

1 **Plant-associated microbiomes in arid lands: Diversity, ecology and biotechnological potential**

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17 **Abstract**

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

23 **Scope** Under such extreme selection pressures, special root-associated bacterial assemblages, endowed with
24 capabilities of plant growth promotion (PGP) and extremophile traits, are selected by the plants. In this review, we
25 provide a general overview on the microbial diversity in arid lands and deserts versus specific microbial
26 assemblages associated with plants. The ecological drivers that shape this diversity, how plant-associated
27 microbiomes are selected, and their biotechnological potential are discussed.

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

33

34 **Keywords:** Plant associated microbiome, Arid land, Extreme environments, Drought, Salinity, Plant Growth
35 Promoting Rhizobacteria, Sustainable agriculture, Biotechnology

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38 **Introduction**

39 Arid areas cover nearly 47% of Earth's land surface. Such extended regions are characterized by various harsh
40 environmental conditions mainly soil deficiency in water and nutrients, high salinity and acidity, low precipitation,
41 high temperatures and UV irradiation (Whitford 2002). All the organisms thriving in these extreme environmental
42 conditions, including plants and bacteria, adopt complex survival strategies to alleviate abiotic stresses. In desert
43 environments, microorganisms are the first colonizers (Mapelli et al. 2012; Borin et al. 2010). They possess special
44 adaptation mechanisms, partly related to their ability of expressing and regulating only those genes required to
45 survive and respond appropriately to the physical and chemical composition of these particular habitats (Bohnert et
46 al. 1995; Begley et al. 2002; Boor 2006; Colica et al. 2014). They are able to create stable associations with higher
47 organisms like fungi, lichens and mosses to form the so-called biological soil crusts (BSC) which have a crucial
48 performance in stabilizing soil against erosion and in the restoration of deserts soils (de-Bashan et al. 2010; Bashan
49 et al. 2012; Xu et al. 2013). BSCs can also be favourable niches for the germination of plant seeds.

50 Microorganism colonization and services in extreme environments are essential for the plant establishment. While
51 microorganisms favour the availability of water and nutrients for the plant, in return plant root system supply carbon
52 sources for growth, representing a stable survival niche (Neilands 1995; Graham and Vance 2000; Richardson et al.
53 2009). In the plant root system, the rhizosphere, the first millimetres of soil surrounding plant root surface, is a thin
54 dynamic layer of high activity and metabolism. Plant rhizosphere represents a suitable survival niche to
55 microorganisms where nutrients are more available. In this compartment, bacteria are the most abundant
56 microorganisms and since they are mostly providing useful services to support root and plant growth they are
57 commonly defined as Plant Growth Promoting Rhizobacteria (PGPR). PGPR exert beneficial effects on the growth
58 of the host plant via direct and indirect mechanisms. They directly promote the plant growth by increasing the
59 availability of nutrients, for instance by fixing atmospheric nitrogen (Graham and Vance 2000; Richardson et al.
60 2009), solubilizing inorganic phosphate and producing siderophores that increase the availability of mineral
61 nutrients such as iron (Neilands 1995; Richardson 2001). PGPR contribute to the modulation of plant hormone
62 balance through the synthesis of hormone-like molecules, mainly auxins, cytokinins and gibberellins (Costacurta and
63 Vanderleyden 1995; Spaepen et al. 2007). Indirect mechanisms include the prevention of attacks of plant pathogens
64 through the synthesis of antibiotics or antifungal compounds and through competition for nutrients (Van Loon et al.

65 1997; McCully 2005; Couillerot et al. 2009; Saharan and Nehra 2011). On their side, plants noticeably contribute to
66 the selection of PGPR by releasing root exudates, which generate a positive selection pressure and increase
67 competitiveness among bacteria in root colonization (Shukla et al. 2013). A fraction of PGPR can also enter in root
68 interior tissues, the so called endosphere, establishing the endophytic populations' community (Hallmann et al.
69 1997; Zinniel et al. 2002; Compant et al. 2005; Cankar et al. 2005; Danhorn and Fuqua 2007; Dias et al. 2009;
70 Rhoden et al. 2015). Plants harbor endophytic bacteria that colonize a variety of internal plant tissues namely shoot,
71 seeds and root tissues (Rosenblueth and Martínez-Romero 2006). In this context, Ulrich et al. (2008) identified
72 *Paenibacillus*, *Methylobacterium* and *Stenotrophomonas* endophytes in the shoot tips and zygotic embryos of
73 Norway spruce (*Picea abies*). In other studies, the endophytic bacteria *Methylobacterium extorquens*, *Pseudomonas*
74 *synxantha*, *mycobacterium sp.* and *Rhodotorula minuta* were isolated from shoot tips of callus cultures of Scots
75 pines (*Pinus sylvestris* L.) (Laukkanen et al. 2000, Pirttila et al. 2000). Beside, different bacterial genera have been
76 identified within the endophytic community of potato (*Solanum tuberosum*) root tissues, for instance *Rheinheimera*,
77 *Dyadobacter*, *Devosia*, *Pedobacter* and *Pseudoxanthomonas* (Manter et al. 2010). In *Mammillaria fraileana* seeds,
78 endophytic bacteria distributed underneath the membrane covering the embryo and in the vascular tissue have been
79 detected in addition to a large population of endophytic bacteria that have been isolated from stems and roots (Lopez
80 et al. 2011). For instance, *Bacillus megaterium*, *Pseudomonas putida* and *Enterobacter sakazakii* have been isolated
81 from the vascular cylinder, while *Azotobacter vinelandii* has been isolated from the root cortex.

82 This symbiotic association can be established without harming the plant (Lopez et al. 2011). Hence, several
83 endophytes are of great importance given the beneficial effects that they offer to their host plants. Some endophytes
84 are endowed with promoting growth potential (Dias et al. 2009; Bae et al. 2009; Lopez et al. 2011; Etesami et al.
85 2014) and biocontrol activities against phytopathogens (Melnick et al. 2013; Falcão et al. 2014). These particular
86 characteristics lead them to be employed in several biotechnological applications. Thanks to their secondary
87 metabolites, endophytes are employed as medicinal remedies (Strobel 2007; Qin et al. 2011) and as a tool for
88 phytoremediation of organic contaminants giving their ability to degrade xenobiotics (Lodewyckx et al. 2002;
89 Kuiper et al. 2004; Germaine et al. 2006; Doty 2008). They also play an important role in soil fertility and
90 improvement of sustainable production of non-food crops for biomass and biofuel production (Ryan et al. 2008).

91 In stressful conditions mimicking arid and desert environments, it has been shown that biotic resistance of *Quercus*
92 *pubescens* to insect pest infestation is not affected by warming and drought stresses. Leaf palatability is rather

93 influenced by the variability of trichome density implicated in such induced adaptation (Backhaus et al. 2014).
94 Similarly, in salt stressed plants, adaptation implies a complex regulation machinery involving Ethylene Responsive
95 Factor (ERF) (Klay et al. 2014). There is an increasing body of literature showing that arid soils may favour the
96 selection of bacteria capable of providing suitable services to alleviate plant drought stress (Marasco et al. 2012;
97 Marasco et al. 2013a; Shelef et al. 2013) suggesting that this adaptation may be manifesting in the bacterial
98 assemblages.

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

108 Plants surviving in arid ecosystems can sustain specific root associated PGPR communities that are selected by the
109 environmental factors peculiar of the different locations (Marasco et al. 2013a; Ferjani et al. 2015; Mapelli et al.
110 2013). Plant and cultivar type as well as nutrients richness of the soil, are pivotal factors for PGPR recruitment
111 (Zhang et al. 2014; Latour et al. 1996). This selection gives rise to diverse PGPR communities with common
112 capabilities for improving plant functionalities under the harsh conditions determined by drought and saline stresses
113 in arid environments.

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

119

120 **Microbial diversity associated to plants growing in arid lands and deserts**

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

131 The Sonoran and Mohave deserts in North America present BSCs bacterial communities dominated by
132 *Cyanobacteria* and a few proportion of bacteria related to *Acidobacteria*, *Actinobacteria*, *Bacteroidetes*,
133 *Proteobacteria*, *Chloroflexi* and *Deinococcus* phyla. The bacterial communities in the Atacama Desert, the oldest
134 and driest desert located in South America, showed the dominance of *Actinobacteria* and *Chloroflexi* with a low
135 abundance of *Acidobacteria* and *Proteobacteria* (Neilson et al. 2012). These data have been confirmed also by the
136 characterization of the bacterial community in the Tataouine Desert, a part of the world largest Sahara Desert in
137 South Tunisia (Chanal et al. 2006). The common diversity traits observed in the bacterial communities of different
138 deserts may be attributed to the largely common harsh environmental conditions of all these deserts, which are
139 however affected by microbial cell inputs determined by the circulation of the airborne dust associated to sand
140 storms (Nagy et al. 2005).

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

144 Several studies confirmed that the so called rhizosphere effect holds as well in desert ecosystems. 16S rRNA gene
145 sequences produced by PCR-DGGE analysis of the bacterial community associated with the roots of *Larrea*
146 *tridentate* located in the Mohave Desert of southern California, revealed a predominance of *Proteobacteria*
147 (*Bradyrhizobiaceae*, *Rhodospirillaceae*, *Pseudomonadaceae*, *Aurantimonadaceae*, *Enterobacteriaceae*,
148 *Xanthomonadaceae*, and *Alcaligenaceae*), *Bacteroidetes* (*Chitinophagaceae* and *Flexibacteraceae*), *Firmicutes*

149 (*Bacillaceae*), and *Actinobacteria* (*Micrococcaceae*) (Jorquera et al. 2012). In arid, yet cultivated soils in Egypt, the
150 bacterial communities associated to the rhizosphere of pepper and medical plants plants were prevalently colonized
151 by *Firmicutes* and *Proteobacteria*, while the bulk soil was characterized by the abundance of *Actinobacteria* and
152 *Firmicutes* (Marasco et al. 2012; Koberl et al. 2011). In the same case study, Marasco et al. (2012) found different
153 distribution of cultivable bacterial genera in different fractions of root system. *Bacillus* spp. (68% of the isolates)
154 were mainly isolated from the endosphere, while *Klebsiella* spp. were dominating the isolate collections from the
155 rhizosphere and the root surrounding soil, representing 61% and 44% of the isolates, respectively (Marasco et al.
156 2012). Ferjani et al. (2015) observed in date palms from South Tunisian oases a rhizosphere community completely
157 different from that in the root surrounding soil, supporting the consideration that date palm root exudates are
158 strongly shaping the bacterial community. A rhizosphere effect was also observed in the halophyte *Salicornia* sp.
159 sampled from the Chotts and Sebkha saline systems in the South of Tunisia (Mapelli et al. 2013).
160 All these studies proved that arid environments select very diverse bacterial communities that are shaped by the
161 resources made available by the plant roots (Figure 1).

162

163 **Ecological drivers selecting the plant-associated microbiome**

164 Over the past decade, many research works have been focused on the plant associated microbiome selection.
165 Progress in molecular tools has increased our understanding of the composition, the function and the ecological
166 drivers of plant associated microbial assemblages. Despite the various microenvironments of the plant, including the
167 phyllosphere, carposphere and endosphere, the rhizosphere has been the most investigated. A particular attention has
168 been addressed to explore the PGPR diversity in this compartment in relation to different ecological drivers. The
169 rhizosphere is defined as the soil fraction adhering to root plant strongly influenced by root exudates. It is well
170 documented that the composition of root exudates depends on plant type, growth stage and environmental conditions
171 (Duineveld et al. 1998; Gabriele et al. 2001; Appuhn and Joergensen 2006; Van Overbeek and Van Elsas 2008;
172 Cavaglieri and Etcheverry 2009). Further studies showed how the composition of root exudates determines the
173 recruitment of plant-associated bacteria. It has been shown that root exudates have a significant role in shaping the
174 abundance of rhizosphere bacterial communities in herbaceous and arboreal plants (Zhang et al. 2014). Besides, it
175 has been recently demonstrated that plant genotypic variations can also influence the rhizosphere associated
176 microbiome (Haney et al. 2015). Interestingly, it has been shown in the same work that accessions of *Arabidopsis*

177 *thaliana* inhibited specifically some *Pseudomonadacea* species, namely *P. brassicacearum*, *P. fluorescens* and *P.*
178 *syringae*, without affecting most of the microbiome. Hence, plant genotype is a crucial factor in determining plant
179 associated bacteria that influence the plant health and physiology according to specific biotic and abiotic stresses.
180 Furthermore, it has been proved that *Olea europaea* L. genotype has a more relevant impact on endophytic
181 communities in olive leaves compared to the soil type, the environmental conditions and the geographic location
182 (Müller et al. 2015). This study has been performed on 10 *Olea europaea* L. cultivars leaves sampled from olive
183 trees growing at a single agricultural site in Spain and from nine wild olive trees developing in natural habitats in
184 Greece, Cyprus and on Madeira Island. A strong correlation between bacteria endophytic composition and plant
185 genotypes has been highlighted.

186 In addition to the selection operated by plants, abiotic stresses are the selective forces contributing to shape the
187 bacterial community associated to roots (Figure 2). A complex interaction between environmental and abiotic
188 factors was shown to play an important role in shaping bacterial diversity, as well as to affect the properties of soils.
189 It has been demonstrated that the biological state of agricultural soils and land use history play an important role in
190 shaping the bacterial communities (Paula et al. 1992; Latour et al. 1996; Lazarovits and Nowak 1997; Garbeva et al.
191 2008). In fact, plant growth potential of PGPR is more stimulated in nutrient-deficient soil than in a nutrient-rich
192 ones (Egamberdiyeva 2007). In a comparative study, Yanxia et al. (2009) showed that bacterial communities in the
193 soybean rhizosphere were more stable in clayey soil comparing to the sandy soil (Yanxia et al. 2009). Both soil
194 types and land use history parameters were shown to affect bacterial community to a greater extent than plant
195 species. Different plant types (maize, oat, barley and grass) were cultivated under greenhouse conditions in soils
196 with different land use histories. The previous land use was the main significant factor affecting the composition of
197 the *Burkholderia* community (Salles et al. 2004). Also the soil type showed an effect on *Pseudomonas* diversity, but
198 the soil factor exerted a preeminent influence on the bacterial communities' composition. Besides, Latour et al.
199 (1996) evaluated the bacterial diversity of roots associated bacteria of two different plant species. They
200 demonstrated that both soil type and host plant affect the bacterial diversity, though, the soil is the dominant factor
201 (Latour et al. 1996). In another research study, microbial diversity has been assessed near *Reaumuria negevensis*
202 plant growing in the Negev Desert (Saul-Tcherkas and Steinberger 2011). It has been demonstrated that bacterial
203 communities' abundance is closely related to seasonal variations. In fact, *Actinobacteria* was the dominant phylum
204 in all seasons except in winter. However, in winter season, *Acidobacteria* phylum reaches its highest density

205 (56.3%) and substitute *Actinobacteria* phylum, which decreases to 4.2%. Beside, *Proteobacteria* phylum increases
206 in the winter season. In the other hand, *Bacteroidetes* and *Chloroflexi* phyla were higher in the summer season and
207 lower in winter and autumn, though, *Gemmatimonadetes* phylum increased in autumn.
208 Therefore, multiple ecological players shape the plant recruited microbiome. This peculiar plant associated bacterial
209 assemblages are presumably involved in an adaptation strategy that allows the plants to overcome harsh conditions
210 in arid lands.

211

212 **Functional services of plant-associated microbiomes in arid areas**

213 Considering the importance and the potential use of plant growth promoting rhizobacteria for agronomic and
214 environmental applications, several studies focused not only on the bacterial diversity but also on the PGPR
215 ‘ecological role’. In this context, the interest in exploring PGPR bacteria naturally adapted to harsh arid ecosystems
216 is widely increased especially for those associated to plants exposed to water shortage and salinity (Marasco et al.
217 2013b; Daffonchio et al. 2015).

218 In this context, a research work has been carried out to assess the microbial diversity and promoting growth potential
219 of grapevine (*Vitis vinifera*) rhizobacteria sampled from three distinct Mediterranean sites: Tunisia, Egypt and Italy
220 (Marasco et al. 2013a). Basing on cultivation dependent and independent approaches, the bacterial community
221 associated to grapevine root system (root tissues, rhizosphere, and root-surrounding soil) has been assessed. A
222 phylogenetic study showed the affiliation of the different root associated bacteria to five phyla: *Acidobacteria*,
223 *Actinobacteria*, *Firmicutes*, *Proteobacteria* and *Bacteroidetes*. *Alphaproteobacteria* was dominant in all
224 rhizospheric soils sampled from the different countries. According to DGGE analysis, soil endophyte fractions
225 presented a limited diversity compared to the other root system samples. It has been explained that this low
226 microbial diversity can be the result of a strong bacterial selection in the root system that imposes specific
227 physiological requirements within the endosphere. However, a considerable endosphere and rhizosphere bacterial
228 diversity has been reported in the different latitudinal sites examined. Despite this diversity, it has been
229 demonstrated that bacterial PGP potential remained unchanged in the different rhizobacterial collections even
230 though bio-pedo-climatic conditions were completely different in the studied sites (different cultivars, soil type and
231 climate) (Figure 2). This functional redundancy in grapevine root associated bacteria proves the strong functional
232 equilibrium of promoting growth bacteria despite the environmental variation. Such a property may protect

233 grapevine from harsh conditions and ensure its survival regardless environmental constraints, mainly in arid systems
234 (Marasco et al. 2013a).

235 A recent work on the date palm rhizosphere in the oasis ecosystems of Southern Tunisia, reported that the shape of
236 rhizobacterial communities is correlated with geo-climatic features along a north-south aridity transect (Ferjani et al.
237 2015). Such bacterial community segregation between the different oases was associated with the harsher conditions
238 in the southern oases close to the Grand Erg Oriental desert, respect to the mountain oases. The cultivable bacteria
239 associated to the date palm rhizosphere belonged to *Proteobacteria*, *Actinobacteria* and *Firmicutes*, with
240 *Gammaproteobacteria* dominating followed by *Actinobacteria*. The majority (85%) of isolates affiliated to the
241 different phyla showed multiple plant growth promotion activities (Table 1). Identifying environmental factors
242 contributing to microbial community variation at a large spatial scale can help in assessing microbial communities
243 usable for desert farming. Date palm root system showed a complex diversity that exhibited a reservoir of PGPR
244 adapted to thrive in the harsh conditions of the desert oases (Ferjani et al. 2015).

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

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

257 An assessment of the bacterial diversity associated to pepper (*Capsicum annuum* L.) cultivated in a traditional farm
258 subjected to desert farming practices in Egypt showed the presence of a dense and diverse bacterial population in the
259 rhizosphere and the root surrounding soil. Conversely, the bacterial community associated to the endosphere was
260 much less abundant presumably due to the selection exerted by the plant root tissues that select specific bacterial

261 colonizers. Most of the isolates (95%) presented *in vitro* multiple plant growth promoting (PGP) activities and stress
262 resistance capabilities. It has been also demonstrated that under desert farming, PGP bacteria are able of enhancing
263 plant photosynthetic activity and biomass synthesis (up to 40%) under drought stress (Marasco et al. 2012).
264 To evaluate long-term agriculture impact on arid soil in organic desert farming in Sekem (Egypt), Koberl et al.
265 (2011) analysed microbial communities of the desert soil as well as those associated with cultivated medicinal plants
266 *Matricaria chamomilla*, *Calendula officinalis* and *Solanum distichum*. The desert soil was dominated by two
267 phylotypes affiliated to *Ochrobactrum sp.* and *Rhodococcus sp.* which were also found in all samples from the
268 rhizosphere and endorhiza of all the three medicinal plants. However, the rhizosphere and the endosphere of the
269 medicinal plants presented a clear plant-specific effect since they shared only 20% of the bacterial community with
270 the bulk desert soil. It has been demonstrated that indigenous desert microorganisms promote plant health in desert
271 agro-ecosystems via an antagonist potential towards phytopathogens (Koberl et al. 2011).
272 All these studies indicate that arid land conditions select efficient PGPR capable of resisting harsh conditions and to
273 sustain crop production under the desert farming practices (Figure 1 and 2).

274

275 **Biotechnological potential of PGP microbes and feasibility of their application**

276 Many studies have shown the important role of associated root bacteria in increasing crop yield and soil fertility
277 (Desai et al. 2012; Deivanai et al. 2014; Nadeem et al. 2014; Kumar et al. 2014) not only in the normal conditions
278 but also under biotic and abiotic stresses. This potential is currently applied for desert farming (Koberl et al. 2011)
279 and for restoration and reforestation of eroded desert lands (Chanway 1997; Bashan et al. 2012). It has been proved
280 that one of the consistent strategies for enhancing *in vivo* effect of PGP microbes on plants is multiple inoculations
281 and stress protecting bioformulations (Adesemoye et al. 2008; Wang et al. 2012).

282 Beside, PGPR contribute to protect plant health against fungal, bacterial, nematode and even viral diseases in arid
283 environments which are propitious to phyto-pathogens attacks (Rodríguez-Díaz et al. 2008; Almaghrabi et al. 2013).

284 Fungal biocontrol has been mostly explored given its wide extension and devastating effect on crop yield (Ait Kaki
285 et al. 2013; Siddiqui 2006; Recep et al. 2009; Muñoz et al. 2009). A research study on rhizobacteria associated with
286 some desert plants in Saudi Arabia has been carried out to identify and to select effective isolates against
287 phytopathogenic fungi. This investigation allowed the identification of successful isolates to *Bacillus spp.*,

288 *Enterobacter spp.* and *Pseudomonas spp.* Based on plant growth promotion properties, resilience to harsh conditions
289 and antagonistic potentials, the strains have been proposed as biofertilizer candidates (El-Sayed et al. 2014).
290 Nevertheless, the application of such inoculum in agrobiolgy, cannot cover the broad-spectrum disease control
291 given the variability of cultivar varieties, environmental conditions and soil types. It can be only applied in niche
292 applications especially with weakly domesticated crop in growth substrates lacking antagonists (Cassells and
293 Rafferty-McArdle 2012). However, despite significant biocontrol activities against plant pathogens has been proved
294 for PGPR in laboratory and in the greenhouse, field results are still uncertain since autochthonous community
295 outcompete the added allochthonous formulation.

296 The biotechnological potential enclosed in the extreme arid and saline environments is not limited to the agriculture
297 application. Raddadi et al. 2013 reported the production of halo-alkalitolerant endoglucanase by *Paenibacillus*
298 *tarimensis* isolated from the inland saline system Chott El Fjej in South Tunisia. These cellulases were functional in
299 a broad pH range, at high temperature and salt concentration up to 5M NaCl and 4.6M KCl. Consequently, they are
300 promising candidate for industrial applications (Raddadi et al. 2013). Strains and enzymes isolated from arid
301 extreme environments could be applied in bioremediation of polluted soils (Mapelli et al. 2012), especially under
302 phytoremediation approaches for those strains capable to thrive in the root ecosystem. Indeed, phytoremediation
303 processes have been proposed for enhancing plant adaptation and growth in soil and water contaminated with
304 organic pollutants (Afzal et al. 2014) (Figure 2).

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

311

312

313 **Conclusion**

314 Drought stress is an environmental threat affecting plant yield and productivity. As discussed in this review, arid
315 ecosystems harbour diverse microbial communities. In such ecosystems, PGPR associated to plant roots can be very

316 active in supporting plant improvement, health and resistance to drought stress. Major efforts have still to be
317 implemented for the understanding of the factors that regulate the plant microbe interactions in the root system and
318 the mechanisms that are behind the drought resistance conferred to the plants by the root-associated bacteria. As
319 well, despite a huge body of literature is available about PGPR, the ecological factors determining their recruitment
320 by the plant and the assemblage of effective bacterial communities in the rhizosphere and the endosphere remain
321 elusive. It is evident that the assemblage of these bacterial communities is driven by different ecological factors,
322 including soil type, land history, cultivar variety, abiotic stresses, geo-climatic factors and by the type of plant and
323 its growing conditions. However, we are still far from understanding the relative weight of these factors in the
324 establishment of the root meta-organism. The clarifications of these factors regulating the recruitment and the
325 assemblage of drought resistance-inducing PGPR communities by the plant roots will allow to move PGPR from a
326 prominent biotechnological tools yet to be exploited for agricultural, environmental and industrial purposes to a
327 huge implementable biotechnological resource for agriculture.

328

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

602 **Figure 1:** Location in world map and distribution of the arid lands and desert ecosystems sites where studies were
603 conducted on the diversity of plant-associated microbial assemblages as reported in Table 1. Microbial
604 communities' diversity is shaped by the abiotic factors (arid conditions) and by the plant-related factors (Fig. 2).
605 Microorganisms were detected by culture-dependent (green dots and letters), and-independent approaches (red dots
606 and letters) or both (black dot). *Gammaproteobacteria* (Gp) are the most encountered class in almost all the
607 prospected sites. *Alphaproteobacteria* (Ap) and *Firmicutes* (F) showed also high occurrence. Independently from
608 each bacterial community components, PGP functional redundancy is noticed leading to functional services. These
609 PGPR from arid lands hold the potential to sustain crop production under the desert farming practices. Detected
610 Phyla: P, *Proteobacteria* (Gp, *Gammaproteobacteria*; Ps, *Pseudomonas*; Az, *Azotobacter*; En, *Enterobacter*; Ch,
611 *Chryseomonas*; Hm, *Halomonas*; Ku, *Kushneria*; Cr, *Chromohalobacter*); (Ap, *Alphaproteobacteria*; Or,
612 *Ochrabactrum*; Ag, *Agrobacterium*); (Bp, *Betaproteobacteria*; Ac, *Achromobacter*); F, *Firmicutes* (Bc, *Bacillus*;
613 Ly, *Lysinibacillus*; Br, *Brevibacillus*; Pn, *Paenibacillus*; Vg, *Virgibacillus*; Mr, *Marinococcus*); A, *Actinobacteria*
614 (Rh, *Rhodococcus*; Ns, *Nesterenkonia*) and B, *Bacteroidetes*; (Sp, *Sphingobacteria*).

615

616 **Figure 2:** Plant associated bacterial assemblages: Ecological drivers, functions and applications.

617 In arid environments, plants recruit diverse bacterial communities to undertake the harsh environmental conditions.
618 Within the phyllosphere and the rhizosphere plant compartments, bacteria colonizing the rhizosphere and the
619 endosphere are the most investigated. They are shaped by several ecological drivers. Plant related factors determine
620 the plant associated microbiome depending on the plant type, its growth stage and the composition of its root
621 exudates. Beside, plant genotype is also a crucial factor in determining plant associated bacteria depending on the
622 cultivar or the ecotype. Abiotic stresses contribute to this bacterial communities' recruitment. Abiotic factors are
623 related to the typical climate of the arid lands and deserts characterized by seasonal variations, high UV radiations
624 and temperature and low precipitations. The biological state of agricultural soils and the land use history that affect
625 the soil nutrients richness, structure, moisture and salinity, are also key ecological drivers. Despite the microbial
626 diversity of PGP bacteria, functional redundancy has been shown. It proves a strong functional equilibrium although

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

636

637

table

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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)	<i>Larrea tridentat</i> (Rhizosphere)	<i>Proteobacteria</i> <i>Bacteroidetes</i> <i>Firmicutes</i>	Jorquera et al. 2012
"Le Frecce" 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
Mornag Vineyards (North Tunisia)	<i>Vitis vinifera</i> (Roots endosphere)	<i>Actinobacteria</i> <i>Alphaproteobacteria</i>	Marasco et al. 2013a

Semi-arid (7)	<i>Vitis vinifera</i> (Rhizosphere)	<i>Betaproteobacteria</i> <i>Sphingobacteria</i> <i>Alphaproteobacteria</i> <i>Betaproteobacteria</i>	
Sebkha and Chott (Southern Tunisia)	<i>Salicornia</i> (Rhizosphere)	<i>Betaproteobacteria</i> <i>Alphaproteobacteria</i>	Mapelli et al. 2013
Hypersaline soils (8)		<i>Firmicutes</i>	

CULTURE-DEPENDENT APPROACH

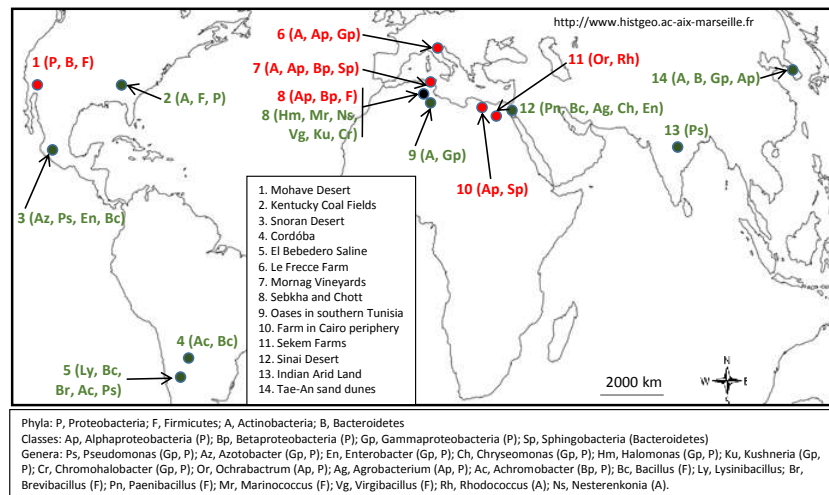
Arid land	<i>Pennisetum glaucum</i> L (Rhizosphere)	<i>Pseudomonas</i> (PS, PH, Si, Am) (9)	Sandhya et al. 2010
India	<i>Pennisetum glaucum</i> L (Rhizosphere)		
Arid (13)	<i>Zea mays</i> L (Rhizosphere)		
Southern Sonoran Desert (North America)	<i>Mammillaria fraileana</i> (Endosphere, Roots cortex)	<i>Azotobacter vinelandii</i> (NF)	Lopez et al. 2011
Subtropical, hot, dry (3)	<i>Mammillaria fraileana</i> (Endosphere, Roots cylinder)	<i>Pseudomonas Putida</i> (PS) <i>Enterobacter sakazakii</i> (PS) <i>Bacillus megaterium</i> (PS)	
El Bebedero saline	<i>Prosopis strombulifera</i> (Roots endosphere)	<i>Lysinibacillus fusiformis</i> (NF, PH)	Sgroy et al. 2009

(San Luis, Argentina)		<i>Bacillus subtilis</i> (NF, ACC, PH)	
Saline system (5)		<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)	
Tae-An sand dunes (Chungnam- South Korea)	<i>Calystegia soldanella</i> (Rhizosphere)	<i>Gammaproteobacteria</i>	Park et al. 2005
Desert (14)	<i>Calystegia soldanella</i> (Roots)	<i>Bacteroidetes, Actinobacteria</i>	
		<i>Gammaproteobacteria</i>	
	<i>Elymus mollis</i> (Rhizosphere)	<i>Alphaproteobacteria, Actinobacteria</i>	
		<i>Gammaproteobacteria,</i>	
		<i>Bacteroidetes, Actinobacteria</i>	
	<i>Elymus mollis</i> (Roots)	<i>Gammaproteobacteria</i>	
Sinai desert (Egypt)	<i>Panicum turgidum</i> (Rhizosheath)	<i>Paenibacillus macerans</i> (NF)	Othman et al. 2004
Arid to desert (12)		<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</i> L.(Rhizosphere)	<i>Gammaproteobacteria</i> <i>Actinobacteria</i>	Ferjani et al. 2014
Western Kentucky coal fields (USA) Moderate climate (2)	<i>Panicum virgatum</i> L. (Shoot, root and seeds)	<i>Firmicutes</i> <i>Proteobacteria</i> <i>Actinobacteria</i>	Xia et al. 2013
Cordóba (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 Figure 1; (b). Plant Growth Promoting activities: Nitrogen Fixation (NF), Phosphate Solubilization (PS), Phytohormones production (PH), Siderophore production (Si), Ammonia production (Am), 1 aminocyclo-propane-1-carboxylate deaminase production (ACC), antifungal activity (AF), Protease Activity (PA).

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