

## Chapter 2

# Harnessing the Plant Microbiome for Improved Abiotic Stress Tolerance

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**Abstract** The benefits of the green revolution in agriculture are over because current agricultural productivity has touched its limits of effectiveness in increasing plant yield. This problem is complicated by shrinking farmland, high labour costs and biotic and abiotic stresses. In fact, global agriculture and increased production would depend on the application and utilisation of microorganisms of agricultural importance, which will serve as an alternative strategy for higher crop productivity in the future. Efficient microbes play a key role in integrated management practices such as biotic and abiotic stresses and nutrient management to reduce chemical use and improve cultivar performance. On the other hand, high food demand and ever-increasing population increase pressure and urgency of how to exploit the microbiome for high crop yields and reduced losses caused by environmental stresses. This chapter highlights the importance of the designer plant microbiome, a strategy that may provide an effective and sustainable increase in crop yield and ultimately leads to food security by efficiently tackling biotic and abiotic stresses.

**Keywords** Microbiome • Plant nutrition • Abiotic stress

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## 2.1 Introduction: An Overview of Abiotic Stresses in Plants

A plethora of abiotic stresses affects crop plants including drought, extreme temperatures, salinity, nutrient deficiency and flooding which are expected to intensify due to climatic changes (Hussain et al. 2012; Timmusk et al. 2013, 2014; Rolli et al. 2015). Abiotic stresses represent a significant threat to agricultural productivity (Capell et al. 2004). A global water shortage due to significant climatic changes is the leading cause of these abiotic stresses. Drought is the most significant abiotic stress, adversely affecting the productivity and distribution of crop plants worldwide (Hussain et al. 2012; Marasco et al. 2013). For example, drought alone affects up to 45% of the global agricultural land, characterised by high human population (38%) with increased food demands (Bartels and Hussain 2008; Hussain et al. 2012). Plant growth and development face deleterious effects even with short-term water imbalance. Plants exhibit a plethora of responses at physiological, metabolic and molecular levels to survive or tolerate adverse conditions which include stomatal closure, increased aquaporin and H<sup>+</sup>-pyrophosphatase activity and accumulation of a variety of compatible solutes (Bartels and Sunkar 2005; Shinozaki and Yamaguchi-Shinozaki 2007; Marasco et al. 2013; Hussain et al. 2016). Several studies have revealed overall effects of drought on plant growth and development; however, it is difficult to understand the damage caused to plants at the cellular and molecular levels under water deficit conditions (Zhu 2002; Chaitanya et al. 2003; Chaves and Oliveira 2004).

Salinity limits agricultural production in arid and semiarid areas, characterised by low annual precipitation, where agriculture is dependent on irrigation (Agrawal et al. 2013). Increased salt ion concentrations (such as Na<sup>+</sup> and Cl<sup>-</sup>, but also others including Ca<sup>2+</sup>, K<sup>+</sup>, CO<sub>3</sub><sup>2-</sup>, NO<sub>3</sub><sup>-</sup>, SO<sub>4</sub><sup>2-</sup>) in soil reduce water uptake by roots which ultimately results in the accumulation of toxic salt ions within plant cells (Tester and Davenport 2003). Plants have the ability to tackle this problem such as low Na<sup>+</sup> concentration by actively maintaining translocation into vacuolar compartments via ATP-dependent ion pumps. However, excessive NaCl in irrigation water results in osmotic stress (Zhang et al. 2009a, b). Any imbalance in intracellular ion homeostasis leads to the damaging effects, for example, cell signalling pathways including those that lead to the synthesis of osmotically active metabolites, specific proteins, nutritional disorders, assimilation, membrane disorganisation, reduced cell division and expansion, genotoxicity and certain free radical scavenging enzymes that control ion and water flux (Zhang et al. 2009a, b) which ultimately impaired optimal growth and development.

Abiotic stresses such as drought, salinity and extreme temp are often interconnected and induce a similar set of plant responses by activating the same or interacting pathways (Shinozaki and Yamaguchi-Shinozaki 2000; Seki et al. 2001, 2002; Kreps et al. 2002). A general response such as compatible solute accumulation and the synthesis of stress proteins and antioxidants at cellular level in many crop plants have been reported for all these stresses (Cushman and Bohnert 2000; Bartels and Sunkar 2005; Chinnusamy et al. 2005; Bartels and Hussain 2008; Hussain et al. 2011, 2012).

Efforts to enhance plant performance under abiotic stress have met with little success due to an incomplete understanding of the stress tolerance mechanisms in plants. Several groups have studied the complex mechanisms involved in stress response and adaptation—such as stress signalling, readjusting metabolism and reprogramming gene expression—to improve stress tolerance (Ma et al. 2011; Marasco et al. 2016; Thao and Tran 2016). However, for agricultural and environmental sustainability, the development of stress-tolerant plants is a viable approach, which seems imperative to fulfil the growing demands for quality food (Castiglioni et al. 2008). However, current breeding methods lack suitable methodological means to manage crop production in stress environment (Ashraf and Foolad 2007). In contrast, genetic engineering of crop plants can play a major role in developing stress-tolerant plants. Combining transgenic approaches with current breeding methods can be used to develop enhanced stress tolerance of crop plants (Capell et al. 2004). Current transgenic approaches aim to transfer to the target plant one or several different genes involved in several pathways including regulatory transcription factors, compatible solutes/osmoprotectants (proline, glycine betaine, polyamines) and proteins (LEA, heat shock, aquaporin) for generating stress-tolerant plants (Wang et al. 2003; Vinocur and Altman 2005; Valliyodan and Nguyen 2006; Bhatnagar-Mathur et al. 2007; Kathuria et al. 2007; Sreenivasulu et al. 2007; Marasco et al. 2016; Thao and Tran 2016). The bottleneck of transgenic approaches has been and continues to be the identification of key genes and their use in transgenic crops with improved stress tolerance without sacrificing yield (Bartels and Hussain 2008).

The last century has witnessed several significant, diverse and unexpected discoveries related to the plant-associated microbiome by molecular and omics tools combined with novel microscopic techniques (Mendes et al. 2011; Bulgarelli et al. 2012; Lundberg et al. 2012; Bhattacharyya et al. 2016; Berg et al. 2016; Timmusk et al. 2017). A wide range of agriculturally important microbiomes has been extensively exploited for increased growth and disease management in plants. It is expected that plant-associated beneficial microbiomes can significantly contribute to alleviating abiotic stresses using a variety of mechanisms (Hayat et al. 2010; Mapelli et al. 2013; Vejan et al. 2016). The sustainability of crop plants challenged by environmental stresses becomes more important and needs nonconventional solutions such as the use of microbiomes (Schaeppi and Bulgarelli 2015). Strengthening microbial traits beneficial to plants, the environment or both offers a promising avenue for the development of sustainable future agriculture. Microbial collection and utilisation can serve as a valuable tool and key determinants in managing plant health and productivity under an array of biotic and abiotic stresses (Celebi et al. 2010; Mengual et al. 2014; Rolli et al. 2015; Berg et al. 2016; Marasco et al. 2016). The identification, characterisation and utilisation of beneficial microbiomes which enhance abiotic stress tolerance in plants would help to sustain the next generation in agriculture worldwide (Jorquera et al. 2012; Nadeem et al. 2014). Diverse mechanisms which these microbes use to confer stress have been reviewed elsewhere (Lugtenberg and Kamilova 2009; Yang et al. 2009; Grover et al. 2010; Zelicourt et al. 2013; Nadeem et al. 2014). In this chapter, we will highlight advantages of the plant-associated microbiome approach, in particular, increasing

plant tolerance to different abiotic stresses, which pose a serious threat to global crop productivity.

## 2.2 Exploring the Plant-Associated Microbiome for Improving Abiotic Stress Tolerance in Plants

### 2.2.1 Drought Stress

Recent data have revealed that the plant-associated microbiome can influence several plant traits including growth and biotic and abiotic stress tolerance (Mendes et al. 2011; Lau and Lennon 2012; Marasco et al. 2012, 2013; Bainard et al. 2013; Sugiyama et al. 2013; Berg et al. 2014; Rolli et al. 2015; Panke-Buisse et al. 2015). Drought stress represents a serious threat to agriculture worldwide. The contribution of the plant-associated microbiome to plant adaptation to drought stress is poorly understood. Rolli et al. (2015) tested in vivo eight isolates, over 510 strains, for their ability to support grapevine and *Arabidopsis* growth under drought stress; they demonstrated that plant growth-promoting activity is stress dependent and not a per se feature of the strains. Similarly, a pepper plant inoculated with selected strains under irrigated and drought conditions exhibited a stress-dependent plant growth-promoting pattern by increasing shoot and leaf biomass and shoot length and enhancing photosynthesis in drought-challenged grapevine, with a profound positive effect on drought-sensitive rootstock. Overall, these results indicate that the tested bacteria significantly contributed to plant adaptation to drought via stress-induced plant growth promotion. Certain PGPR, such as *Achromobacter piechaudii* ARV8, enhance drought stress tolerance in pepper and tomato by 1-aminocyclopropane-1-carboxylate (ACC) deaminase. The mechanisms which render drought stress tolerance in plants remain largely speculative. However, it is possible that the breakdown of plant ACC by bacterial ACC will inhibit ethylene synthesis which ultimately reduces plant stress and enables normal plant growth (Glick et al. 2007; Arshad et al. 2008; Duan et al. 2009; Yang et al. 2009). Another study highlighted the positive influence of bacterial priming on wheat seedlings under drought stress (Timmusk et al. 2014, 2017); this method increased plant biomass by 78% and improved photosynthesis fivefold under severe drought. Furthermore, three of seven volatiles from bacterially primed drought-stressed wheat seedlings have been used to assess plant performance under drought stress in early stages of stress development (Timmusk et al. 2014). Wheat inoculated with *Burkholderia phytofirmans* PsJN had an increased photosynthesis, better water use efficiency, and high chlorophyll content and grain yield than the control under water deficit in the field conditions (Naveed et al. 2014a). Similarly, maize inoculated with both *B. phytofirmans* and *Enterobacter* sp. FD17 performed better compared to controls (Naveed et al. 2014b). Three bacterial strains isolated from extremely water-stressed soil, viz. *Pseudomonas putida*, *Pseudomonas* sp. and *Bacillus megaterium*, stimulated plant

growth under drought conditions (Marulanda et al. 2009). Similarly, Sandhya et al. (2009) reported that inoculation of sunflower seedlings with *Pseudomonas* sp. strain GAP-45 enhanced survival and plant biomass under drought stress. It is possible that inoculated bacteria can efficiently colonise the root-adhering soil resulting in stable soil aggregates and ultimately enhanced stress tolerance. In a similar study, maize plants inoculated with *Pseudomonas* strain GAP-45 showed increased compatible solutes and antioxidant under water deficit conditions (Sandhya et al. 2010). In tomato, grapevine, olive and pepper plants, microbes isolated from roots of plants growing under extreme dry conditions improved the growth of another host species under similar growth conditions (Marasco et al. 2013). This stress-resistance solution strategy has the potential to save time, effort and costs. Kohler et al. (2008) inoculated lettuce with *Pseudomonas mendocina* and arbuscular mycorrhizal fungi (*Glomus intraradices* or *G. mosseae*) which resulted in antioxidant catalase activity under severe drought conditions pointing to possible use of microbes in alleviation of oxidative stress. Similarly, the accumulation of 14-3-3 protein along with glutathione and ascorbate has played important roles in maintaining plant metabolic functions and conferring protection under drought conditions. Lavender plants inoculated with *Glomus intraradices* and *Glomus* sp. strain accumulated these compounds and exhibited high drought tolerance by improving water contents, root biomass and N and P contents (Porcel et al. 2006; Marulanda et al. 2007). Plant growth-promoting bacteria have improved growth in sunflower, pea, sorghum, tomato, pepper, rice, common bean and lettuce under drought conditions (Alami et al. 2000; Creus et al. 2004; Mayak et al. 2004; Dodd et al. 2005; Cho et al. 2006; Marquez et al. 2007; Figueiredo et al. 2008; Arshad et al. 2008; Kohler et al. 2008; Sandhya et al. 2009; Kim et al. 2013; Perez-Montano et al. 2014; Marasco et al. 2016).

### 2.2.2 Salinity Stress

Extreme climatic conditions and the misuse of agricultural land over the past few decades have led to high salinity, which is a limiting factor to global crop productivity (Wicke et al. 2011). Several approaches, in addition to molecular technologies, have been implicated for addressing salinity such as soil reclamation and management practices. However, these methods are expensive and not always practical and sustainable for controlling salinity. In contrast, the use of natural plant growth-promoting bacteria as inoculants for crop plants growing on salt-affected land is gaining momentum (Tiwari et al. 2011; Shabala et al. 2013; Paul and Lade 2014; Qin et al. 2014; Ruiz et al. 2015). A growing body of research has shown that microbial communities increase productivity and improve plant health following adverse environmental stresses (Berendsen et al. 2012; Zuppinger-Dingley et al. 2014; Sloan and Lebeis 2015).

It is proposed that microbes inhabiting sites exposed to frequent stress conditions develop adaptive tolerant traits and are potential candidates as plant growth

promoters under stress conditions (Yang et al. 2016b). Halotolerant microbes thrive under soil salinity stress and express traits to help plants to survive high salinity. Upadhyay et al. (2009) isolated 130 rhizobacterial strains from wheat plants sown under saline conditions and showed that 24 isolates tolerated relatively high levels (8%) of NaCl stress. The authors attributed this tolerance to different genes, hormones and proteins such as *nifH*, indole-3-acetic acid (IAA), siderophores and gibberellin. Similarly, halotolerant bacterial strains isolated from Korea enhanced plant growth under salinity stress by reducing ethylene production via ACC deaminase activity (Siddikee et al. 2010). The availability of new halotolerant diazotrophic bacteria, with traits such as IAA, phosphorus solubilisation and ACC deaminase activity, isolated from roots of *Salicornia brachiata* (extreme halophyte) represents other potential candidates (Jha et al. 2012). Arora et al. (2014) demonstrated that 17 of 20 bacteria isolated from halophytes and other salt-tolerant plant species happily grew in 7.5% NaCl in culture and two of these grew in 10% NaCl. Plant-associated microbiomes have improved growth in canola, pepper, tomato, bean, wheat and lettuce (Yildirim and Taylor 2005; Barassi et al. 2006; Upadhyay et al. 2009; Ali et al. 2014; Leite et al. 2014; Zhao et al. 2016).

There are reports that the involvement of arbuscular mycorrhizal fungi (AMF) has increased host plant tolerance to salinity stress. Co-inoculation of AMF plants with *Glomus* sp. has increased growth in saline soils possibly due to increased phosphate and decreased Na<sup>+</sup> concentration in shoots compared to uninoculated controls (Giri and Mukerji 2004). AMF treatment has improved salt tolerance in maize, mungbean, clover, tomato and cucumber due to P acquisition, improved osmoregulation by proline accumulation and reduced NaCl concentration (Jindal et al. 1993; Al-Karaki et al. 2001; Feng et al. 2002; Ben Khaled et al. 2003; Grover et al. 2010; Velazquez-Hernandez et al. 2011). However, research on the ability of bacterial and AM species to induce protective proteins and osmoprotectants is needed. The above reports suggest that plants under stress may readily recruit diverse bacterial strains with broad implications for plants grown under salt stress. This phenomenon has been collectively termed induced systemic tolerance (Yang et al. 2009).

### 2.2.3 *Extreme Temperature Stress (Low and High)*

The Intergovernmental Panel on Climate Change (IPCC: 2007) reported that global temperatures are predicted to increase by 1.8–3.6 °C by the end of this century due to climate changes. High temperatures are a major obstacle in crop production as well as microbial colonisation, which results in major cellular damage such as protein degradation and aggregation. All organisms respond to high temperature by producing a specific group of polypeptides known as heat shock proteins (HSPs). Stress adaptation in microorganisms represents a complex multilevel regulatory process that may involve several genes (Srivastava et al. 2008), such that microbes develop different adaptation strategies to combat the stress. Certain microbes perform better at high temperatures, and these microbes may be important for crop

plants under high temperature (Yang et al. 2016a). Srivastava et al. (2008) isolated *P. putida* strain NBR10987, which exhibited thermotolerance in the drought-stressed rhizosphere of chickpea and was attributed to the stress sigma factor  $\delta_s$  overexpression and thick biofilm formation. Certain bacterial strains combat stress by producing exopolysaccharides (EPS) which possess unique water holding and cementing characteristics and play vital roles in stress tolerance by water retention and biofilm formation. Sorghum seedlings inoculated with *Pseudomonas* AKM-P6 strain had improved tolerance to heat stress through enhanced physiological and metabolic performance indicating a unique interaction of inducible proteins in heat tolerance using microbes (Ali et al. 2009).

Low-temperature stress is an important limiting factor to crop productivity because it adversely affects plant growth and development. Grapevines inoculated with *B. phytofirmans* PsJN increased tolerance to low nonfreezing temperatures and resistance to grey mould. Similarly, endophyte inoculation resulted in higher and faster accumulation of stress-related proteins and metabolites, which lead to more effective resistance to low temperature, indicating a positive priming effect on plants (Theocharis et al. 2012). Similarly, Barka et al. (2006) noted that grapevine roots inoculated with *B. phytofirmans* PsJN resulted in better root growth, higher plant biomass and increased physiological activity at low temperature (4 °C). Further analysis revealed that bacterised plantlets significantly increased proline, starch and phenolic levels compared with uninoculated control plantlets, which enhanced grapevine plantlets to tolerate low temperature. Low temperature usually inhibits soybean symbiotic activities (nodule infection and nitrogen fixation), but inoculation of soybean with both *Bradyrhizobium japonicum* and *Serratia proteamaculans* resulted in faster growth at 15 °C (Zhang et al. 1995, 1996). Switchgrass inoculated with *B. phytofirmans* PsJN had enhanced growth under glasshouse conditions (Kim et al. 2012). According to Mishra et al. (2009), wheat seedlings inoculated with *Pseudomonas* sp. strain PPERs23 highly improved root and shoot lengths resulting in dry root/shoot biomass and total phenolics, chlorophyll and amino acid contents. Furthermore, inoculated wheat seedlings had enhanced physiologically available iron, anthocyanins, proline, protein and relative water contents and reduced  $\text{Na}^+/\text{K}^+$  ratio and electrolyte leakage, resulting in enhanced cold tolerance (Mishra et al. 2009). Many studies have explored several bacterial strains for enhanced cold stress tolerance in plants (Selvakumar et al. 2008a, b, 2009, 2010a, b). It is apparent from the above studies that *B. phytofirmans* PsJN has a wide host spectrum, which includes grapevines, maize, soybean, sorghum, wheat and switchgrass with promising results under different abiotic stresses.

### 2.2.4 Heavy Metal Stress

Heavy metal contamination due to increased industrialisation has recently received attention because heavy metals cannot be degraded (Kidd et al. 2009; Ma et al. 2011; Rajkumar et al. 2012). Various physiochemical and biological

techniques developed to remove contaminants have failed due to being expensive, environmentally unsafe and unacceptable by the public (Boopathy 2000; Vidali 2001; Doble and Kumar 2005). Phytoremediation using plants to eliminate soil contaminants is cost-effective and environmentally friendly with high public acceptance technology (Hadi and Bano 2010; Beskoski et al. 2011; Fester et al. 2014; Arslan et al. 2015). Another viable and promising alternative is the application of plant-associated microbiomes whereby microbial activities in the rhizosphere increase plant metal uptake by several ways like altering mobility and bioavailability of metals (Rajkumar et al. 2010; Ma et al. 2011; Aafi et al. 2012; Yang et al. 2012). Several plant growth-promoting substances, such as plant growth hormones (IAA, cytokinins and gibberellins), siderophores and ACC deaminase, are produced by plant-associated microbiomes to improve plant growth in heavy metal-contaminated soils (Babu and Reddy 2011; Luo et al. 2011, 2012; Wang et al. 2011; Bisht et al. 2014; Kukla et al. 2014; Waqas et al. 2015; Ijaz et al. 2016; Santoyo et al. 2016). High soil contamination could reduce plant growth including root growth and expansion mainly due to oxidative stress, which limits the rate of phytoremediation (Gerhardt et al. 2009; Hu et al. 2016). The lack of nutrients and reduced microbial density also limit phytoremediation (Gerhardt et al. 2009). Common heavy metals include manganese (Mn), cadmium (Cd), lead (Pb), chromium (Cr), zinc (Zn), aluminium (Al) and copper (Cu). Some metalloids also show toxicity such as antimony (Sb) and arsenic (As) (Durube et al. 2007; Park 2010; Wuana and Okieimen 2011; Pandey 2012).

Rhizosphere bacteria deserves close attention among the microbes involved in phytoremediation (Arora et al. 2005) as these can directly improve process efficiency by altering soil pH and oxidation/reduction reactions (Khan et al. 2009; Kidd et al. 2009; Uroz et al. 2009; Wenzel 2009; Rajkumar et al. 2010; Afzal et al. 2011; Ma et al. 2011). *Microbacterium* sp. G16 and *Pseudomonas fluorescens* G10 significantly increased the solubility of lead (Pb) in *Brassica napus* compared with uninoculated controls and were mainly attributed to IAA, siderophores, ACC deaminase and phosphate solubilisation (Sheng et al. 2008). Similarly, co-inoculation of *Zea mays* with *Azotobacter chroococcum* or *Rhizobium leguminosarum* improved plant growth and biomass in Pb-contaminated soil (Hadi and Bano 2010; Hussain et al. 2013). Several endophyte genera like *Bacillus* sp., *Serratia*, *Enterobacter*, *Burkholderia* sp., *Agrobacterium* and others have increased the phytoremediation rate and biomass production in metal-contaminated soils (Wani et al. 2008; Kumar et al. 2009; Mastretta et al. 2009; Luo et al. 2012; Nonnoi et al. 2012; Afzal et al. 2014; Glick 2014, 2015; Hardoim et al. 2015; Ijaz et al. 2016; Singh et al. 2016; Zheng et al. 2016; Feng et al. 2017).

Moreover, mycorrhizal fungi play significant role in phytoremediation due to hyperaccumulators of heavy metals with heavy metal tolerance (Zarei et al. 2010; Orłowska et al. 2011).



### 2.2.5 Nutrient Deficiency Stresses

Beneficial microbes can be used to enhance the sustainability of current agricultural systems. Members of the rhizosphere microbiome are playing significant roles in plant nutrient management (Adhya et al. 2015). Well-known examples include nitrogen-fixing rhizobia and mycorrhizal fungi involved in phosphorus uptake (Hawkins et al. 2000; Richardson et al. 2009; Miransari 2011). Plants usually get nutrients from the rhizosphere and from the phyllosphere (Turner et al. 2013). Plant nutrient management requires optimal use of soil, water, atmospheric factors and NPK fertilisers (Miao et al. 2011), along with a beneficial microbiome to help improve nutrient use efficiency. A plethora of research is available on the usefulness of symbionts such as mycorrhizal fungi for channelling nutrients and minerals such as phosphorus, water and other essential macro- and microelements from soil to growing plants (Gianinazzi et al. 2010; Adeleke et al. 2012; Johnson and Graham 2013; Salvioli et al. 2016) and for modelling and improved soil structure and aggregates (Miller and Jastrow 2000) in crops such as cereals, pulses, fruits and oilseeds to meet their nutritional requirements (Jeffries and Barea 2001; Johnson et al. 2012; Salvioli and Bonfante 2013). Apart from *Rhizobium* and *Bradyrhizobium*, several other bacterial endophytes have been reported to establish symbiosis with plants for bioavailable nitrogen fixation in unspecialised host tissues even in the absence of nodules (Zehr et al. 2003; Gaby and Buckley 2011; Guimaraes et al. 2012; Santi et al. 2013). For example, *Cyanobacteria* are in symbiotic association with a range of plants from different clads, such as gunnera, cycads and lichens, and form heterocysts suitable for biological nitrogen fixation (BNF) with nitrogenase (Berman-Frank et al. 2003; Santi et al. 2013). Another study revealed that 74 and 77 of 102 bacteria associated with sugarcane roots successfully fix nitrogen and solubilise phosphorus, respectively (Leite et al. 2014). Similarly, analysis of the cowpea rhizosphere using 16S rRNA sequencing revealed that *Burkholderia* and *Achromobacter* species along with *Rhizobium* and *Bradyrhizobium* can nodulate cowpea and support BNF (Guimaraes et al. 2012). Some reports have indicated that algal genera such as *Anabaena*, *Aphanocapsa* and *Phormidium* can fix atmospheric nitrogen in paddy fields (Shridhar 2012; Hasan 2013).

Considering the importance of essential plant nutrients, it would be logical to discover bacterial species that affect macro- and micronutrient uptake in plant species under different deficient and toxic conditions (Leveau et al. 2010; Mapelli et al. 2012). Microbiomes can also facilitate the uptake of several trace elements such as iron (Zhang et al. 2009a, b; Marschner et al. 2011; Shirley et al. 2011) and calcium (Lee et al. 2010). Collectively, members of the plant microbiome play essential roles in degrading organic compounds which are required not only for their survival but also for plant growth in nutrient-poor soils (Leveau et al. 2010; Mapelli et al. 2012; Turner et al. 2013; Bhattacharyya et al. 2015).

### **2.2.6 Establishing a Functional Plant Microbiome in Agriculture**

It is important to understand microbe–microbe and plant–microbe interactions to generate/develop a beneficial soil microbiome. However, it is unknown whether such beneficial microbial communities would be stable in agricultural soils. Under natural conditions, two factors, i.e. soil type and plant roots, usually determine the composition and association of microbial communities with plant roots. The influence of soil type and plant roots on the rhizomicrobiome has been reviewed extensively (Berg and Smalla 2009; Philippot et al. 2013; Bulgarelli et al. 2013, 2015; Lareen et al. 2016). Physiochemical properties of soils have a direct influence on specific microbes and plant root exudates (Hamel et al. 2005; Dumbrell et al. 2010) whereby soil type mostly determines the soil biome and plant root exudates tend to establish a favourable rhizobiome. Collectively, soil type and plant species are important players which determine the composition of rhizosphere and recruit diverse microbial communities for the establishment of a favourable rhizobiome to increase crop yields and reduce losses to biotic and abiotic stresses (Bulgarelli et al. 2012, 2015; Peiffer et al. 2013; Philippot et al. 2013; Schlaeppi et al. 2014; Tkacz et al. 2015; Lebeis et al. 2015; Yeoh et al. 2016). These factors significantly contribute to the selective enrichment of beneficial microbes in the rhizobiome, which may help to identify heritable traits to improve plant health and productivity (Tkacz and Poole 2015). Consequently, this mechanistic approach has the potential to create a microbiome that can improve plant traits following species or genotype-driven selection in the composition of rhizobiome structure as revealed in maize, barley, potato, *Arabidopsis*, *Brassica rapa* and sugarcane (Rasche et al. 2006; Bulgarelli et al. 2012, 2015; Lundberg et al. 2012; Peiffer et al. 2013; Lebeis et al. 2015; Panke-Buisse et al. 2015; Yeoh et al. 2016).

## **2.3 Customised Adjustment of the Plant Microbiome: A Revolution in Progress**

Recent studies have highlighted the potential of customised or synthetic microbial communities to reap maximum benefits in crop production in terms of plant growth, yield and resistance to abiotic and biotic challenges (Mendes et al. 2011; Lau and Lennon 2012; Berendsen et al. 2012; Bainard et al. 2013; Bulgarelli et al. 2015; Lebeis 2015). Using the plant microbiome in crop production is not a new concept. The plant microbiome is a key determinant of plant health and productivity (Berendsen et al. 2012; Ziegler et al. 2013; Chaparro et al. 2014) and has received considerable attention in recent years (Lebeis et al. 2012; Bulgarelli et al. 2013). Manipulation of the plant microbiome can increase tolerance to biotic and abiotic stresses (Barka et al. 2006; Jha et al. 2012; Jorquera et al. 2012; Berg et al. 2013), increase agricultural production (Yang et al. 2009; Bakker et al. 2012; Turner et al. 2013), reduce chemical

inputs (Adesemoye et al. 2009; Adesemoye and Egamberdieva 2013; Jha et al. 2015) and reduce greenhouse gas emissions (Singh et al. 2010), resulting in more sustainable agricultural productivity. This is vital for sustaining the ever-growing global population. Furthermore, identified naturally occurring beneficial microbes are now being used in agriculture for significant improvement of crop plant performance (Zolla et al. 2013; Nadeem et al. 2014).

Despite the fact that the richness of species and diversity of microbial communities recruited in plant microbiomes are mostly unknown, assembling a specific trait-associated microbiome is critical into new plant hosts for the development of improved production systems. There is ample evidence that many molecules, microbes, plant species and mechanisms support the establishment of a rhizobiome with the potential to play significant roles in enhanced plant productivity in the future (Berendsen et al. 2012; Miller and Oldroyd 2012; Bakker et al. 2013; Oldroyd 2013; Qiu et al. 2014; Zhang et al. 2015). Some strategies have been worked out to reshape the rhizobiome and redirect microbial activity by bringing about change in root exudates using conventional and modern breeding approaches (Bakker et al. 2012). Efforts to develop PGPB and/or PGPF consortia by mimicking or partially reconstructing the plant microbiome/rhizobiome are in progress. Tomato plants inoculated with these PGP consortia (*Bacillus amyloliquefaciens* IN937a, *Bacillus pumilus* T4, AMF *Glomus intraradices*) in greenhouse conditions resulted in full yield with 30% fewer inputs (Adesemoye et al. 2009). Similarly, Atieno et al. (2012) reported increased biomass in two soybean cultivars after inoculation with *B. japonicum* 532C, RCR3407 and *B. subtilis* MIB600. In another study, co-inoculation of soybean with *B. japonicum* E109 and *Bacillus amyloliquefaciens* LL2012 indirectly improved soybean nodulation efficiency. Phytohormones produced by *Bacillus amyloliquefaciens* LL2012 helped to improve nodulation efficiency in *B. japonicum* E109 (Masciarelli et al. 2014). Mengual et al. (2014) employed a consortium of *B. megaterium*, *Enterobacter* sp., *Bacillus thuringiensis* and *Bacillus* sp. along with composted sugar beet residues on *Lavandula dentata* L. to help restore soils by increasing phosphorus bioavailability, soil nitrogen fixation and foliar NPK contents. Hence, the success of a rational design of a plant microbiome depends on several factors including smart integration of all players in the system. In this context, genetic diversity of the local soil microbiome can help to improve and stabilise the effects of microbial inoculants. Therefore, it is recommended that microbiome profiling be implemented for the determination, monitoring and targeted application of microbial inoculants under field conditions.

## 2.4 Conclusion and Future Perspectives

The growing body of research relating to the plant microbiome is bringing into focus its importance for plant health, growth and productivity. While most research findings are preliminary, intensive research is required to unravel the intricacies of this highly complex phenomenon to understand microbe community dynamics and

communication to exploit this largely untapped resource. Opportunities for exploiting the plant microbiome for raising crops are numerous and diverse. Plant-associated microbes would play a significant role in stress management in plants and provide excellent models for understanding stress tolerance mechanisms. Another strategy would be to generate transgenic plants harbouring beneficial genes from microbes, similar to transgenic plants harbouring ACC deaminase gene from bacteria. However, considering the timeframe and other issues involved in the development of transgenic plants, it would be more cost-effective and environmentally friendly to develop easy-to-handle microbial inoculants to alleviate abiotic stresses.

While several studies have shown significant improvements to stress tolerance using PGPM to crops under field conditions (Celebi et al. 2010; Mengual et al. 2014; Rolli et al. 2015), others have revealed inconsistent or negative results (Nadeem et al. 2014). One promising strategy for a stable beneficial outcome is to use a microbial consortium in the field to tailor the rhizobiome to respond to specific biotic and abiotic stresses without compromising plant growth and productivity (Trabelsi and Mhamdi 2013). Therefore, the mechanisms by which microbes confer stress tolerance to their hosts need further research to develop suitable microbial consortia for ready-to-use formulations under different biotic and abiotic stresses. However, this will require concerted efforts at interdisciplinary levels from microbiologists, molecular biologists, plant physiologists, plant breeders, soil scientists and agronomists. Recent developments in this field provide opportunities to understand how the microbe–microbe and plant–microbe interactions mediate the functional relationship between different players.

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