, while the bulk soil was characterized by the abundance of *Actinobacteria* and *Firmicutes* (Marasco et al. 2012; Koberl et al. 2011). In the same case study, Marasco et al. (2012) found different distribution of cultivable bacterial genera in different fractions of root system. *Bacillus* spp. (68 % of the isolates) were mainly isolated from the endosphere, while *Klebsiella* spp. were dominating the isolate collections from the rhizosphere and the root surrounding soil, representing 61 and 44 % of the isolates, respectively (Marasco et al. 2012). Ferjani et al. (2015) observed in date palms from South Tunisian oases a rhizosphere community completely different from that in the root surrounding soil, supporting the consideration that date palm root exudates are strongly shaping the bacterial community. A rhizosphere effect was also observed in the halophyte *Salicornia* sp. sampled from the Chotts and Sebkhah saline systems in the South of Tunisia (Mapelli et al. 2013).

All these studies proved that arid environments select very diverse bacterial communities that are shaped by the resources made available by the plant roots (Fig. 1).

Ecological drivers selecting the plant-associated microbiome

Over the past decade, many research works have been focused on the plant associated microbiome selection. Progress in molecular tools has increased our understanding of the composition, the function and the ecological drivers of plant associated microbial assemblages. Despite the various microenvironments of the plant, including the phyllosphere, carposphere and endosphere, the rhizosphere has been the most investigated. A particular attention has been addressed to explore the PGPR diversity in this compartment in relation to different ecological drivers. The rhizosphere is defined as the soil fraction adhering to root plant strongly influenced by root exudates. It is well documented that the composition of root exudates depends on plant type, growth stage and environmental conditions (Duineveld et al. 1998; Gabriele et al. 2001; Appuhn and Joergensen 2006; Van Overbeek and Van Elsas 2008; Cavaglieri and Etcheverry 2009). Further studies showed how the composition of root exudates determines the recruitment of plant-associated bacteria. It has been shown that root exudates have a significant role in shaping the abundance of rhizosphere bacterial communities in herbaceous and arboreal plants (Zhang et al. 2014). Besides, it has been recently demonstrated that plant genotypic variations can also influence the rhizosphere associated microbiome (Haney et al. 2015). Interestingly, it has been shown in the same work that accessions of *Arabidopsis thaliana* inhibited specifically some *Pseudomonadaceae* species, namely *P. brassicacearum*, *P. fluorescens* and *P. syringae*, without affecting most of the microbiome. Hence, plant genotype is a crucial factor in determining plant associated bacteria that influence the plant health and physiology according to specific biotic and abiotic stresses. Furthermore, it has been proved that *Olea europaea* L. genotype has a more relevant impact on endophytic communities in olive leaves compared to the soil type, the environmental conditions and the geographic location (Müller et al. 2015). This study has been performed on 10 *Olea europaea* L. cultivars leaves sampled from olive trees growing at a single agricultural site in Spain and from nine wild olive trees developing in natural habitats in Greece, Cyprus and on Madeira Island. A strong correlation between bacteria endophytic composition and plant genotypes has been highlighted.

Table 1 Diversity of plant associated bacterial assemblages in desert and arid land systems

Sites and characteristics	Host plant/Plant part	Dominant Phyla / Isolated Strains (PGPR traits)	References
CULTURE-INDEPENDENT APPROACH			
Mohave desert (Southwest North America) Dry/Arid (1) ^a	<i>Larrea tridentat</i> (Rhizosphere)	<i>Proteobacteria</i> <i>Bacteroidetes</i> <i>Firmicutes</i>	Jorquera et al. 2012
“Le Frece” farm (North Itlay) Humid (6)	<i>Vitis vinifera</i> (Roots endosphere) <i>Vitis vinifera</i> (Rhizosphere)	<i>Actinobacteria</i> <i>Alphaproteobacteria</i> <i>Gammaproteobacteria</i>	Marasco et al. 2013a
Farm in Cairo periphery (Cairo -North West Egypt) Arid (10)	<i>Vitis vinifera</i> (Roots endosphere, Rhizosphere)	<i>Sphingobacteria</i> <i>Alphaproteobacteria</i>	Marasco et al. 2013a
Sekem farms (Egypt) Arid (11)	<i>Matricaria chamomilla</i> L. (Rhizosphere, Roots endosphere) <i>Calendula officinalis</i> L. (Rhizosphere, Roots endosphere) <i>Solanum distichum</i> (Rhizosphere, Roots endosphere)	<i>Ochrobactrum</i> sp. <i>Rhodococcus</i> sp.	Korbel et al. 2011
Momag Vineyards (North Tunisia) Semi-arid (7)	<i>Vitis vinifera</i> (Roots endosphere) <i>Vitis vinifera</i> (Rhizosphere)	<i>Actinobacteria</i> <i>Alphaproteobacteria</i> <i>Betaproteobacteria</i> <i>Sphingobacteria</i> <i>Alphaproteobacteria</i> <i>Betaproteobacteria</i>	Marasco et al. 2013a
Sebkha and Chott (Southern Tunisia) Hypersaline soils (8)	<i>Salicornia</i> (Rhizosphere)	<i>Betaproteobacteria</i> <i>Alphaproteobacteria</i> <i>Firmicutes</i>	Mapelli et al. 2013
CULTURE-DEPENDENT APPROACH			
Arid land India Arid (13)	<i>Pennisetum glaucum</i> L (Rhizosphere) <i>Pennisetum glaucum</i> L (Rhizosphere) <i>Zea mays</i> L (Rhizosphere)	<i>Pseudomonas</i> (PS, PH, Si, Am) ^b	Sandhya et al. 2010
Southern Sonoran Desert (North America) Subtropical, hot, dry (3)	<i>Mammillaria fraileana</i> (Endosphere, Roots cortex) <i>Mammillaria fraileana</i> (Endosphere, Roots cylinder)	<i>Azotobacter vinelandii</i> (NF) <i>Pseudomonas Putida</i> (PS) <i>Enterobacter sakazakii</i> (PS) <i>Bacillus megaterium</i> (PS)	Lopez et al. 2011
El Bebedero saline (San Luis, Argentina) Saline system (5)	<i>Prosopis strombulifera</i> (Roots endosphere)	<i>Lysinibacillus fusiformis</i> (NF, PH) <i>Bacillus subtilis</i> (NF, ACC, PH) <i>Brevibacterium halotolerans</i> (NF, ACC, AF, PH) <i>Bacillus licheniformis</i> (NF, ACC, PH) <i>Bacillus pumilus</i> (NF, ACC, AF, PH) <i>Achromobacter xylosoxidans</i> (NF, ACC, PH) <i>Pseudomonas putida</i> (Si, NF, ACC, PH)	Sgroy et al. 2009
Tae-An sand dunes (Chungnam- South Korea) Desert (14)	<i>Calystegia soldanella</i> (Rhizosphere) <i>Calystegia soldanella</i> (Roots) <i>Elymus mollis</i> (Rhizosphere)	<i>Gammaproteobacteria</i> <i>Bacteroidetes</i> , <i>Actinobacteria</i> <i>Gammaproteobacteria</i> <i>Alphaproteobacteria</i> , <i>Actinobacteria</i> <i>Gammaproteobacteria</i> ,	Park et al. 2005

Table 1 (continued)

Sites and characteristics	Host plant/Plant part	Dominant Phyla / Isolated Strains (PGPR traits)	References		
Sinai desert (Egypt) Arid to desert (12)	<i>Elymus mollis</i> (Roots)	<i>Bacteroidetes</i> , <i>Actinobacteria</i> <i>Gammaproteobacteria</i>	Othman et al. 2004		
	<i>Panicum turgidum</i> (Rhizosphere)	<i>Paenibacillus macerans</i> (NF) <i>Bacillus circulans</i> (NF) <i>Agrobacterium radiobacter</i> (NF) <i>Chryseomonas luteola</i> (NF) <i>Bacillus circulans</i> (NF)			
	<i>Panicum turgidum</i> (Intact root)	<i>Bacillus circulans</i> (NF) <i>Enterobacter agglomerans</i> (NF)			
	Oases (Southern Tunisia) Arid (9)	<i>Phoenix dactylifera L.</i> (Rhizosphere)		<i>Gammaproteobacteria</i> <i>Actinobacteria</i>	Ferjani et al. 2015
	Western Kentucky coal fields (USA) Moderate climate (2)	<i>Panicum virgatum L.</i> (Shoot, root and seeds)		<i>Firmicutes</i> <i>Proteobacteria</i> <i>Actinobacteria</i>	Xia et al. 2013
Cordoba (Argentina) Cultivation under drought conditions (4)	<i>Helianthus annuus</i> (Roots)	<i>Achromobacter xiloxidans</i> (NF, AF, PH) <i>Bacillus sp.</i> (NF, AF, PH)	Forchetti et al. 2007		
Sebkha and Chott (Southern Tunisia) Hypersaline soils (8)	<i>Salicornia</i> (Rhizosphere)	<i>Halomonas taeheungii</i> (ACC, PA, Am) <i>Halomonas xinjiangensis</i> (ACC, PA, Am) <i>Halomonas elongate</i> (NF, PA, Am), <i>H. eurihalina</i> (NF, PA, Am), <i>H. indalina</i> (NF, PA, Am), <i>Kushneria marisflavi</i> (NF, PA, Am), <i>Chromohalobacter canadensis</i> (NF, PA, Am) <i>Marinococcus</i> (PA, Am), <i>Nesterenkonia</i> (PA, Am), <i>Virgibacillus</i> (PA, Am)	Mapelli et al. 2013		

^a Site number in Fig. 1

^b Plant Growth Promoting activities

NF Nitrogen Fixation, PS Phosphate Solubilization, PH Phytohormones production, Si Siderophore production, Am Ammonia production, ACC 1 aminocyclo-propane-1-carboxylate deaminase production, AF antifungal activity, PA Protease Activity

In addition to the selection operated by plants, abiotic stresses are the selective forces contributing to shape the bacterial community associated to roots (Fig. 2). A complex interaction between environmental and abiotic factors was shown to play an important role in shaping bacterial diversity, as well as to affect the properties of soils. It has been demonstrated that the biological state of agricultural soils and land use history play an important role in shaping the bacterial communities (Paula et al. 1992; Latour et al. 1996; Lazarovits and Nowak 1997; Garbeva et al. 2008). In fact, plant growth potential of PGPR is more stimulated in nutrient-deficient soil than in a nutrient-rich ones (Egamberdiyeva 2007). In a

comparative study, Yanxia et al. (2009) showed that bacterial communities in the soybean rhizosphere were more stable in clayey soil comparing to the sandy soil (Yanxia et al. 2009). Both soil types and land use history parameters were shown to affect bacterial community to a greater extent than plant species. Different plant types (maize, oat, barley and grass) were cultivated under greenhouse conditions in soils with different land use histories. The previous land use was the main significant factor affecting the composition of the *Burkholderia* community (Salles et al. 2004). Also the soil type showed an effect on *Pseudomonas* diversity, but the soil factor exerted a preminent influence on the bacterial

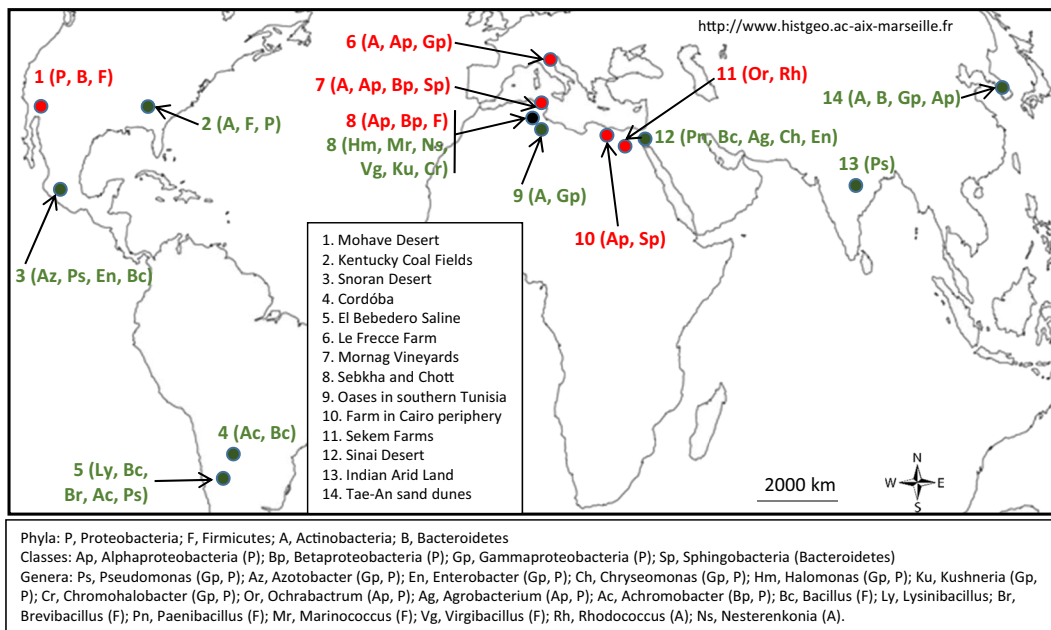


Fig. 1 Location in world map and distribution of the arid lands and desert ecosystems sites where studies were conducted on the diversity of plant-associated microbial assemblages as reported in Table 1. Microbial communities' diversity is shaped by the abiotic factors (arid conditions) and by the plant-related factors (Fig. 2). Microorganisms were detected by culture-dependent (green dots and letters), and-independent approaches (red dots and letters) or both (black dot). Gammaproteobacteria (Gp) are the most encountered class in almost all the prospected sites. Alphaproteobacteria (Ap) and Firmicutes (F) showed also high occurrence. Independently from each bacterial community components, PGP functional redundancy is noticed leading to functional services.

communities' composition. Besides, Latour et al. (1996) evaluated the bacterial diversity of roots associated bacteria of two different plant species. They demonstrated that both soil type and host plant affect the bacterial diversity, though, the soil is the dominant factor (Latour et al. 1996). In another research study, microbial diversity has been assessed near *Reaumuria negevensis* plant growing in the Negev Desert (Saul-Tcherkas and Steinberger 2011). It has been demonstrated that bacterial communities' abundance is closely related to seasonal variations. In fact, *Actinobacteria* was the dominant phylum in all seasons except in winter. However, in winter season, *Acidobacteria* phylum reaches its highest density (56.3 %) and substitute *Actinobacteria* phylum, which decreases to 4.2 %. Besides, *Proteobacteria* phylum increases in the winter season. In the other hand, *Bacteroidetes* and *Chloroflexi* phyla were higher in the summer season and lower in winter and autumn, though, *Gemmatimonadetes* phylum increased in autumn.

These PGPR from arid lands hold the potential to sustain crop production under the desert farming practices. Detected Phyla: P, *Proteobacteria* (Gp, *Gammaproteobacteria*; Ps, *Pseudomonas*; Az, *Azotobacter*; En, *Enterobacter*; Ch, *Chryseomonas*; Hm, *Halomonas*; Ku, *Kushneria*; (Ap, *Alphaproteobacteria*; Or, *Ochrobactrum*; Ag, *Agrobacterium*); (Bp, *Betaproteobacteria*; Ac, *Achromobacter*); F, *Firmicutes* (Bc, *Bacillus*; Ly, *Lysinibacillus*; Br, *Brevibacillus*; Pn, *Paenibacillus*; Vg, *Virgibacillus*; Mr, *Marinococcus*); A, *Actinobacteria* (Rh, *Rhodococcus*; Ns, *Nesterenkonia*) and B, *Bacteroidetes*; (Sp, *Sphingobacteria*)

Therefore, multiple ecological players shape the plant recruited microbiome. This peculiar plant associated bacterial assemblages are presumably involved in an adaptation strategy that allows the plants to overcome harsh conditions in arid lands.

Functional services of plant-associated microbiomes in arid areas

Considering the importance and the potential use of plant growth promoting rhizobacteria for agronomic and environmental applications, several studies focused not only on the bacterial diversity but also on the PGPR 'ecological role'. In this context, the interest in exploring PGPR bacteria naturally adapted to harsh arid ecosystems is widely increased especially for those associated to plants

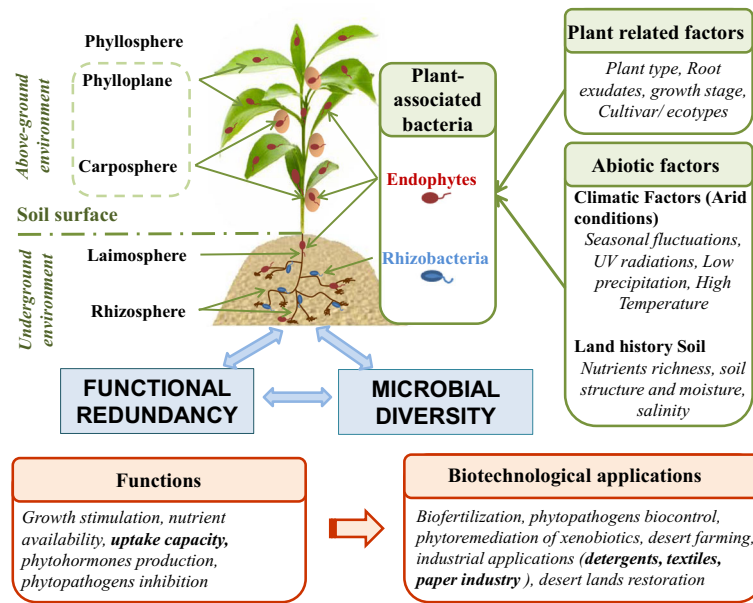


Fig. 2 Plant associated bacterial assemblages: Ecological drivers, functions and applications. In arid environments, plants recruit diverse bacterial communities to undertake the harsh environmental conditions. Within the phyllosphere and the rhizosphere plant compartments, bacteria colonizing the rhizosphere and the endosphere are the most investigated. They are shaped by several ecological drivers. Plant related factors determine the plant associated microbiome depending on the plant type, its growth stage and the composition of its root exudates. Beside, plant genotype is also a crucial factor in determining plant associated bacteria depending on the cultivar or the ecotype. Abiotic stresses contribute to this bacterial communities' recruitment. Abiotic factors are related to the typical climate of the arid lands and deserts characterized by seasonal variations, high UV radiations and temperature and low precipitations. The biological state of agricultural soils and the land use history that affect the soil nutrients richness, structure, moisture and salinity, are also key ecological drivers. Despite the microbial

diversity of PGP bacteria, functional redundancy has been shown. It proves a strong functional equilibrium although the environmental variations. This distinctive characteristic can preserve plants from harsh conditions and ensure their survival regardless arid systems environmental constraints. These functions consist on plant growth promotion under harsh salinity and drought conditions, phytohormones production, facilitation of mineral and nutrient availability and uptake capacity as well as the promotion of plant health via antagonistic potential towards phytopathogens. PGP bacteria are endowed with diverse biotechnological potentials. They can be evolved in agricultural applications as biofertilizers and agents for phytopathogens biocontrol. They may be further used in phytoremediation for xenobiotic polluted soils. PGP bacteria can also be employed in industrial application, such as detergents, textiles and paper industries, thanks to their high resistance to salinity and high temperature in addition to their thermostability and tolerance of harsh chemical compounds

exposed to water shortage and salinity (Marasco et al. 2013b; Daffonchio et al. 2015).

In this context, a research work has been carried out to assess the microbial diversity and promoting growth potential of grapevine (*Vitis vinifera*) rhizobacteria sampled from three distinct Mediterranean sites: Tunisia, Egypt and Italy (Marasco et al. 2013a). Basing on cultivation dependent and independent approaches, the bacterial community associated to grapevine root system (root tissues, rhizosphere, and root-surrounding soil) has been assessed. A phylogenetic study showed the affiliation of the different root associated bacteria to five phyla: *Acidobacteria*, *Actinobacteria*, *Firmicutes*, *Proteobacteria* and *Bacteroidetes*. *Alphaproteobacteria* was dominant in all rhizospheric soils sampled from the different countries. According to DGGE analysis, soil

endophyte fractions presented a limited diversity compared to the other root system samples. It has been explained that this low microbial diversity can be the result of a strong bacterial selection in the root system that imposes specific physiological requirements within the endosphere. However, a considerable endosphere and rhizosphere bacterial diversity has been reported in the different latitudinal sites examined. Despite this diversity, it has been demonstrated that bacterial PGP potential remained unchanged in the different rhizobacterial collections even though bio-pedoclimatic conditions were completely different in the studied sites (different cultivars, soil type and climate) (Fig. 2). This functional redundancy in grapevine root associated bacteria proves the strong functional equilibrium of promoting growth bacteria despite the

environmental variation. Such a property may protect grapevine from harsh conditions and ensure its survival regardless environmental constraints, mainly in arid systems (Marasco et al. 2013a).

A recent work on the date palm rhizosphere in the oasis ecosystems of Southern Tunisia, reported that the shape of rhizobacterial communities is correlated with geo-climatic features along a north-south aridity transect (Ferjani et al. 2015). Such bacterial community segregation between the different oases was associated with the harsher conditions in the southern oases close to the Grand Erg Oriental desert, respect to the mountain oases. The cultivable bacteria associated to the date palm rhizosphere belonged to *Proteobacteria*, *Actinobacteria* and *Firmicutes*, with *Gammaproteobacteria* dominating followed by *Actinobacteria*. The majority (85 %) of isolates affiliated to the different phyla showed multiple plant growth promotion activities (Table 1). Identifying environmental factors contributing to microbial community variation at a large spatial scale can help in assessing microbial communities usable for desert farming. Date palm root system showed a complex diversity that exhibited a reservoir of PGPR adapted to thrive in the harsh conditions of the desert oases (Ferjani et al. 2015).

The rhizosphere of the halophyte *Salicornia* sp. obtained from the Sebkhia and Chott hypersaline ecosystems in Southern Tunisia showed a high bacterial diversity and a large collection (475 isolates) of halophilic and halotolerant bacteria has been established. Twenty *Halomonas* isolates showed resistance to a wide set of abiotic stresses and performed different PGP activities *in vitro* mainly phosphate solubilisation, ammonia and indole-3-acetic acid production and potential nitrogen fixation. These results demonstrate the relevant potential of these bacteria to promote plant growth under the harsh salinity and drought conditions (Mapelli et al. 2013).

In another study, the rhizosphere of cactus plants growing on barren mineral substrates in North American deserts has been shown to contain dense layers of bacteria and fungi. The dominant bacterial groups were represented by *Pseudomonads*, *Bacilli* and *Actinomyces* that have been shown to be able to dissolve several rock types and minerals, releasing significant amounts of useful minerals for plants (Bashan and de-Bashan 2010). Several PGPR strains may enhance root hair size and number, facilitating the mineral uptake capacity of the plant (de Freitas and Germida 1992).

An assessment of the bacterial diversity associated to pepper (*Capsicum annuum* L.) cultivated in a traditional farm subjected to desert farming practices in Egypt showed the presence of a dense and diverse bacterial population in the rhizosphere and the root surrounding soil. Conversely, the bacterial community associated to the endosphere was much less abundant presumably due to the selection exerted by the plant root tissues that select specific bacterial colonizers. Most of the isolates (95 %) presented *in vitro* multiple plant growth promoting (PGP) activities and stress resistance capabilities. It has been also demonstrated that under desert farming, PGP bacteria are able of enhancing plant photosynthetic activity and biomass synthesis (up to 40 %) under drought stress (Marasco et al. 2012).

To evaluate long-term agriculture impact on arid soil in organic desert farming in Sekem (Egypt), Koberl et al. (2011) analysed microbial communities of the desert soil as well as those associated with cultivated medicinal plants *Matricaria chamomilla*, *Calendula officinalis* and *Solanum distichum*. The desert soil was dominated by two phylotypes affiliated to *Ochrobactrum* sp. and *Rhodococcus* sp. which were also found in all samples from the rhizosphere and endorhiza of all the three medicinal plants. However, the rhizosphere and the endosphere of the medicinal plants presented a clear plant-specific effect since they shared only 20 % of the bacterial community with the bulk desert soil. It has been demonstrated that indigenous desert microorganisms promote plant health in desert agro-ecosystems via an antagonist potential towards phytopathogens (Koberl et al. 2011).

All these studies indicate that arid land conditions select efficient PGPR capable of resisting harsh conditions and to sustain crop production under the desert farming practices (Figs. 1 and 2).

Biotechnological potential of PGP microbes and feasibility of their application

Many studies have shown the important role of associated root bacteria in increasing crop yield and soil fertility (Desai et al. 2012; Deivanai et al. 2014; Nadeem et al. 2014; Kumar et al. 2014) not only in the normal conditions but also under biotic and abiotic stresses. This potential is currently applied for desert farming (Koberl et al. 2011) and for restoration and reforestation of eroded desert lands (Chanway 1997; Bashan et al.

2012). It has been proved that one of the consistent strategies for enhancing *in vivo* effect of PGP microbes on plants is multiple inoculations and stress protecting bioformulations (Adesemoye et al. 2008; Wang et al. 2012).

Beside, PGPR contribute to protect plant health against fungal, bacterial, nematode and even viral diseases in arid environments which are propitious to phyto-pathogens attacks (Rodríguez-Díaz et al. 2008; Almaghrabi et al. 2013). Fungal biocontrol has been mostly explored given its wide extension and devastating effect on crop yield (Ait Kaki et al. 2013; Siddiqui 2006; Recep et al. 2009; Muñoz et al. 2009). A research study on rhizobacteria associated with some desert plants in Saudi Arabia has been carried out to identify and to select effective isolates against phytopathogenic fungi. This investigation allowed the identification of successful isolates to *Bacillus spp.*, *Enterobacter spp.* and *Pseudomonas spp.* Based on plant growth promotion properties, resilience to harsh conditions and antagonistic potentials, the strains have been proposed as biofertilizer candidates (El-Sayed et al. 2014).

Nevertheless, the application of such inoculum in agrobiolgy, cannot cover the broad-spectrum disease control given the variability of cultivar varieties, environmental conditions and soil types. It can be only applied in niche applications especially with weakly domesticated crop in growth substrates lacking antagonists (Cassells and Rafferty-McArdle 2012). However, despite significant biocontrol activities against plant pathogens has been proved for PGPR in laboratory and in the greenhouse, field results are still uncertain since autochthonous community outcompete the added allochthonous formulation.

The biotechnological potential enclosed in the extreme arid and saline environments is not limited to the agriculture application. Raddadi et al. 2013 reported the production of halo-alkalitolerant endoglucanase by *Paenibacillus tarimensis* isolated from the inland saline system Chott El Fjej in South Tunisia. These cellulases were functional in a broad pH range, at high temperature and salt concentration up to 5 M NaCl and 4.6 M KCl. Consequently, they are promising candidate for industrial applications (Raddadi et al. 2013). Strains and enzymes isolated from arid extreme environments could be applied in bioremediation of polluted soils (Mapelli et al. 2012), especially under phytoremediation approaches for those strains capable to thrive in the root ecosystem. Indeed, phytoremediation processes have

been proposed for enhancing plant adaptation and growth in soil and water contaminated with organic pollutants (Afzal et al. 2014) (Fig. 2).

Furthermore, arid environment present deficiency in nitrogen compound, which implies symbiotic association between nitrogen fixing organisms and plants to increase the level of nitrogen and the plant growth in arid lands. *Rhizobia* are widely described as the most efficient nitrogen fixing bacteria especially rhizobium-legume symbiosis system (Zahran et al. 1999). Moreover, Requena et al. reported a combination between PGPR, arbuscular mycorrhizal fungi and *Rhizobium spp.* isolated from semi-arid environment for legume plant inoculation to establish Mediterranean semi-arid ecosystems revegetation (Requena et al. 1997).

Conclusion

Drought stress is an environmental threat affecting plant yield and productivity. As discussed in this review, arid ecosystems harbour diverse microbial communities. In such ecosystems, PGPR associated to plant roots can be very active in supporting plant improvement, health and resistance to drought stress. Major efforts have still to be implemented for the understanding of the factors that regulate the plant microbe interactions in the root system and the mechanisms that are behind the drought resistance conferred to the plants by the root-associated bacteria. As well, despite a huge body of literature is available about PGPR, the ecological factors determining their recruitment by the plant and the assemblage of effective bacterial communities in the rhizosphere and the endosphere remain elusive. It is evident that the assemblage of these bacterial communities is driven by different ecological factors, including soil type, land history, cultivar variety, abiotic stresses, geo-climatic factors and by the type of plant and its growing conditions. However, we are still far from understanding the relative weight of these factors in the establishment of the root meta-organism. The clarifications of these factors regulating the recruitment and the assemblage of drought resistance-inducing PGPR communities by the plant roots will allow to move PGPR from a prominent biotechnological tools yet to be exploited for agricultural, environmental and industrial purposes to a huge implementable biotechnological resource for agriculture.

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