

Microbe-Mediated Tolerance in Plants Against Biotic and Abiotic Stresses

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7.1 Introduction: A Glimpse of Plant Productivity Under Environmental Stresses

A plethora of data suggested that significant climatic changes have welcomed the twenty-first century (Kumar and Verma 2018). Many research reports have pointed that environmental stresses constitute significant threat to future food security around the globe (Battisti and Naylor 2009) with the ever-increasing world population which would be at least nine billion by 2050 (Singh et al. 2011; Hussain et al. 2012, 2014). Current estimates have revealed that over 800 million people are experiencing food shortage and malnutrition worldwide. Agricultural sustainability is threatened by a multitude of factors including unpredictable climate variation, population and reduction in soil health (Cushman and Bohnert 2000). Global food production is limited by several reasons, primarily by extreme climatic stresses which cause 20–30% vield losses globally (Savary et al. 2012; Dikilitas et al. 2018). Similarly, diseases can significantly affect virtually all crop plants with the potential to reduce both yield and quality, and an estimated 20-40% global harvest is lost to diseases alone (Savary et al. 2012; Dikilitas et al. 2018). Indiscriminate and widespread use of pesticides and weedicides for disease eradication has negatively impacted the environment; therefore, development of resistant/tolerant crop plant is human friendly and an effective strategy to enhance productivity (Hussain et al. 2011), which causes major loss of beneficial microbial diversity from the soil (Kumar and Verma 2018). However, benefits of green revolution are now over

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mainly due to uncontrolled world population, narrow range of germplasm resources, lengthy breeding process and extreme climatic stresses (Hussain et al. 2012).

Therefore, it is well conceived that conventional breeding alone cannot keep pace with future food needs of the world population. Selective breeding and genetic modifications have played a promising role for the improvement of all major crop plants in order to meet the human food requirements (Capell et al. 2004; Bartels and Hussain 2008; Hussain et al. 2012). Combining general breeding schemes and current molecular strategies have been wisely utilized to develop crop plant with enhanced stress tolerance (Capell et al. 2004; Hussain et al. 2012). Plants overexpressing several different genes have shown improved tolerance to different environmental stresses and promotion of plant health and yield (Roy et al. 2014; Hussain et al. 2016) under both laboratory and greenhouse conditions. Currently, plant engineering approaches have been designed to transfer important genes playing significant role (synthesis of osmolytes, antioxidants and stress-related proteins such as Lea, HSP) in biochemical pathways (Wang et al. 2003; Vinocur and Altman 2005; Valliyodan and Nyugen 2006; Sreenivasulu et al. 2007; Kathuria et al. 2007; Bartels and Hussain 2008; Hussain et al. 2012, 2014; Marasco et al. 2016; Thao and Tran 2016). However, identification and isolation of key genes and acceptance of transgenic products at community level pose the main bottleneck of this strategy. Similarly, several research reports have revealed that crop health, adaptation and tolerance to various stresses are not only linked to the genome of the plant but evidence suggest that these might also be intricately influenced by multiple environmental factors (Munns and Gilliham 2015; Tiwari et al. 2017). Potentially, plant-associated microbes represent possible strategies to decrease the negative effects of chemical fertilizers, pesticides, herbicides and abiotic stresses.

There is now overwhelming research evidence that plant microbiome including symbiotic associations through numerous mechanisms help (Vandenkoornhuyse et al. 2015) significantly to sustainable plant yield management strategies (Berendsen et al. 2012; Mendes et al. 2013; Wagg et al. 2014; Mueller and Sachs 2015; Gouda et al. 2018). Emerging plant-associated microbiome-based technologies have received attention which offer potential increase in plant growth and development, nutrient acquisition, health, enhanced biotic/abiotic stress tolerance and host immune regulation leading to enhanced crop yields (Mayak et al. 2004; Glick et al. 2007; Marulanda et al. 2009; Yang et al. 2009; Berendsen et al. 2012; Bakker et al. 2013; Mendes et al. 2013; Turner et al. 2013; Berg et al. 2014; Lakshmanan et al. 2014: Ngumbi and Kloepper 2016). Several researchers have reported the beneficial impact of integration and utilization of mycorrhizal fungi (Rodriguez and Redman 2008; Bonfante and Anca 2009; Singh et al. 2011; Aroca and Ruiz-Lozan 2012; Azcon et al. 2013), bacteria for atmospheric nitrogen fixation (Lugtenberg and Kamilova 2009) and PGPR (Kloepper et al. 2004; Mayak et al. 2004; Glick et al. 2007; Kim et al. 2009; Glick 2012; Pineda et al. 2013; Chauhan et al. 2015) on crop plants for enhanced tolerance to various biotic and abiotic stresses (Timmusk and Wagner 1999; Mayak et al. 2004; Dimpka et al. 2009; Sandhya et al. 2009; Grover et al. 2011; Kasim et al. 2013; Coleman-Derr and Tringe 2014; Nadeem et al. 2014; Hussain et al. 2018). However, this should be noted that this is a vast but still largely

an untrapped area which calls for more systematic and intensive research efforts for completely realizing its potential in increasing yields in a changing climate (Hussain et al. 2018).

Similarly, very little is known of how plants strategically prioritize their requirements, such as investing energy resources into defence at the expense of other vital functions, to modify the internal system to enhance tolerance to different environmental stresses (Schenk et al. 2012a, b). With the availability of high-throughput molecular tools, several diverse and unexpected research discoveries have revealed the underlying responses of plant adaptation to stress tolerance using plant-related microbiome (Mendes et al. 2011; Bulgarelli et al. 2012; Lundberg et al. 2012; Berg et al. 2016; Timmusk et al. 2017; White et al. 2017; Hussain et al. 2018). Although several different PGPRs have helped plants in mitigating various stresses, the mechanisms involved remain mostly unexplored. Meanwhile, several plant-associated microbes have been characterized for improved growth, development and stress management which significantly contributed to our understanding to design strategies for the use of these PGPRs (Hayat et al. 2010; Lakshmanan et al. 2012; Mapelli et al. 2013; Vejan et al. 2016). Integration and exploitation of plant-associated microbes hold great promise which can play important roles in improving plant health, growth and development (Rolli et al. 2015; Wallenstein 2017), by managing plant tolerance to various environmental stresses (Mapelli et al. 2013; Vejan et al. 2016) and enhancing plant productivity for food security (Lugtenberg and Kamilova 2009; Celebi et al. 2010; Mengual et al. 2014; Rolli et al. 2015; Berg et al. 2016; Marasco et al. 2016). Overall, sustainable agriculture challenged by abiotic stresses needs nonconventional strategies like the use of plant-related microbiomes (Schaeppi and Bulgarelli 2015; Bulgarelli et al. 2015). Taken together, the identification, characterization and use of microbes which enhance plant abiotic stress tolerance by diverse mechanisms would help to sustain agriculture in the future (Jorquera et al. 2012; Bhardwaj et al. 2014; Nadeem et al. 2014).

Innumerable reviews have highlighted several plant traits which are used by microbes for developing stress tolerance (Rosenblueth and Martinez-Romero 2006; Hardoim et al. 2008; Lugtenberg and Kamilova 2009; Rodriguez et al. 2009; Yang et al. 2009; Grover et al. 2011; Friesen et al. 2011; Singh et al. 2011; de Zelicourt et al. 2013; Bulgarelli et al. 2013; Nadeem et al. 2014; Qiu et al. 2014; Wellenstein 2017). It is the need of the time to join hands for exploring microbial traits beneficial to both plants and the environment because this strategy has a huge potential for sustainable agriculture in the future (Lally et al. 2017). This chapter highlights the advantages of the plant-related microbial community approach, especially increasing plant tolerance to various environmental stresses which constitute a serious threat to food security around the globe.

7.2 Plants and Their Microbial Environment: Exploring Plant Microbiome Diversity

It is well established that virtually the whole plant is populated by an uncountable number of microorganisms (Quiza et al. 2015) and has been classified mainly on the basis of plant part they colonized such as endophyte (present inside the plant part), epiphyte (aerial plant part like leaves and twigs) and rhizosphere (on the roots under the soil) (Ali et al. 2012; Penuelas and Terradas 2014; Bai et al. 2015; Santoyo et al. 2016). Under natural conditions, plants establish multiple mutually beneficial interactions with these microbes (Schenk et al. 2012a, b) for improvement of plant characters such as seed germination and vigour, growth and development, plant health (environmental stress tolerance) and crop productivity (Mendes et al. 2013; Quiza et al. 2015).

Despite their potential utility for plant productivity and other traits, progress in identification, characterization and utilization of these extremely complex microbial communities has been hampered mainly due to technological limitations (Hussain et al. 2018). Historic documents that report the use of microbes in agriculture date back to 1800, and rhizobium bacteria were first recommended for use in legume crops to enhance growth, development and uptake of nutrients from the soil (Jones et al. 2014). Initial efforts to use microbes have focused on exploring the functional roles of few members of plant-associated microbial groups which met with limited success largely because of the fact that most microbes are not culturable (Amann et al. 1995; Andreote et al. 2009; Schenk et al. 2012a, b; Balbontin et al. 2014; Larimer et al. 2014; van der Heijden et al. 2015). However, several individual microbes helping in improving plant health, growth and development, such as atmospheric nitrogen-fixing microbes (Olivares et al. 2013; de Bruijin 2015) and mycorrhizal fungi (Smith and Read 2008; Chagnon et al. 2013; van der Heijden et al. 2015), have been successfully characterized. On the other hand, concerted efforts to study microbial system recognize the utility of saprophytic or symbiotic interactions with plants ranging from beneficial to pathogenic (Mendes et al. 2013; Ouiza et al. 2015). It is further noticed that pathogenic microbes despite their detrimental effects may use plant-derived organic substances for growth, hence may indirectly play a functional role in nutrient cycling and modifying plant environment (Schenk et al. 2012a, b), while beneficial microbes promote plant growth by improving nutrient acquisition (Mishra et al. 2012; Santoyo et al. 2012; Bulgarelli et al. 2013; Santoyo et al. 2016; Calvo et al. 2017), synthesizing growth regulators (Glick 2012) and suppressing different stresses by biosynthesis of pathogen-inhibiting compounds (Glick 2012; Santoyo et al. 2012; Martinez-Absalon et al. 2014; Hernandez-Leon et al. 2015) and other mechanisms (Smith and Read 2008; Berg 2009; Schenk et al. 2012a, b; Chagnon et al., 2013; Olivares et al., 2013; de Bruijin 2015; van der Heijden et al. 2015; Orozco-Mosqueda et al. 2018).

Lederberg and McCray (2001) used for the first time plant microbiome representing microbes occupying plants with beneficial outcomes such as plant health and plant productivity. Technically speaking, the term microbiome has been broadly applied to microbial community composition and their interaction (Beneficial or pathogenic) with specific hosts or environment (Mendes et al. 2011; Lakshmanan et al. 2012; Boon et al. 2014; Ofek et al. 2014; Panke-Buisse et al. 2015; Lareen et al. 2016). The current focus of plant-microbe interaction research involves three aspects. These include microbes involved in nutrient acquisition by symbiosis between plants and arbuscular mycorrhizal fungi (AMF) (Smith and Smith 2011; Sessitsch and Mitter 2014) and atmospheric nitrogen-fixing rhizobia (Oldroyd et al. 2011; Lundberg et al. 2012), microbes improving plant tolerance to various stresses (Doornbos et al. 2011; Ferrara et al. 2012; Marasco et al. 2012; Kavamura et al. 2013; Zolla et al. 2013) and disease-causing microbes (Kachroo and Robin 2013; Mendes et al. 2011, 2013; Wirthmueller et al. 2013; Quecine et al. 2014). Previous research efforts considered the plant-microbe association initially in relation to plant diseases (Mendes et al. 2013). However, advanced research in this field demonstrated that a huge amount of microbes are involved in beneficial functions to plants (Mendes et al., 2013; Bhardwaj et al. 2014; Santoyo et al. 2016, 2017). However, apart from well-known mutualistic interactions among plant and microbes, other characterized or uncharacterized useful microbes often are not included in field-based plant production strategies.

7.3 Shaping Plant Microbiome: Technical Progress

Extensive research efforts have attributed several functions to plant-associated microbes. However, these microbial communities, comprising of several diverse microbial strains, represent an extremely complex and dynamic fraction of plant microbiome (Farrar et al. 2014; Mueller and Sachs 2015). Therefore, research studies have partitioned plant microbiome and targeted different fractions separately. A plant environment has been divided into three major components such as rhizosphere, endosphere and phyllosphere based on the microbial presence where these can live and develop (Hardoim et al. 2008; Hirsch and Mauchline 2012; Haney and Ausubel 2015; Haney et al. 2015; Nelson 2018; Orozco-Mosqueda et al. 2018). In fact, new developments and technical advances resulted in enhanced research in this unexplored field (Porras-Alfaro and Bayman 2011; Berendsen et al. 2012; Bakker et al. 2013; Bulgarelli et al. 2013; Philippot et al. 2013; Schlaeppi et al. 2013; Turner et al. 2013; Guttman et al. 2014; Berg et al. 2014; Knief 2014; Lebeis 2014; Schaeppi and Bulgarelli 2015; Santoyo et al. 2017). Keeping in view the plant nutrition, it is important to characterize microbes that are involved in nutrient recycling and uptake for plants under various extreme soil situations (Leveau et al. 2010; Mapelli et al. 2012; Tajini et al. 2012; Krey et al. 2013; Lally et al. 2017). The scientific literature provides several examples of well-characterized microbes like bacteria (PGPR) and fungi (PGPF) with both antagonistic and synergistic interactions which contribute to enrich plant growth (Verma et al. 2010; Murray 2011; Rout and Callaway 2012; Bhardwaj et al. 2014). Furthermore, these microbes produce different phytohormones like auxin and siderophores (Khalid et al. 2004; Cassan et al. 2009; Abbasi et al. 2011; Filippi et al. 2011; Yu et al. 2011) which play critical roles in host nutrition, growth and health and provide protection to plants from biotic and abiotic

stresses (Berendsen et al., 2012; Bakker et al. 2013; Bulgarelli et al. 2013; Mendes et al. 2013; Rastogi et al. 2013; Berg et al. 2014; Lakshmanan et al. 2014; Prashar et al. 2014; Bell et al. 2014; Mueller and Sachs 2015; Wallenstein 2017; Hussain et al. 2018).

Well-explored systems for mutualistic interactions include *Rhizobia* spp. and arbuscular mycorrhizae (AM) that exchange plant carbohydrates and important amino acids (Moe 2013) for fixing atmospheric nitrogen and insoluble phosphate bioavailability (Spaink 2000, Luvizotto et al. 2010; Leite et al. 2014) for plants. Microbes inhabiting in rhizosphere also help plants by providing many trace elements such as iron (Zhang et al. 2009; Marschner et al. 2011; Shirley et al. 2011) and calcium (Lee et al. 2010). Likewise, plant microbiome also plays essential functions in degrading non-bioavailable organic compounds required not only for microbes own survival but also for plant's vital functions like growth and development in nutrient-poor and nutrient-contaminated soils (Leveau et al. 2010; Mapelli et al. 2012; Turner et al. 2013; Bhattacharyya et al. 2015). Taken together, shaping and strengthening plant microbiome will have a significant and positive effect on sustainable agriculture in the future (Mitter et al. 2017).

Many reports have designated microbiome as the second genome, while some other researchers treated microbiome as a holobiont to demonstrate the critical roles played by microbial communities associated with plants (Zilber-Rosenberg and Rosenberg 2008; Grice and Segre 2012; Agler et al. 2016; Clavel et al. 2016; Paredes and Lebeis 2016; Zmora et al. 2016). Currently, an effort to explore plant microbiome comprising of several different microbial communities is largely hindered due to several factors, mainly because of methodological constraints (Bulgarelli et al. 2013). Therefore, development and validation of protocols is essential for exploring the whole plant microbiome diversity (Calvo et al. 2017; Hussain et al. 2018). With the advent of next-generation sequencing, selection under artificial ecosystem and other molecular techniques like florescent tagging especially for studying unculturable species (endophytes) are now a gradually routine in research (Swenson et al. 2000; Bulgarelli et al. 2012; Hernández-Salmerón et al. 2016). A huge body of data are accumulated as a result of these technological advancements in the field (Martinez-Absalon et al. 2014; Hernandez-Leon et al. 2015; Hernández-Salmerón et al. 2016; Orozco-Mosqueda et al. 2018). On the other hand, integration of different computational models is also essential for dissection of this complex and dynamic hidden treasure (Farrar et al. 2014; Mendes and Raaijmakers 2015) with the aim of searching for new beneficial microbes and effectively manipulating plant microbiome for increasing plant productivity (Hussain et al. 2018).

Taken together, investment in research aimed at exploring microbial traits that are beneficial to plants and environment constitutes an ideal approach towards nextgeneration sustainable plant productivity (Schaeppi and Bulgarelli 2015; Goswami et al. 2016; Khan et al. 2016; Compant et al. 2016). Despite the above-mentioned facts, assessing and accessing the microbiome of important local plants and native habitats represents a yet unexplored field to exploit synergism between microbes and plant traits in modern agriculture. However, understanding microbe-microbe dynamics is critical to identify key factors that help to shape and establish microbial communities. Therefore, information extracted from the indigenous plant-associated microbiome constitutes an integral part for designing/engineering a microbiome to be used for sustaining agriculture in the future.

7.4 Reinstating a Functional Plant Microbiome: Smart Solution to a Complex Problem

Researchers are suffering from information gap which is negatively affecting the ability to manage and manipulate the rhizosphere microbiome (rhizobiome) while the strategy to use microbes for increasing plant productivity is not new. Current data reveal the potential of engineering rhizosphere microbiome which offers a unique opportunity to achieve maximum benefits in plant production despite different challenges (Bakker et al. 2012; Berendsen et al. 2012; Bainard et al. 2013; Qiu et al. 2014; Bulgarelli et al. 2015; Yadav et al. 2015). It is noteworthy that rhizosphere represents an extremely competitive environment for microbes, while these microbes play a critical role in plant growth and productivity (Berendsen et al. 2012; Ziegler et al. 2013; Chaparro et al. 2014). Therefore, plenty of progress has been achieved in engineering sustainable plant productivity through engaging microbial communities (Bakker et al. 2012; Lebeis et al. 2012; Bulgarelli et al. 2013; Su et al. 2015).

Huge research endeavours have resulted in isolation, identification and characterization of hundreds of bacterial/fungal strains with known beneficial effects and are currently being utilized in developing microbial consortia (Patel and Sinha 2011; Kim and Timmusk 2013; Dong and Zhang 2014). Several researches have demonstrated the importance of microbial consortia approach which has contributed significantly towards increased agricultural production with less chemical inputs, reduced emission of greenhouse gases and high tolerance to different stresses (Barka et al. 2006; Adesemoye et al. 2009; Yang et al. 2009; Singh et al. 2010; Bakker et al. 2012; Jha et al. 2012; Jorquera et al. 2012; Adesemoye and Egamberdieva 2013; Berg et al. 2013; Turner et al. 2013; Egamberdieva et al. 2017). This is crucial for keeping pace with the rapidly growing world population (Zolla et al. 2013; Nadeem et al. 2014). Another way to extract maximum benefits out of this approach is to exploit knowledge from microbes with publically available genome sequences and synthetically develop a microbiome that can help to improve plant traits as reported for a few important plants including wheat, rice, Arabidopsis, maize, Brassica rapa, potato, barley, sugarcane and rice (Rasche et al. 2006; Bulgarelli et al. 2013, 2015; Lundberg et al. 2012; Peiffer et al. 2013; Lebeis et al. 2015; Panke-Buisse et al. 2015; Raajimakers 2015; Yeoh et al. 2016). Furthermore, it is expected that microbes in their natural habitats have the potential to contribute significantly in the improvement of crop productivity under environmental challenges.

Consequently, research reports have demonstrated the potential of these microbes which have positively impacted many plant traits including growth, development and productivity under various environmental stresses (Bhattacharya and Jha 2012; Goh et al. 2013; Coleman-Derr and Tringe 2014; Schlaeppi et al. 2014; Tkacz et al. 2015;

Lebeis et al. 2015; Yeoh et al. 2016). It is extremely vital to understand thoroughly both way interactions (microbe-microbe and plant-microbe) for the successful engineering of beneficial soil microbiome (rhizosphere). Similarly, available data have revealed the genetic and molecular basis of these interactions (Bloemberg and Lugtenberg 2001; Wang et al. 2005; Lim and Kim 2013; Timmusk et al. 2014; Vargas et al. 2014; Kim et al. 2015; Busby et al. 2017; Lally et al. 2017; Iannucci et al. 2017), and this information can be used for genetically modifying either partner using genetic engineering protocols for enhanced plant productivity. However, it is worthy to note that microbiome interactions are dynamic and complex depending on several factors including soil biochemistry, plant genotypes and external environment which heavily influence the composition and colonization of several bacterial communities with plant roots. Additionally, these factors involved are in crucial functions such as triggering plant-genotype-specific physiological responses, resulting in different exudation patterns in roots (Hamel et al. 2005; Bais et al. 2006; Hartmann et al. 2009; Dumbrell et al. 2010; Oburger et al. 2013). As a result of increased interest in this research, these factors (different soil types, different native plant species and microbial communication) have been extensively reviewed on the rhizomicrobiome (Tarkka et al. 2008; Berg and Smalla 2009; De-la-Pena et al. 2012; Philippot et al. 2013; Bulgarelli et al. 2013, 2015; Lareen et al. 2016). A broader picture of these interactions revealed that these factors played significant roles in the selective enrichment of microbial communities in rhizosphere microbiome (Berendsen et al. 2012; Miller and Oldroyd 2012; Schenk et al. 2012a, b; Sugiyama and Yazaki 2012; Morel and Castro-Sowinski 2013; Oldroyd 2013), by coordinating the establishment and recruitment of diverse bacterial communities for engineering a specific rhizobiome with positive impact on plant productivity (Bulgarelli et al. 2013, 2015; Peiffer et al. 2013; Philippot et al. 2013; Schlaeppi et al. 2014; Su et al. 2015; Tkacz et al. 2015; Lebeis et al. 2015; Yadav et al. 2015; Yeoh et al. 2016).

Multiple studies have reported positive interaction between specific plants and belowground soil-dwelling microbial communities (Micallef et al. 2009; Inceoglu et al. 2013). This clearly highlighted the fact that plant root exudates play critical roles in identification and recruitment of specific microbes which result in changes in composition and diversity of microbes in the rhizosphere (Haichar et al. 2008; Badri et al. 2009, 2013; Moe 2013; Weston and Mathesius 2013). Based on the above discussion, some useful approaches have been devised to reinstate the rootassociated microbiome and re-route microbial activity by enhancing root exudates through more systematic breeding efforts (Bakker et al. 2012; Huang et al. 2014a, b; Reyes-Darias et al. 2015; Yuan et al. 2015; Corral-Lugo et al. 2016; Webb et al. 2016). Root exudates not only serve as food for root-associated microbes but also act as a signal molecule for the initiation of diverse physical and chemical interactions around plant roots (Berendsen et al. 2012; Hawes et al. 2012; Baetz and Martinoia 2013; Chaparro et al. 2013; Vacheron et al. 2013; Huang et al. 2014a, b; Reyes-Darias et al. 2015; Yuan et al. 2015; Corral-Lugo et al. 2016; Webb et al. 2016). Significant growing evidence suggested that progress has been made towards the development of PGPR and/or PGPF consortia using knowledge derived from plant ecosystem for mimicking or partially reconstructing the plant microbiome/

rhizobiome (Adesemoye et al. 2009; Atieno et al. 2012; Masciarelli et al. 2014; Mengual et al. 2014). It is worthy to note that the success of a tailored design of a plant microbiome depends on several factors including identification of the genetic components of the microbiome control and smart integration of critical players in the system. Similarly, it is speculated that changes in root system architecture (RSA) through breeding techniques may help in the recruitment of beneficial plant-specific rhizobiome. However, more systematic and detailed investigations will be required to study these interactions.

7.5 Plant Microbiome and Biotic Stress

Pathogen-free plants present the important and most ignored trait of the plantassociated microbes. Different pathogens especially viruses, bacteria and fungi are responsible for biotic stresses, and crop productivity is significantly reduced ($\geq 15\%$) by these stresses worldwide (Strange and Scott 2005; Haggag et al. 2015). Stress (both biotic and abiotic) is a major challenge to agricultural yield, and huge economic losses urgently require the development of resistant crop plants. Gusain et al. (2015) have revealed adverse impacts of biotic stress on plants in detail. Several microorganisms belonging to different genera (Burkholderia, Pseudomonas, Bacillus, Azotobacter and Azospirillum) are the major group of PGPR that are involved in eliciting induced systemic resistance (ISR) response in plants (Alstrom 1991; Van Peer et al. 1991; Wei et al. 1991; Riggs et al. 2001; Shaharoona et al. 2006; Lebeis 2015; Tiwari et al. 2017; Hussain et al. 2018). Similarly, some microbial species belonging to a symbiotic group of rhizobacteria are also involved directly or indirectly with different PGPRs and can evoke ISR in plants (Elbadry et al. 2006). Inoculation of plants or their parts with PGPR which exhibits resistance to different pathogens of biotic stress (Ngumbi and Kloepper 2016). Zamioudis et al. (2013) demonstrated that P. fluorescens WCS417 is able to promote important plant traits in A. thaliana. This report further revealed that the improvement of different traits occurs via an auxin-dependent and JA-independent mechanism resulting in ISR (Zamioudis et al., 2013). Thus, PGPR/PGPF interactions with their host plant revealed the power to unravel mechanisms which act as the prime barrier of plant defence (Badri et al. 2009; De-la-Pena et al. 2012; Dangl et al. 2013). In fact, PGPR and PGPF are also involved in induction of immune "priming", by secreting signalling compounds which do not result in direct immune activation, but just activate and govern the immune responses against different pathogens (Conrath 2006; Badri et al. 2009; De-la-Pena et al. 2012; Dangl et al. 2013), even in distal tissues.

The defensive capacity of plants represents a physiological condition which is evoked by different signalling molecules known as elicitors. Thus, elicitors are molecules that induce different plant immune responses. Several reports have described two mechanisms which constitute plant immune responses include induced systemic resistance (ISR) and systemic acquired resistance (SAR). Thus, rhizobacteria infection triggers induced systemic resistance (ISR; Ortiz-Castro et al. 2008), while arbuscular mycorrhizae (AM) can produce mycorrhizal-induced resistance (MIR; Pozo and Azcon-Aguilar, 2007; Zamioudis and Pieterse, 2012) suggesting that microbial exploitation is common which gives strength to plants to face pathogen attacks. PGPR-mediated ISR requires interaction between bacteria and plant root which renders plants resistance to some pathogenic microorganisms by the activation of plant natural defences (Raaijmakers et al. 1995; Lugtenberg and Kamilova 2009; Prathap and Ranjitha 2015). ISR is triggered by the interaction of usually non-pathogenic microorganisms in roots and further extending to shoots (Ramos-Solano et al. 2008). Activation of ISR primes the plants to respond faster and stronger against the attack of several pathogenic species including bacteria, protists, nematodes, virus, fungi, viroids and insects (Verhagen et al. 2004; Conrath 2006; Berendsen et al. 2012; Walters et al. 2013).

Therefore, it is known that ISR is a non-specific defence reaction, but it provides strength to the plants to fight different plant diseases (Kamal et al. 2014). Several reports have shown that root inoculation with several different PGPRs rendered the entire plant tolerant to lethal pathogens (Schuhegger et al. 2006; Choudhary et al. 2007; Tarkka et al. 2008). Hence, research has proved ISR as one of the PGPR-mediated mechanisms which reduce plant disease by bringing about critical changes in the host plants at physical and biochemical levels (Pieterse et al. 2002). Since then, the PGPR-elicited ISR is regarded as vital biocontrol mechanism and is under intensive research in plants such as maize, bean, *Arabidopsis*, wheat, tomato, rice, tobacco, radish, soybean, cucumber and carnation (Bevivino et al. 1998; van Loon et al. 1998; Ruy et al. 2004; Compant et al. 2005; Han et al. 2005; Landa et al. 2006; Rashedul et al. 2009; Senthilkumar et al. 2009; Filippi et al. 2011; Neeraj 2011; Pereira et al. 2011; Mavrodi et al. 2012; Martins et al. 2013). However, understanding the metabolic pathway participating in this method is not yet complete (Ramos Solano et al. 2008), which necessitates multidisciplinary intensive research efforts.

On the other hand, it is established that phytohormones such as ethylene and jasmonic acid behave as a signalling agent in ISR, and plant defence response is dependent on these molecules (van Loon 2007). In contrast to the above-mentioned two phytohormones, salicylic acid (SA) acts as a key determinant in SAR. However, a study has shown some overlap between ISR and SAR in some cases (Lopez-Baena et al. 2009). In fact, well-known biotic elicitors are cell wall polysaccharides, along with some others including different phytohormones and signalling molecules (Shuhegge et al. 2006; van Loon 2007; Ramos Solano et al. 2008; Berg 2009; Fouzia et al. 2015; Kanchiswamy et al. 2015; Ulloa-Ogaz et al. 2015; Wang et al. 2015; Meena et al. 2016; Goswami et al. 2016; Islam et al. 2016; Ramadan et al. 2016; Raza et al. 2016a, b; Santoro et al. 2016; Sharifi and Ryu 2016; Gouda et al. 2018).

7.6 Microbiome for Abiotic Stress Alleviation in Crop Plants

Virtually, stress is defined as any factor which negatively affects plant health, growth, and productivity (Foyer et al. 2016). Due to climate change, plants are frequently subjected to various environmental stresses (Hussain et al. 2018). Because expanding the agricultural land is near impossible, increasing demands for food place a serious threat to current crop production systems. Hence, a scientifically improved farming method is required for keeping pace with unprecedented demands and maintaining the soil fertility under intense farming. Currently, sustainable agriculture is based on several improved agricultural techniques (Kumar 2016; Mus et al. 2016; Passari et al. 2016; Perez et al. 2016; Shrestha 2016; Suhag 2016; Ubertino et al. 2016). On the other hand, heavy investment in stress-related research has increased our understanding of the molecular mechanisms implicated in environmental stress tolerance (Tripathi et al. 2015, 2016, 2017; Pontigo et al. 2017; Singh et al. 2017). Therefore, in the development of stress tolerance coupled with better nutritional value, crop plants significantly contributed towards sustainable agricultural development. Engaging beneficial microbes is one possible way to address stress tolerance in plants (Vejan et al. 2016). Following this, recent research has shown that a strain of Bacillus amyloliquefaciens living in rice rhizosphere is able to reduce various abiotic stresses via cross-talk with pathways regulating stresses and phytohormones (Tiwari et al. 2017). Similarly, it is known that several soil-inhibiting microbes such as Paecilomyces formosus can help reduce plant stress caused by different factors especially heavy metals such as nickel (Bilal et al. 2017). The advantages of using root-associated microbes include their capacity to alleviate negative effects of different abiotic stresses in a wide range of crop plants (Timmusk and Wagner 1999; Mayak et al., 2004; Sandhya et al. 2010; Kasim et al. 2013; Tkacz and Poole 2015) and also their capability to simultaneously tackle several biotic and/or abiotic stresses (Ramegowda et al. 2013; Sharma and Ghosh 2017). Consequently, these beneficial microorganisms are under intensive research as one of the most climate-friendly agents for safe crop management practices.

Currently, plant rhizobiome has attracted extreme attention for tackling plant stresses and enhancing plant yields by several mechanisms to fuel new innovations in sustainable crop production as part of the next green revolution (Marulanda et al. 2009; Yang et al. 2009; Mendes et al. 2011; Bulgarelli et al. 2012; Lau and Lennon 2012; Lundberg et al. 2012; Marasco et al. 2012, 2013; Bainard et al. 2013; Sugiyama et al. 2013; Berg et al. 2014; Bonilla et al. 2015; Panke-Buisse et al. 2015; Prosser 2015; Rolli et al. 2015; Jez et al. 2016; Premachandra et al. 2016; Fierer 2017; Goodrich et al. 2017; Hussain et al. 2018). In fact, isolation and characterization of microbes constitute an integral part to identify beneficial microbes. Extensively researched microbial communities include the symbiotic bacteria (Spaink 2000; Lugtenberg and Kamilova 2009; Luvizotto et al. 2010; Leite et al. 2014), mycorrhizal fungi (Khan et al. 2008; Ruiz-Lozano et al. 2011; Sheng et al. 2011; Singh et al. 2011; Aroca and Ruíz-Lozan 2012; Bashan et al. 2012; Azcon et al. 2013) and PGP rhizobacteria (Kloepper et al. 2004; Glick 2012; Rout and Callaway 2012; Bhardwaj et al. 2014; Gabriela et al. 2015). PGPR contains a huge range of well-studied rhizosphere bacteria (Gupta et al. 2015) which are able to produce several different enzymes and metabolites that play critical roles in host nutrition, growth and health and protect plants from environmental stresses (Dimpka et al. 2009; Kim et al. 2009; Yang et al. 2009; Grover et al. 2011; Timmusk and Nevo 2011; Berendsen et al. 2012; Bulgarelli et al. 2013; Mendes et al. 2013; Berg et al. 2014; Prashar et al. 2014; Rastogi et al. 2013; Ding et al. 2013; Kim et al. 2013; Pineda et al. 2013; Timmusk

et al. 2014; Chauhan et al. 2015; Lidbury et al. 2016; Ofaim et al. 2017; Sanchez-Canizares et al. 2017; Syed Ab Rahman et al. 2018). Currently, efforts have been directed at exploring and utilizing naturally occurring, soil-inhibiting microbes for enhanced plant yield under changing climate (Yang et al. 2009; Nadeem et al. 2014; Bhattacharyya et al. 2016; Bashiardes et al. 2018; Jansson and Hofmockel 2018; Yuan et al. 2018). Convincing evidence has witnessed beneficial effects of plantassociated microbes, and this partnership has significantly contributed to establishing smart solutions under nutrient deficiency and mitigating other stresses using diverse mechanisms (Hayat et al. 2010; Mapelli et al. 2013; Vejan et al. 2016).

7.7 Drought Stress

Drought is one of the serious agricultural problems worldwide resulting in reduced growth, development and plant yield (Vinocur and Altman 2005; Hussain et al. 2012, 2014; Naveed et al. 2014a, b; Tiwari et al. 2016). It is also noteworthy that the frequency and intensity of water deficit are expected to increase in the future due to rapid environmental deterioration. Recent investigation revealed that different microbes have the power to support vital plant traits such as plant growth and development through interaction with plant root system under drought stress (Hussain et al. 2012; Huang et al. 2014a, b) to ensure tolerance to environmental stresses (Mendes et al. 2011; Ngumbi 2011; Lakshmanan et al. 2012; Marasco et al. 2012, 2013; Bainard et al. 2013; Sugiyama et al. 2013; Berg et al. 2014; Edwards et al. 2015; Rolli et al. 2015; Panke-Buisse et al. 2015; Hussain et al. 2018). Several approaches have been chalked out and applied to address the drought-associated negative impact on crop productivity. However, use of plant-associated microbes offers a sustainable solution to abiotic stresses by diverse mechanisms (Faroog et al. 2009; Budak et al. 2013; Cooper et al. 2014; Hussain et al. 2014; Porcel et al. 2014). Kang et al. (2014) reported that inoculated soybean with Pseudomonas putida H-2-3 mitigated drought impact by decreasing antioxidant activity, producing different osmolytes, enhancing chlorophyll contents, improving shoot length and productivity. Similarly, two maize cultivars inoculated with Burkholderia phytofirmans strain PsJN showed 70% and 58% increase in root biomass and with Enterobacter sp. strain FD, 47% and 40%, respectively, under water deficit (Naveed et al. 2014a, b). Similarly, several other researchers reported a positive impact of these microbes on roots in different plants like maize and wheat (Yasmin et al. 2013; Timmusk et al. 2013, 2014). Inoculated plants showed promising results compared to noninoculated control plants under low water condition which led to the conclusion that an increase in root biomass resulted in enhanced water uptake by plants under water deficit stress. Timmusk et al. (2014) have also demonstrated the positive effects on shoot biomass in corn and wheat under drought when inoculated with PGPR.

Crop plants treated with PGPR demonstrated several adjustments at molecular, biochemical and physiological levels for improving several traits such as growth and development, nutrient and water use efficiency, high chlorophyll content for increased photosynthesis, biocontrol activity and ultimately enhanced crop yield by bringing about alterations in root and shoot, phytohormonal activity, high relative water content, EPS production, osmotic adjustment due to osmolyte accumulation, ACC deaminase activity and antioxidant defence (Bano et al. 2013; Kasim et al. 2013; Marasco et al. 2013; Huang et al. 2014a, b; Naveed et al. 2014a, b; Naseem and Bano 2014; Sarma and Saikia 2014; Timmusk et al. 2014; Cohen et al. 2015; Fasciglione et al. 2015; Ortiz et al. 2015; Rolli et al. 2015; Ma et al. 2016a, b; Tiwari et al. 2016; Yang et al. 2016a). PGPR treatment has improved the growth of important crops like rice, wheat, sorghum, maize, sunflower, soybean, pea, tomato, lettuce and pepper under water deficit (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. 2003; Kohler et al. 2008; Sandhya et al. 2010; Castillo et al. 2013; Kasim et al. 2013; Kim et al. 2013; Lim and Kim 2013; Perez-Montano et al. 2014; Naseem and Bano 2014; Sarma and Saikia 2014; Timmusk et al. 2014, 2017; Marasco et al. 2016).

7.8 Salinity Stress

Salinity is a major environmental stress and globally challenging plant growth and productivity (Wicke et al. 2011; Hussain et al. 2014). Researchers have adopted several approaches for tackling salinity problem including agronomic practices, physiological adjustments and molecular (genetic) engineering. However, despite appreciated utility, these practices are not environmentally friendly and practically sustainable due to the incomplete understanding of stress tolerance mechanism and rapidly deteriorating climate. On the other hand, a growing evidence highlighted that different microbial communities improved plant health with enhanced productivity by altering the selectivity of Na⁺, K⁺ and Ca²⁺ and sustaining a higher K⁺/Na⁺ ratio in roots under high salinity stress (Barassi et al. 2006; Berendsen et al. 2012; Damodaran et al. 2013; Zuppinger-Dingley et al. 2014; Fasciglione et al. 2015; Sloan and Lebeis 2015; Bacilio et al. 2016; Bharti et al. 2016; Kasim et al. 2016; Mahmood et al. 2016; Sharma et al. 2016; Khan et al. 2017; Shahzad et al. 2017; Timmusk et al. 2017; de la Torre-Gonzalez et al. 2017). Consequently, engaging both PGPR and PGPF has demonstrated a promising success under salinity stress (Upadhyay et al. 2011; Shukla et al. 2012; Bharti et al. 2016; Yang et al. 2016b). Crop plants growing on salty soil which are inoculated with PGPR/PGPF performed better with optimal yield (Tiwari et al. 2011; Shabala et al. 2013; Paul and Lade 2014; Qin et al. 2014; Ruiz et al. 2015). Similarly, multiple reports have demonstrated practical utility of microbial communities where plants like rice, barley, wheat, canola, tomato, mung bean, maize, oat, lettuce and peanuts have developed significantly higher biomass in high salt condition (Mayak et al. 2004; Upadhyay et al. 2009; Ahmad et al. 2011; Jha et al. 2012; Shukla et al. 2012; Nautiyal et al. 2013; Ali et al. 2014; Chang et al. 2014; Jha and Subramanian 2014; Leite et al. 2014; Timmusk et al. 2014; Fasciglione et al. 2015; Suarez et al. 2015; Bharti et al. 2016; Mahmood et al. 2016; Sharma et al. 2016; Zhao et al. 2016).

It is well documented that microbes living in harsh environments modify their physiology accordingly and serve as potential candidates for enhancing plant growth and productivity under stress conditions (Rodriguez et al. 2008; Timmusk et al. 2014). Several researchers isolated bacterial strains from plant roots challenged with high salt stress. Researchers isolated 130 rhizobacterial strains from wheat roots facing salinity stress, and 24 out of 130 isolates showed good growth in culture at 8% of NaCl stress (Upadhyay et al. 2009; Siddikee et al. 2010; Upadhyay et al. 2011: Arora et al. 2014). Different PGPR strains mitigate stress using various mechanisms. For example, Korean halotolerant strain inoculation resulted in enhanced growth because bacterial ACC deaminase activity negatively affected ethylene production under stress (Siddikee et al. 2010). Wheat inoculated with EPSproducing PGPR demonstrated high biomass by binding with cations and zero negative effect on plants under salinity stress (Upadhyay et al. 2011; Vardharajula et al. 2011). A plethora of research has used several PGPR strains including Hartmannibactor diazotrophicus E19, Pseudomonas alcaligenes PsA15, Bacillus polymyxa BcP26, Mycobacterium phlei MbP18, P. fluorescens, P. aeruginosa, P. stutzeri and B. amyloliquefaciens that have been successfully utilized in different plant species for mitigating salinity stress (Egamberdiyeva 2007; Bano and Fatima 2009; Tank and Saraf 2010; Bal et al. 2013; Nautiyal et al. 2013; Suarez et al. 2015).

Plants inoculated with PGPF showed significant tolerance to high salinity condition (Giri and Mukerji 2004; Grover et al. 2011; Velazquez-Hernandez et al. 2011) due to diverse mechanisms like osmotic adjustment, root growth, increased phosphate and decreased Na⁺ concentration in shoots, improved photosystem II efficiency and antioxidant systems and reduced ROS compared to un-inoculated controls (Shukla et al. 2012; Navarro et al. 2014; Ruiz-Lozano et al. 2016). Therefore, maize, rice, cucumber, mung bean, clover, citrus and tomato have shown improved salt tolerance after PGPF treatment which could serve as potential tool for alleviating salt stress especially in stress-sensitive crop plants (Jindal et al. 1993; Al-Karaki et al. 2001; Feng et al. 2002; Ben Khaled et al. 2003; Yang et al. 2009; Grover et al. 2011; Velazquez-Hernandez et al. 2011; Shukla et al. 2012; Navarro et al. 2014; Ruiz-Lozano et al. 2016).

7.9 Heavy Metal Stress

Researchers have shown that industrialization leads to heavy metal accumulation with a huge impact on plant and human health (Qin et al., 2015; Wu et al., 2015). However, the heavy metal problem has received research priority around the globe in recent years due to non-degradable nature of these contaminants (Duruibe et al. 2007; Kidd et al. 2009; Ma et al. 2011; Rajkumar et al. 2012; Ma et al. 2016a, b). Apart from heavy metals, some metalloids such as antimony (Sb) and arsenic (As) are also contributing a huge toxicity (Duruibe et al. 2007; Park 2010; Wuana and Okieimen 2011; Pandey 2012). Heavy metals also constitute significant threat to agricultural productivity and soil health. Many biophysiochemical approaches adopted to reclaim contaminated soils have failed because

these were environmentally unsafe, deleterious to soil structure, and unacceptable to the community (Boopathy 2000; Vidali 2001; Doble and Kumar 2005; Glick 2010). Phytoremediation strategy uses different plants supported by microbial communities to clean up heavy metal contaminants in soil and is believed to be a sustainable and cost-effective technology with no negative impact on environment and accepted by the communities (Broos et al. 2004; Hadi and Bano 2010; Afzal et al. 2011; Beskoski et al. 2011; Chen et al. 2014; Fester et al. 2014; Arslan et al. 2017; Hussain et al. 2018). The only limitation of phytoremediation is that plants used for soil reclamation (heavy metals) suffer from negative effects on plant growth due to nutrient shortage and heavy metal-based oxidative stress (Gerhardt et al. 2009; Hu et al. 2016). However, microbe-assisted phytoremediation represents a novel and working alternative (Jamil et al. 2014), whereby microbial activities increase soil reclamation using several unique mechanisms such as efflux, volatilization, metal complexation and enzymatic detoxification (Rajkumar et al. 2010; Ma et al. 2011; Aafi et al. 2012; Yang et al. 2012; Fatnassi et al. 2015; Ghosh et al. 2015; Zhang et al. 2015; Kumar and Verma 2018). It is an established fact that microbes promote plant growth and development by restricting ethylene production and production of plant growth substances such as IAA, cytokinins and gibberellins, siderophores, EPS and ACC deaminase under different stresses including heavy metal stress (Ahmad et al. 2011; Babu and Reddy 2011; Luo et al. 2011, 2012; Wang et al. 2011; Verma et al. 2013; Bisht et al. 2014; Kukla et al. 2014; Waqas et al. 2015; Ijaz et al. 2016; Santoyo et al. 2016; Deng and Cao 2017).

Waqas et al. (2015) have mentioned a few PGPR genera among rhizosphere microbes which demand more intensive research because these can be actively involved in phytoremediation process. These microbes are able to enhance process efficiency by bringing changes in soil pH and other allied oxidation/reduction processes (Khan et al. 2009; Kidd et al. 2009; Uroz et al. 2009; Wenzel 2009; Rajkumar et al. 2010; Ma et al. 2011). Recently, it has been demonstrated that soybean inoculation with *Paecilomyces formosus* exhibited significantly improved growth in soils with Ni accumulation (Bilal et al. 2017).

Similarly, Jamil et al. (2014) reported the positive impact of *Bacillus licheniformis* strain NCCP-59 inoculation with rice, whereby rice seeds exhibited improved germination in Ni-accumulated soil compared to control plants, indicating the ability of *Bacillus licheniformis* strain NCCP-59 to confer protection against Ni toxicity. Recently, a huge data have demonstrated that common heavy metals that include mercury (Hg), manganese (Mn), chromium (Cr), arsenic (As), cadmium (Cd), lead (Pb), chromium (Cr), zinc (Zn), nickel (Ni), aluminium (Al) and copper (Cu) can be efficiently removed by microbes using a plethora of mechanisms in different crop plants such as rice, *Brassica*, maize, lettuce and others (Sheng et al. 2008; Hadi and Bano 2010; Mani et al. 2016; Jing et al. 2014; Adediran et al. 2015; Hristozkova et al. 2016; Mani et al. 2016; Stella et al. 2017; Hussain et al. 2018). A wide diversity of PGPRs including *Bacillus* sp., *Rhizobia, Serratia, Azospirillum, Enterobacter, Klebsiella, Burkholderia* sp. and *Agrobacterium* have efficiently improved the phytoremediation efficiency by enhancing biomass in heavily 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; Ghosh et al. 2015; Hardoim et al. 2015; Jha et al. 2015; Deng et al. 2016; Ijaz et al. 2016; Singh et al. 2016; Zheng et al. 2016; Feng et al. 2017).

7.10 Nutrient Deficiency Stress

Despite continuous depletion of soil fertility, soil microbes are playing a vital role in enhancing crop productivity in conventional agricultural production systems (Berendsen et al. 2012). Exploring and utilizing plant microbiome is one of the nonconventional solutions required for maintaining the sustainability of crop plants which are facing nutrient deficiency (Schaeppi and Bulgarelli 2015). The main challenge is the efficient monitoring of processes mediated by these microbes because global attention has been diverted towards their role in plant nutrition only recently (Lebeis et al. 2012; Bulgarelli et al. 2013; Turner et al. 2013; Wei et al. 2016). Plant symbiosis with microbes (rhizobia, bradyrhizobia and AMF) represents one of the widely researched plant-microbe interactions (Hawkins et al. 2000; Jefferies and Barea 2001; Richardson et al. 2009; Miransari 2011; Wu et al. 2016), where these microbes participate in crucial functions for maintaining adequate plant nutrient and high productivity by developing nitrogen-fixing nodules and mycorrhizal arbuscules, respectively (Adesemoye et al. 2009; Miao et al. 2011; Adesemoye and Egamberdieva 2013; Adhya et al. 2015).

Generally, rhizobial symbiosis only occurs in leguminous plants, while AMFbased symbiosis is widespread, and over 80% of land plants experience this symbiosis (Guimaraes et al. 2012; Oldroyd 2013; Hussain et al. 2018). It has been observed that apart from *Rhizobium* and *Bradyrhizobium*, several other bacterial endophytes establish symbiosis or symbiosis-like relationship with plants for bioavailable nitrogen fixation in unspecialized host tissues using nodule-less system (Zehr et al. 2003; Gaby and Buckley 2011; Guimaraes et al. 2012; Santi et al. 2013). *Cyanobacteria*, for example, establish symbiotic relationship with several plants and develop heterocysts instead of nodules which are suitable for BNF using nitrogenase (Berman-Frank et al. 2003; Santi et al. 2013). Leite et al. (2014) reported that sugarcane root-associated bacteria are helpful in fixing nitrogen and solubilizing phosphorus, respectively. Apart from the above reports, some algal genera such as *Anabaena*, *Aphanocapra* and *Phormidium* are also actively involved in fixing nitrogen in fieldgrown rice by some unknown mechanisms (Shridhar 2012; Hasan 2013).

Similarly, a recent work reported the benefits of mycorrhizal fungi-based symbiosis for making available nutrients and minerals such as phosphorous and essential minor elements (Hartmann et al. 2009; Gianinazzi et al. 2010; Tian et al. 2010; Adeleke et al. 2012; Jin et al. 2012; Carvalhais et al. 2013; Johnson and Graham 2013; Lareen et al. 2016; Salvioli et al. 2016) to many crop plants for meeting their nutritional requirements (Johnson et al. 2012; Philippot et al. 2013; Salvioli and Bonfante 2013; Schlaeppi et al. 2014). Furthermore, research reports also highlighted the significant role of AMF in improving soil structure and establishing

beneficial microbes (Bulgarelli et al. 2012; Peiffer et al. 2013; Dell Fabbro and Prati 2014; Tkacz et al. 2015; Wu et al. 2016). Recently, Symanczik et al. (2017) demonstrated that naranjilla (*Solanum quitoense*) inoculated with AMF showed improved plant growth and enhanced nutrition and soil water retention due to the successful establishment of AMF symbiosis which led to the high acquisition of phosphorous (up to 104%) compared to control plants. Furthermore, this study proved that highly diverse belowground systems like AMF play a significant role in maintaining soil structure and aggregation by hyphae and exudates which is essential for sustainable soil productivity (Van der Heijden et al. 2008; De Vries et al. 2013; Wagg et al. 2014). On the other hand, there are published reports revealing many non-AMF involved in AMF like symbiotic benefits to plants (Cai et al. 2014; Ghanem et al. 2014; Pandey et al. 2016).

Keeping the importance of nutrients in plant life, it would be logical to identify bacterial and AMF strains that effectively increase macro- and micronutrient uptake in plants under nutrient deficiency stress (Leveau et al. 2010; Mapelli et al. 2012; Pankaj et al. 2016; Wang et al. 2017). As a matter of fact, rhizospheric microbes can also help in the uptake of many trace elements such as iron and calcium (Zhang et al. 2009; Lee et al. 2010; Marschner et al. 2011; Shirley et al. 2011) from the soil with improved plant root system (Cummings and Orr 2010; Qiang et al. 2016). Taken together, it is safe to conclude that microbes residing in the rhizosphere are especially playing a vital role in degrading insoluble organic compounds which are not only required for their own life but also needed for proper plant growth under nutrient deficiency stress (Leveau et al. 2010; Mapelli et al. 2012; Turner et al. 2013; Bhattacharyya et al. 2015; Pankaj et al. 2016; Wang et al. 2017).

7.11 Extreme Temperature Stress

Rapid climate changes have increased the frequency of global temperature fluctuations. As a result of these changes, extreme temperatures (hot and cold) have now been treated as significant abiotic stress (Hussain et al. 2018; Kumar and Verma 2018). Reports have predicted that global temperatures will increase by 1.8–3.6 °C by the end of this century due to extreme changes (International Panel on Climate Change (IPCC 2007)). High temperatures are not only considered a major obstacle in crop growth and productivity but also negatively impact microbial colonization (Carson et al. 2010). Both plants and microbes respond to high temperature by producing heat shock proteins (HSPs) which help to avoid major cellular damage such as protein degradation and aggregation (Rodell et al. 2009; Alam et al. 2017). Stress adaptation in microbes constitutes a complex regulatory mechanism that may comprise of many gene expressions (Srivastava et al. 2008), helping microbes in developing strategies to mitigate the stress (Kumar and Verma 2018; Yang et al. 2016a).

As have been mentioned, high soil temperature significantly affects the performance of plant-associated microbes. However, several microbes have been isolated from hot environments, and these microbes performed significantly under heat stress. And based on observation, these microbes may be suitable candidates to use with crop plants under high temperature. In a study, wheat cultivars Olivin and Sids1 were treated with Bacillus amyloliauefaciens UCMB5113 or Azospirillum brasilense NO40, and young seedlings were tested for effect of short-term heat stress (Abd El-Daim et al. 2014). Few stress-associated genes also showed raised transcripts in leaves of control plants. However, such genes exhibited much lower expression in plants inoculated with microbes compared to control plants (Abd El-Daim et al. 2014). Similarly, low reactive oxygen species production was observed with non-significant changes in metabolome in wheat seedling treated with bacteria under high temperature. Certain microbes mitigate heat stress by exopolysaccharide (EPS) synthesis. EPS has the ability to hold water and has cementing characteristics which lead to confer stress tolerance mainly by biofilm synthesis traits (Hussain et al. 2018). Pseudomonas putida strain NBR10987 was isolated from chickpea rhizosphere under drought. Inoculated chickpea plants exhibited thermotolerance. Detailed investigations showed that thermotolerance in chickpea was due to stress sigma factor (δ s) overexpression as well as thick biofilm synthesis (Srivastava et al. 2008). Similarly, inoculation of sorghum seedlings with two Pseudomonas strains AKM-P6 and NBR10987 improved thermotolerance manifested by better physiological and metabolic performance through diverse mechanisms (Redman et al. 2002; Ali et al. 2009; Grover et al. 2011). McLellan et al. (2007) noticed induction of small heat shock HSP101 and HSP70 proteins and enhanced heat tolerance in Arabidopsis when inoculated with fungus Paraphaeosphaeria quadriseptata.

Plants primed with microbes adapted for low temperature show high growth and development under cold stress. Therefore, researchers used microbes to mitigate negative effects of low temperature stress. Various bacterial strains have been used to enhance cold stress tolerance in plants (Selvakumar et al. 2008a, b, 2009, 2010a, b). Several low temperature-adapted bacterial strains such as *Brevundimonas terrae*, Pseudomonas cedrina, and Arthrobacter nicotianae have demonstrated multifunctional plant growth-promoting attributes (Yadav et al. 2014). Similarly, B. phytofirmans PsJN conferred not only high stress tolerance to low non-freezing temperatures but also grapevine plants showed resistance to grey mold (Meena et al. 2015). Barka et al. (2006) used Burkholderia phytofirmans PsJN to inoculate grapevine roots and concluded that inoculated plants physiologically performed better as manifested by their fast root growth and high plant biomass at low temperature (4 °C). Theocharis et al. (2012) showed positive priming effect of endophyte on plant at low temperature mainly due to high accumulation of several stress proteins. It is known that soybean symbiotic activities are inhibited by low temperature but soybean seedlings inoculated with both Bradyrhizobium japonicum and Serratia proteamaculans responded to symbiosis at low temperature (15 °C) and showed higher growth (Zhang et al. 1995, 1996). Mishra et al. (2009) noted that wheat seedlings primed with Pseudomonas sp. strain PPERs23 exhibited higher root/shoot ratio with increased dry root/shoot biomass, and other physiological traits such as increased iron, anthocyanins, proline, protein and relative water contents and reduced Na⁺/K⁺ ratio and electrolyte leakage also contributed to enhanced cold tolerance (Mishra et al. 2009). The above-mentioned studies clearly highlighted the importance of cold-adapted microbes like *Burkholderia phytofirmans* PsJN inoculated in plant species such as grapevines, maize, soybean, sorghum, wheat and switch grass that seems to be promising agents for low-temperature stress tolerance (Kim et al. 2012).

7.12 Future Perspective

Feeding the growing population requires high and stable yields using smart crop production technologies. The current agriculture in developing countries apparently relied on the cultivation of high-yield, moderately stress-tolerant varieties further fuelled by agrochemicals. It is not surprising that abiotic stresses, especially high temperature, drought and salinity, are considered by researchers as the most significant threats to agriculture (Trabelsi and Mhamdi 2013; Busby et al. 2017). Given this, we have to either develop stress-tolerant crop plants or look for alternative and more realistic agricultural practices (Bulgarelli et al. 2012; Mengual et al. 2014). Developing more sustainable solutions to agricultural problems seems logical under rapidly changing global climate and uncontrolled human growth (Hussain et al. 2014). Opportunities for exploiting the plant-associated microbes for raising successful crops are uncountable and diverse which can play a promising role for effectively tackling stresses in sustainable next-generation agriculture (Vandenkoornhuyse et al. 2015; Hussain et al. 2018).

The development and integration of smart agricultural tools and practices will depend on the successful use of all players in the system. Moderate success has been achieved towards the development of model host-microbiome systems for poplar, rice, sorghum, maize, miscanthus, tomato and Medicago truncatula (Johnston-Monje and Raizada 2011; Sessitsch et al. 2011; Knief et al. 2012; Peiffer et al. 2013; Ramond et al. 2013; Spence et al. 2014; Edwards et al. 2015; Hacquard and Schadt 2015; Lakshmanan 2015; Tian et al. 2015; Li et al. 2016; Hussain et al. 2018). However, great variation and success depend on many factors including the individual plant species, genotype, native soil microbiota, microbiome and interplay between these players with their specific traits that interact with each other under given climatic conditions. Under such circumstances, it is recommended that established microbiomes are most likely suitable candidates for generating diverse but functionally variable associations to select on a trial basis (Mueller and Sachs 2015). Hence, novel methods to utilize the plant-associated microbiome in next-generation agriculture could be helpful in enhancing crop productivity under different stresses (Bakker et al. 2012; Marasco et al. 2012; Prudent et al. 2015; Celebi et al. 2010; Mengual et al. 2014; Nadeem et al. 2014; Rolli et al. 2015). Novel versions of the most recent and advanced technologies especially omics approaches, methods and techniques are also offering its open-ended services for generation and interpretation of data from the field level to assess the real impacts of the inoculants on crop plants (Baetz and Martinoia 2013; White et al. 2017).

7.13 Conclusion

Several reports have shown promising results of significant stress tolerance in crop plants primed with plant growth-promoting microbes (PGPM) under field conditions with some negative findings as well. Application of microbial consortium represents one promising strategy for beneficial outcome in field-based agriculture to collectively respond to specific environmental stresses with no apparent impact on plant growth and productivity. Development and application of multispecies consortia have the potential to address inconsistency in performance (Hernández-Salmerón et al. 2016). Therefore, the mechanisms by which microbes confer stress tolerance to their hosts need further exploration to develop ideal microbial consortia for use under different stresses. Recent strategies like the use of omics approaches in this field provide powerful insights to understand how different players interact with each other and establish the functional relationship among microbe-microbe and plant-microbe under stress.

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