

Review Article

Phytomicrobiomes: A Tool for a Better Crop Management and Ensured Sustainability

Ankita Sharma*, Rehan and Reena Nair

Department of Horticulture (Vegetable Science), COA, Jawaharlal Nehru Krishi Vishwa Vidhyalaya, Jabalpur, Madhya Pradesh, India

**Corresponding author*

ABSTRACT

Extreme weather events affect agriculture as it disrupts the availability of food, decreasing the access to food thus affecting its nutritional quality. The demand for food is increasing with the increasing population. To satisfy the demands, crop productivity should be intensified by adopting climate-friendly practices to combat the climate change scenario. Plants host a diverse microbiota with a taxonomically structured microbial community that easily colonizes plant tissues. Plant associated microbiomes support the host by enhancing nutrient uptake, promoting growth, inducing stress tolerance and resistance to pathogens. Phytomicrobiomes are a reservoir for better crop management and the signals hold potential for climate change resilient agricultural practices. To devise strategies for improving crop health and enhancing sustainable production, a systematic phytomicrobiome driven approach need to be addressed to pave ways to tackle crop production and environmental factors. Plant microbiomes promote growth promoting attributes as it has a beneficial, neutral and negative relationship with partners and helps to attain the goal of sustainable agriculture. Plant microbiomes complex structure and chemical communication can be characterized through high-throughput technologies for signaling as these are a vital component of the environmental system. Plant associated microbes have an enormous potential to meet numerous challenges.

Keywords

Phytomicrobiomes,
Sustainability,
Agriculture,
Climate change,
Crop

Introduction

The phytomicrobiomes is a complex and relatively subtle relationship that the plants have with the microbes. Microbes are ubiquitous in nature. Higher plants and microbes have developed a functional mechanism for signaling to communicate among them through sensing by regulating the activity and attaining mutual benefit. This microbial community is associated with the roots and the shoots of the plants. A well-established communication elucidates microbial association, nitrogen-fixing

symbiosis and activates the pathogen response system in plants. Plant-microorganism union gives superior assistance to strengthen molecular, cellular and biochemical phenomenon of the plants to endure abiotic stress resistance and make them flexible to survive ecological difficulties. The plant-associated microbiota form an extensive network of interactions in epiphytic, endophytic and rhizospheric regions on the basis where the organisms colonize in plants and promote plant growth and development. The rhizosphere region in the soil is the hotspot of the microbes and

helps in maintaining the nutrient balance. The root-soil interface consists of a pool of microorganisms that acts as plant growth-promoting rhizobacteria (PGPR). Endophytic microbes dwell in the interior robust tissues of plants. They are endosymbionts that protect the plants by releasing certain compounds. The microorganisms not only confined to the root zone but also actively prevail in the aerial plant parts. Phyllosphere is the aerial parts of the plants colonized by microbes such as fungi, bacteria in a symbiotic relationship with the plants. It governs phytophysiology and promotes overall plant development. To determine the association between the phytomicrobiomes a comprehensive approach involving all the techniques of genomics, proteomics, metabolomics and transcriptomics including genetic engineering is required to know the signaling cascade.

Plant-associated microbiome is tissue-specific and its connection varies in intimacy to complete fusion such as in mitochondria and chloroplast (Backer *et al.*, 2018). Agricultural lands of the farmers are constantly getting degraded and losing their fertility due to extensive application of chemical fertilizers, insecticides, pesticides etc which can be rejuvenated by the use of plant microbiomes as they promote plant growth and can be used as biofertilizers or as bioinoculants as plants provide a diverse ecological niche for microbes. Plant associated microbes are the key factors in promoting root exudation for a better crop stand, superior quality and better yield of field and horticultural crops (Fig. 1–4 and Table 1).

Composition and biomass of phytomicrobiomes

Microorganisms are essential components of the higher plants which are intricate from

their host. Phytomicrobiomes function as holobionts, which is a combination of host and the resident microbes colonizing on it which collectively produces biomass and bulk of energy to the ecosystem and also as a metaorganism. (Vandenkoornhuyse *et al.*, 2015) Plant associated microorganisms have immense potential and impart sustainable and ecological solutions to combat agricultural challenges. Plants are surrounded by abundant colonies of microbes which affects the root and the shoot tissues. The diversity of these microorganisms differs from crop to crop and for the developmental stages of each crop based on the type of stress. Different factors have been reported by Da silva *et al.*, 2014 which control the assembly of the endomicrobiomes and the proteins were identified and expressed in transgenic plants. (Schlaeppli *et al.*, 2013)

The composition and biomass of the microbiome heavily influence the connection between the plants and their surroundings. (Ryan *et al.*, 2009) Among the different compartments of soil and plants where their organisms reside, the root zone harbours microbes such as bacteria in abundance. The bacterial diversity is lower in bulky soil and the composition of microbes varies depending on the environment (Peiffer *et al.*, 2013). A slight shift in the composition, density and diversity of microbes was observed phyllo-microbiomes among the same species of plants. This community of microorganisms helps to impart tolerance towards biotic and abiotic stresses as it activates the antioxidant system of the plants by increasing the content of proline, phenols, antioxidative enzymes such as catalase and peroxidase. The microbial density and biomass were found to be higher in the rhizosphere in comparison to the endosphere or phyllosphere since roots are in direct contact with soil providing a humid, microbe-laden environment.

Phytomicrobiome signaling for climate change resilient agriculture

The signaling molecules that are available in the plants and the microbes play a key role in developing interaction and maintaining communication among them. The most widely studied interaction for the plant-microbe association is the legume-rhizobium system nitrogen fixation symbiosis. The plant releases an isoflavonoid signal which is recognised by the rhizobia, which triggers the formation of nodules and nitrogen-fixing genes. Chemical (isoflavonoid) signals are released by the plants in the rooting zone as root exudates which provide adequate space for microbial strains to synthesise signalling molecule lipo-chitoologosaccharides (LPO).

On the contrary, mycorrhizal fungi also form a symbiotic association with roots of higher plants as it colonizes on the roots and facilitates in phosphorus uptake, increases the absorption of water and nutrients and contributes to parasitism of other plants such as epiphytic orchids. Strigolactons are produced as signals by the plants to the fungus and in turn, fungus produces LCO's. (MacLean *et al.*, 2017) there is a two-way signal exchange to make the relation between plants and microbes beneficial.

Signals get exchanged due to the metabolite (hormones) which regulate plant activity. The activities in the phytomicrobiomes are monitored through quorum signaling and other signaling systems (Hartmann *et al.*, 2014; Smith *et al.*, 2017). Under stress conditions, when a microbe-to-plant signal is needed the plants will produce signals that will trigger the release of signals by microorganisms. This is a POSITIVE CONTROL. When a plant-to-microbe signal impedes the production of microbial signal due to the absence of plants then compounds of root exudates serve as the plant-to-microbe

signal is a NEGATIVE CONTROL.

Depending upon the range of plant species the phytomicrobiomes extract can be classified as Specialist (having an effect on a limited number of plant species) and Generalist (having an effect on a diverse species of plants). The below-ground interaction prepares the plants against environmental stimuli. This leads to the primary regulation mechanism and activation of genes and enzymes to produce secondary defense metabolites. LCO's enhances germination, stimulates plant growth, involved in root nodule formation, elaborates root system, expansion of leaf area, increased photosynthetic rates and accelerates flowering and fruiting due to kinase activity. The microbe-to-plant signals help the germinating seeds to enhance resistance to stress conditions as it has proteomes that fasten organ development in crops. Biotic stresses (diseases) can be controlled which reduces the dependency of farmers on pesticides. Phytomicrobiome-to-plant signals are environment-friendly inputs with low cost which makes the farming system climate resilient due to the temperature shift, change in the pattern of rainfall and wind during the crop growing seasons to enhance global food security.

Quorum sensing mechanism

Quorum sensing is a procedure of interaction between bacterial cells by induction of different chemicals. The microbial groups react rapidly and hinders with the organisms to enhance the uptake and regulate the changing ecological surroundings. Bacteria tend to communicate between themselves. The signalling particles such as N-acyl-homoserine lactones (AHLs) can be used for cell-cell interaction inside bacteria to contemporise some activities and act like a solitary unit. The synthesis of auto-inducers

of N-acyl-homoserine lactones (AHLs) of the gram negative bacteria is regulated responding to the cell-density or the cell “quorum”.

Gram-negative bacteria the synthesis of autoinducers of the N-acyl-homoserine lactone (AHL) type is tightly regulated in response to cell density or the cell “quorum”

Gram-negative bacteria the synthesis of autoinducers of the N-acyl-homoserine lactone (AHL) type is tightly regulated in response to cell density or the cell “quorum”

Gram-negative bacteria the synthesis of autoinducers of the N-acyl-homoserine lactone (AHL) type is tightly regulated in response to cell density or the cell “quorum”

Gram-negative bacteria the synthesis of autoinducers of the N-acyl-homoserine lactone (AHL) type is tightly regulated in response to cell density or the cell “quorum”

Quorum sensing signals induce immune responses and can alter the hormone profile of plants which leads to growth responses (Hartmann and Schikora, 2012). Plants have developed a tendency of detecting materials that are produced by potential pathogens and react by activating their response system. Intercommunication of phytomicrobiomes in the root zone specifies the elements of above-ground plant architecture and symbiotic microbial community above-ground (Tena *et al.*, 2011). The above-ground injury caused due to the attack of pathogens can stimulate generation of signalling compounds in root zone. The metabolites released into the cell at the root zone sense the quality of the ecological niche, space, density and diffusion of microbes in rhizosphere. This environment sensing mechanism regulates the gene expression to optimise the fitness of population. AHL are common in Gram-negative bacteria whereas the cyclic peptides as Quorum Sensing (QS)-signals are found in Gram-positive bacteria. QS Compounds

detect early signals to indicate the presence of pathogens in the adjacent areas for attack. The first demonstration of the reaction of plants towards bacterial AHLs was illustrated for legume crops in *Phaeolus vulgaris* by Joseph and Phillips, 2003 and in *Medicago truncatula* by Mathesius *et al.*, 2003.

In tomato plants, a systematic resistance protein was discovered after the inoculation of the roots with C-4 and C-6 side chain AHL- producing *Serratia liquefaciens* MG1 (Hartmann *et al.*, 2004; Schuhegger *et al.*, 2006). When the roots of the tomato plants were inoculated with *S. liquefaciens* MG 1 then the fungal leaf pathogen *Alternaria alternate* was found to be less effective than the one inoculated with AHL-negative mutant. Salicylic acid was increased along with SA-Ethylene-dependent defence genes (i.e., P_{ra}) in MG- inoculated plants. Synthetic protection of bean and tomato plants against the fungal leaf pathogen *Botrytis cinerea* was induced by *Serratia plymuthica* HROC48, producing C4-/C6- and OHC4- /OHC6-homoserine lactones and the response was reduced with the mutants of AHL-production (Liu *et al.*, 2007).

Rhizoremediation

This is another technique of harnessing the plant-microbiome holobionts. Microbes increase the recycling and dissolution of mineral nutrients by synthesizing Amino acids, vitamins, auxins and gibberellins in the rhizosphere of contaminated soil. Due to an increased microbial activity and plant intervention, the exudation of specialised antimicrobials and signalling molecules such as flavonoids, salicylic acids released by the host plants leads to a degradation and transformation of contaminants (Marihal and Jagadeesh, 2013; Yergeau *et al.*, 2014). Microbes promote the uptake of contaminants and enhance resistance of plants towards

pollutant stress (Taghavi *et al.*, 2005; Nadeem *et al.*, 2013; Bell *et al.*, 2015). Microbial strains have the ability to deteriorate organic pollutants such as pesticides, steroids and antibiotics from the soil strata and root zone. The rhizospheric region has specific strains to degenerate toxic man-made chemicals and pollutants and promotes growth and development of plants. This plant associated technique of bioremediation also known as phytotransformation and phytovolatilization includes a proper management of soil contaminants along with surrounding soil air and water. Besides providing support and establishment in the soil, the plants root modifies the soil conditions through the exudation from various microbe species and help in acclimatizing to the habitat. The characteristics and composition of rhizomicrobiome predicts the rhizoremediation efficiency of the flora as the rhizomicrobiome forms a mega consortium due to root exudation and signalling for sustaining the growth and development of the plants through modification in the physical soil condition and ecology. Rhizoremediation helps in rejuvenating agricultural lands affected due to industrial activities. Martinez *et al.*, (2019) noted that the fungal community composition of ectomycorrhiza on holm oak trees (*Quercus ilex*), affected the performance of the soil contaminated with trace elements, thus controlling the phytoremediation efficiency.

Abiotic stress response in plants

The plant faces various extremities due to the changing climate that leads to stress conditions which hamper the production and productivity of crops thus causing economic loss to the farming community. The development of plants is influenced by the adversities of the climate which limits production and disrupts the normal anatomy

of plants. Salinity stress caused due to prolonged exposure to high salt and mineral content in soil hampers the osmotic and ionic equilibrium of the plant cell. Salinity stress has a detrimental impact on plants as it reduces the mobilization of nutrients, cause hormonal imbalance, formation of reactive oxygen species (ROS) which causes physiological and biochemical changes thus by reducing yield.

The crop species harbour a diverse community of microbes in the rhizosphere region which have enormous potential to endure with salt stress. Plant-growth-promoting-bacteria (PGPB) are salinity tolerant which help the plants to cope with stressful situations. Compounds like 1-aminocyclopropane-1-carboxylate (ACC) deaminase, Volatile organic compounds (VOC), antioxidants and indole-3-acetic acid (IAA) which has the potential of stress avoidance and tolerance are produced by plant associated microbes.

PGPB promotes the growth and development of plants as it produces auxin, gibberellins, and cytokinin and reduces the production of ethylene by ACC deaminase. Auxins produce bacterial strains such as Frankia, Actinobacteria, Streptomyces etc, Cytokinins maintain the totipotent cells of the root and shoot tips and Gibberellins produce bacteria which promote yield (Howell *et al.*, 2003). Abscisic acid (ABA) called the stress hormone is released due to water stress and under saline conditions in the root zone which reduces the impact of stress on plants by accumulating compatible solutes in the root zone and releases Ca^{2+} and K^{+} to mitigate the effect (Numan *et al.*, 2018). Bacterial strains such as *Rhizobium phaseoli* in beans, *Pseudomonas fluorescens* in groundnut, (Ahmed *et al.*, 2011) *Acinetobacter calcoaceticus* in cucurbits (Kang *et al.*, 2014), *Streptomyces spp* in

Tomato and *Micrococcus* in beet (Zhou *et al.*, 2017) were effective in alleviating salt stress. PGPB stimulates the procurement of nutrients and encourages the survival of plants under stress.

When PGPB is used in combination with endophytic microbes then it poses synergetic effects on reducing salinity to enhance the productivity through sustainable approaches by identifying the genes using biotechnological tools which promote plant growth, the mechanism followed to overcome salt stress, exploring the application of mycorrhizae and PGPB under saline conditions and popularizing its role as a biofertilizer for sustainable farming.

OMICS approach to alleviate abiotic stress

Plant-microbe interaction is a complicated and an inter-woven system. Microbial interactions in plants generate diverse signals through integration and fine tuning for crop improvement. A plant has to cope-up with biotic and abiotic stresses and the complex defense signals released by plants due to interaction with microorganisms decide the physiological pathway for tolerance (Schenk *et al.*, 2012). The data driven science of multi-omics and bioinformatics provides information about the composition of microbial community and their functional behaviour in diverse conditions. The responses evoked by the plants at physiological, biochemical and molecular levels due to interconnections are parallel to responses under stress conditions. A multi-omics approach can be adapted to decipher the changes occurring in the plants at genomic, proteomic, transcriptomic and metabolomic levels for a clear understanding of the microbial diversity, density, their behavior in phyllosphere and rhizosphere regions where the connections with the microbes direct the responses of plants

towards various stresses. Stress alleviation and growth-promoting activity in *Trichoderma*-plant interaction reported through *T. Atroviride* on tomato plants were demonstrated by Gravel *et al.*, 2017 to report the impact of genotypic traits of the plants to modulate the interaction between plant and microbe through degradation of Indole acetic acid (IAA) and ACC deaminase in rhizosphere region. The putative sequence was further confirmed through gene silencing done through RNAi.

Superior tolerance to salinity stress in soybean by inoculating *Pseudomonas* sp. AK-1 and *Bacillus* sp due to accumulation of proline and lipoxygenase activity was recorded by Kumari *et al.*, 2015. Gene regulation and identification help in the production of new elite varieties for stress tolerance as the multi-omics approach gives higher yield is efficient and a reliable source. Genomic analysis of the host plant and the associated microbes permits access for the smooth functioning of the system involved in associated interactions.

The genotypic diversity of plants influence the interactive process as Nod factor from the associated microbe influences the smooth functioning of the symbiotic association and root development. The genotypic diversity of plants influence the interactive process as *Nod* factor from the associated microbe influences smooth functioning of symbiotic association and root development.

Meta-omics approaches such as metatranscriptomics and metaproteomics can be applied to exploit the unexplored environmental population of the microbes to generate knowledge about the metabolic pathway, interaction and dominance of microbes in root zone of plants which faces various stresses due to external factors. The physic-chemical factors comprising of

temperature, xenobiotic compounds, acidity and alkalinity can be used to enrich the microbial population *in situ* or directly on microbial habitat (Eyers *et al.*, 2004).

Genomes for biofertilization

Plants need macronutrients for proper growth and development. Nitrogen is produced from ammonia by nitrogen-fixing bacteria which involves an enzyme nitrogenase coded by *Nif* gene. This gene cluster was synthesized and isolated from *E. Coli* through functional expression of nitrogenase and the group was transferred to a diverse species of rhizobia to improve nitrogen fixation in cereals. The regulatory control of the *Nif* gene was redeemed by genetically coded sensors which responded to the root exudates, the chemical signals released by soil bacteria and other biocontrol agents (Temme *et al.*, 2012).

Phosphorus is not available to plants in readily formed assimilate as is present as organic or inorganic form. Plants and microbes (PM) produce organic acids which solubilise phosphates and make it readily available. Phosphate is accumulated as phytate which is hydrolysed and further catalysed by phytase. Eighty-two genes have been synthesized through their phytase families. Microbiome engineering generates the phosphate-solubilising capabilities as an effective alternative to the costly and environment degrading phosphorus fertilizers. (Lopez *et al.*, 2014).

Role of plant microbiota in sustainable agriculture

Plant and microbes encounter is co-evolved and friendly. The sequestration of the soil carbon from the terrestrial carbon cycle can be regulated through the interaction of plant and micro-organisms. There are beneficial

microbial species which decomposes the plant residues and thus vital for proper plant growth, flowering duration and yield (Busby *et al.*, 2017). The interaction between the plants and microbes is conditioned upon its effect on health of plant and could be beneficial or harmful for them. Some of the beneficial plant-microbe interaction involves the symbiotic association of nitrogen-fixing rhizobium and arbuscular mycorrhizal (AM) fungi which provides nitrogen and phosphorus to the host plant under nutrient-deficient conditions. This population of micro-organism dominates over the others due to its symbiotic nature (Cao *et al.*, 2017). Phytohormones (phytohormone-dependent defense pathways, namely, ethylene, jasmonic acid, and salicylic acid) and beneficial enzymes are produced by PGPB which helps in promoting growth and development. Some of these PM interactions are favourable under heavy-metal stress by the plants or microbes or both through enhanced uptake and detoxification.

Some of the microbes causes disease in plants and are harmful for them such as *Pseudomonas syringae*, *Erwinia sp*, *Ralstonia*, *Xanthosomonas* etc., which infects the plants through the natural tissues or their wounds for nutrient acquisition from impoverished soils and to trigger their immune responses. There are several factors which regulates the plant-pathogen interaction like biotic and abiotic factors such as population size, host vulnerability, distinct microbial communities in both rhizosphere (epiphytes, colonize plant surfaces) and endosphere (endophytes, colonising in internal parts of the plants) (Brader *et al.*, 2017). Plant microbiomes enhance resistance in plants against phytopathogenic microbes called as biocontrol agents.

Figure.1 Factors that regulate the plant-microbe interaction

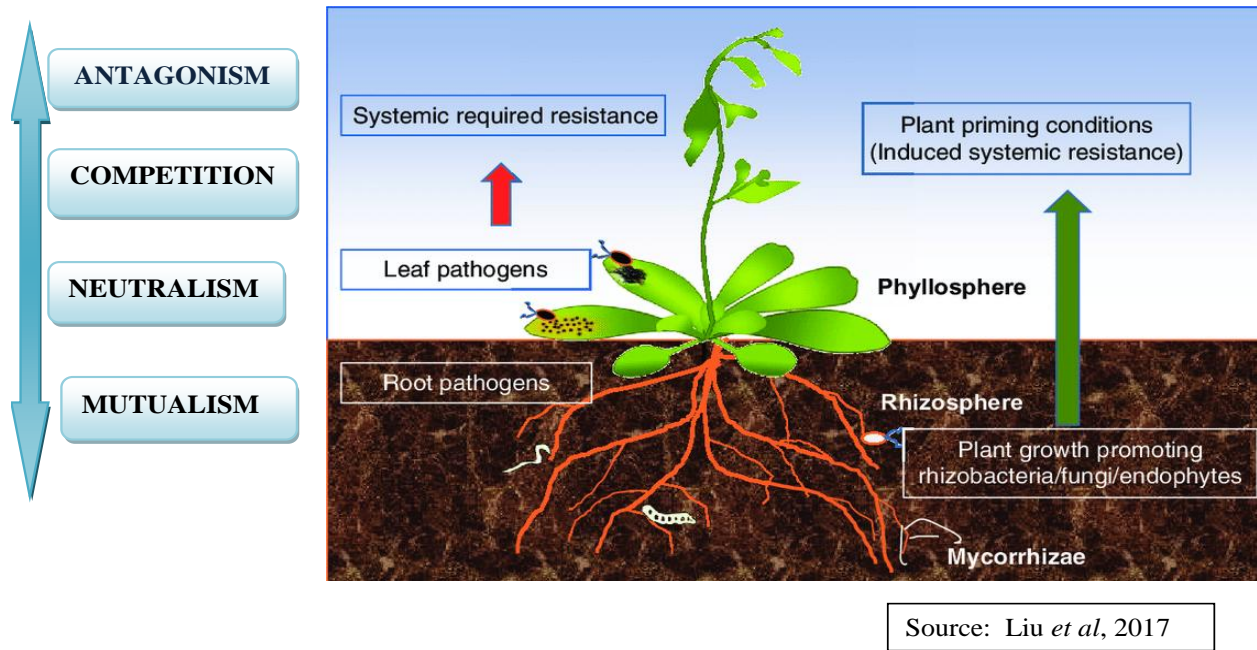


Figure.2 Signalling effect of phytomicrobiomes

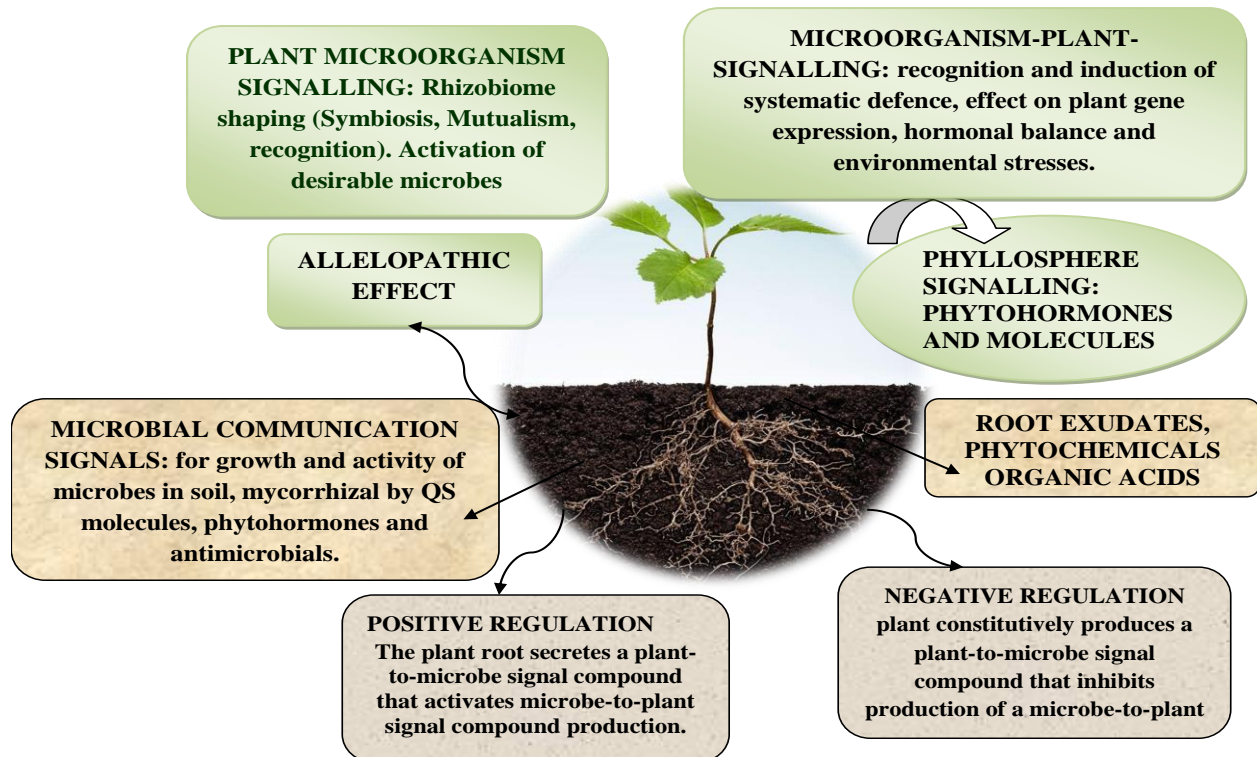


Figure.3 Effect of salinity stress on plant attributes

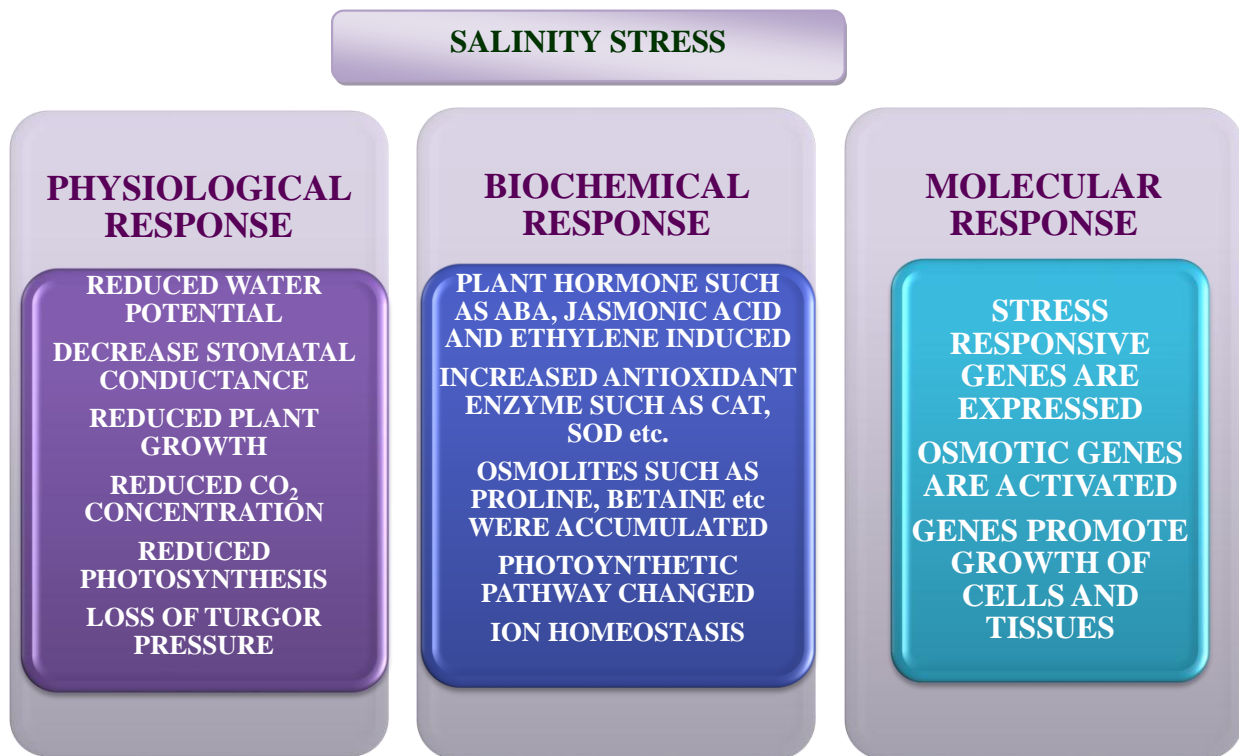


Figure.4 Stress signal transduction

Source: Kumar *et al.*, 2020

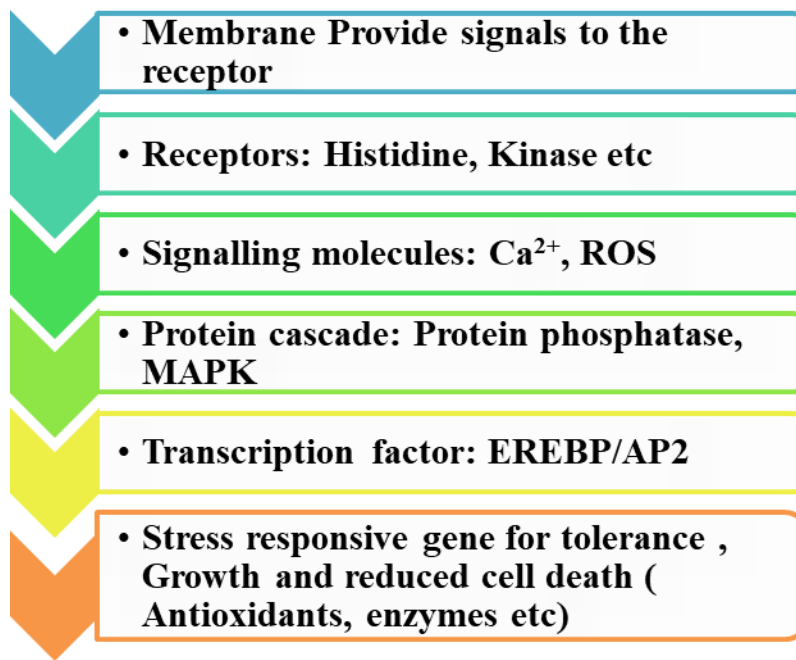


Table.1 Signalling and chemical interaction in crops at rhizosphere

Crop	Microbial strain	Communication signal	Technique used	Reference
Tomato	<i>Pseudomonas syringae</i>	Benzothiadiazole	RT-PCR	Herman <i>et al.</i> , 2008
	<i>Pseudomonas aeruginosa</i>	Pyochelin Phenazine	TLC TLC/HPLC	Audenaert <i>et al.</i> , 2002
Potato	<i>Pseudomonas spp</i>	Phenazine	qPCR and RT-qPCR	Arseneault <i>et al.</i> , 2013
Beans	<i>Pseudomonas aeruginosa</i>	Pyoverdin, Pyochelin, Salicylic acid	TLC and colorimetry	De Meyer <i>et al.</i> , 1997
Rice	<i>Pseudomonas aeruginosa</i>	1-Hydroxy-phenazine, Pyocyanin, Lahorenic acid, Pyochellin	Mass spectrophotometry	Yasmin <i>et al.</i> , 2017
Sunflower	<i>Glomus spp</i>	Benzothiadiazole		Ban R <i>et al.</i> , 2017
Sorghum	<i>Glomus intraradices</i>	Phenazine	RT-PCR	Martínez <i>et al.</i> , 2012

Phytomicrobiomes contribution in global food security

Plant associated microbes and the signals interchanged between higher plants and microorganisms play a vital role in regulating growth, development and productivity of crops under adverse climate conditions (Backer *et al.*, 2018). PGPR and microbe-to-plant signal can be used as an alternative instead of fertilizers for maintaining crop yield and reduce the dependency on pesticides to develop a climate change resilient system of agriculture by reducing the cost of input. Under harsh climate conditions and declining soil fertility, productivity and water quality, the production of agricultural produce need to be increased through already existing arable land. Proper utilization of natural resources and safeguarding the produce from pests and pathogens can be attained by adopting the approach of ‘phytomicrobiome’ to improve the productivity of farm and enhance quality

of produce in a sustainable manner. Excessive indiscriminate use of chemicals in crop production resulted in contamination and posed a negative impact on environment and also on human health and food security. The LCO technique is already being practised in many agricultural lands as this microbial technology has great potential in minimizing the environmental stresses, pollution and increase the quality and quantity of produce substantially with low resource-based inputs for global food security.

In conclusion, a synergetic relation exists between the microbes and the climatic factors which have an impact upon the developmental stages of the crops. The concomitant relationship exists between the plants and the microorganisms and the approach is a low-energy input where they share a mutual benefit. The microbiome on plants is correlated and contributes by providing primary assistance to plants in nutrient and water uptake and in combating

stress conditions. The implementation of advanced *omic* techniques helps in managing the agro-ecosystem as phytomicrobiomes produce sustainable and profitable food material to meet the demands of the population and reduce its side effect on the environment thus enhancing sustainability. *Omic* studies applied in situ are an integral part in improving the production and productivity to ensure food security which can further be embedded with space technologies including remote sensing and other sensor based technologies to understand the potential of these microbial tools in agricultural and other allied sectors. Microbiome-based food products need to be publically and socially accepted for a successful adoption of the technology and maintain multidirectional communication with stakeholders. It should provide economic, environmental and social benefits to improve human health, plant health and reducing contamination. New approaches have a profound effect on phytomicrobiome signalling and plant development. Phenotyping technique is advantageous to determine features such as space occupancy in association to plant light interception. CT scanning methods give fractal dimensions of undisturbed roots. These metabolite based tools when coupled with high-throughput screening gives excellent results. These microbe-mediated techniques also provide support in mitigation of stress under diverse edaphic and environmental conditions. Phytomicrobiomes are well-orchestrated and increases the crop productivity and helps in meeting the demands for food, fibre and fuel by assisting the crops to deal with extreme stress sustainably.

References

Ahmad, M., Zahir, Z. A., Asghar, H. N., and Asghar, M. 2011. Inducing salt

tolerance in mung bean through co-inoculation with rhizobia and plant-growth-promoting rhizobacteria containing 1-aminocyclopropane-1-carboxylate deaminase. *Can. J. Microbiol.* 57, 578–589.

Audenaert, K., Pattery, T., Cornelis, P., and Höfte, M. 2002. Induction of systemic resistance to botrytis cinerea in tomato by *Pseudomonas aeruginosa* 7NSK2: Role of salicylic acid, pyochelin, and pyocyanin. *Mol. Plant-Microbe Interact.* 15, 1147–1156.

Arseneault, T., Goyer, C., and Filion, M. 2013. Phenazine production by *Pseudomonas* sp. LBUM223 contributes to the biological control of potato common scab. *Phytopathology.* 103, 995–1000.

Backer, R., Rokem, J. S., Ilangumaran, G., Lamont, J., Praslickova, D., and Ricci, E. 2018. Plant growth-promoting rhizobacteria: context, mechanisms of action, and roadmap to commercialization of biostimulants for sustainable agriculture. *Front. Plant Sci.* 9:1473.

Bán, R., Baglyas, G., Virányi, F., Barna, B., Posta, K., Kiss, J. and Körösi, K. 2017. The chemical inducer, BTH (benzothiadiazole) and root colonization by mycorrhizal fungi (*Glomus* spp.) trigger resistance against white rot (*Sclerotinia sclerotiorum*) in sunflower. *Acta Biol. Hung.* 68, 50–59.

Brader, G., Compant, S., Vescio, K., Mitter, B., Trognitz, F., Ma, L.-J., and Sessitsch, A. 2017. Ecology and Genomic Insights into Plant-Pathogenic and Plant-Nonpathogenic Endophytes. *Annu. Rev. Phytopathol.* 55, 61–83

Busby, P.E., Soman, C., Wagner, M.R., Friesen, M.L., Kremer, J., Bennett, A., Morsy, M., Eisen, J.A., Leach,

- J.E., and Dangl, J.L. 2017. Research priorities for harnessing plant microbiomes in sustainable agriculture. *PLoS Biol.* 15. e2001793.
- Cao, Y., Halane, M.K., Gassmann, W., and Stacey, G. 2017. The Role of Plant Innate Immunity in the Legume-Rhizobium Symbiosis. *Annu. Rev. Plant Boil.* 68, 535–561.
- Da Silva, D.A.F., Cotta, S.R., Vollú, R.E., Jurelevicius, D., Marques, J.M., Marriel, I.E., and Seldin, L. 2014. Endophytic microbial community in two transgenic maize genotypes and in their near-isogenic non-transgenic maize genotype. *BMC Microbiol.* 14, 332
- De Meyer, G., and Höfte, M. 1997. Salicylic acid produced by the rhizobacterium *Pseudomonas aeruginosa* 7NSK2 induces resistance to leaf infection by *Botrytis cinerea* on bean. *Phytopathology*, 87, 588–593.
- Eyers, L., George, I., Schuler, L., Stenuit, B., Agathos, S. N., and El, F. S. 2004. Environmental genomics: exploring the unmined richness of microbes to degrade xenobiotics. *Appl. Microbiol. Biotechnol.* 66, 123–130.
- Gravel, V., Antoun, H., and Tweddell, R. J. 2007. Growth stimulation and fruit yield improvement of greenhouse tomato plants by inoculation with *Pseudomonas putida* or *Trichoderma atroviride*: possible role of indole acetic acid (IAA). *Soil Biol. Biochem.* 39, 1968–1977.
- Hartmann A., Gantner S., Schuegger R., Steidle A., Dürr C., Schmid M., 2004. *N*-acyl-homoserine lactones of rhizosphere bacteria trigger systemic resistance in tomato plants in *Biology of Molecular Plant-Microbe Interactions*, Vol. 4, eds Lugtenberg B., Tikhonovich I., Provorov N. (St. Paul, Minnesota: MPMI-Press;), 554–556
- Hartmann, A., Rothballer, M., Hense, B. A., and Schröder, P. 2014. Bacterial quorum sensing compounds are important modulators of microbe-plant interactions. *Front. Plant Sci.* 5:131.
- Herman, M., Davidson, J.K., and Smart, C.D. 2008. Induction of plant defense gene expression by plant activators and *Pseudomonas syringae* pv. tomato in greenhouse-grown tomatoes. *Phytopathology*, 98, 1226–1232.
- Howell, S. H., Lall, S., and Che, P. 2003. Cytokinins and shoot development. *Trends Plant Sci.* 8, 453–459.
- Joseph, C. M., and Phillips, D. A. 2003. Metabolites from soil bacteria affect plant water relations. *Plant Physiol. Biochem.* 41, 189–192
- Kang, S.-M., Khan, A. L., Waqas, M., You, Y.-H., Kim, J.-H., and Kim, J.-G., 2014a. Plant growth-promoting rhizobacteria reduce adverse effects of salinity and osmotic stress by regulating phytohormones and antioxidants in *Cucumis sativus*. *J. Plant Interact.* 9, 673–682
- Kumar A, Singh S, Gaurav AK, Srivastava S and Verma JP. 2020. Plant Growth-Promoting Bacteria: Biological Tools for the Mitigation of Salinity Stress in Plants. *Front. Microbiol.* 11:1216.
- Kumari, S., Vaishnav, A., Jain, S., Varma, A., and Choudhary, D. K. 2015. Bacterial-mediated induction of systemic tolerance to salinity with expression of stress alleviating enzymes in soybean (*Glycine max* L. Merrill). *J. Plant Growth Regul.* 34, 558–573.
- Liu, H., Mirzaee, H., Rincon-Florez, V., Moyle, R., Spohn, M., Carvalhais, LC., and Schenk, PM. 2017. Emerging Culture-Independent Tools to Enhance Our Understanding of Soil Microbial

- Ecology: A Paradigm Shift in Terrestrial Biogeochemistry - Scientific Figure on ResearchGate. Available from: https://www.researchgate.net/figure/Overview-of-plant-microbe-interactions-in-the-rhizosphere-and-phylosphere-Plant_fig1_313456433
- Microbial biomass - a paradigm shift in terrestrial biogeochemistry, Imperial College Press, 207-225
- León-Martínez, D.G., Vielle-Calzada, J.-P., and Olalde-Portugal, V. 2012. Expression of phenazine biosynthetic genes during the arbuscular mycorrhizal symbiosis of *Glomus intraradices*. *Braz. J. Microbiol.* 43, 716–738.
- Liu, X., Bimerew, M., Ma, Y., Müller, H., Ovadis, M., and Eberl, L. 2007. Quorum-sensing signaling is required for production of the antibiotic pyrrolnitrin in a rhizospheric biocontrol strain of Bacterial quorum sensing—plant interactions *Serratia plymuthica*. *FEMS Microbiol. Lett.* 270, 299–305.
- Lopez-Arredondo, D.L. 2014. Phosphate nutrition: improving low-phosphate tolerance in crops. *Annu. Rev. Plant Biol.* 65, 95–123
- Lyu, D., Backer, R., Subramanian, S., and Smith, D.L., 2020. Phytomicrobiome Coordination Signals Hold Potential for Climate Change-Resilient Agriculture. *Front. Plant Sci.* 11:634.
- Ma, Z., Hua, G.K.H., Ongena, M., and Höfte, M. 2016. Role of phenazines and cyclic lipopeptides produced by *pseudomonas sp.* CMR12a in induced systemic resistance on rice and bean. *Environ. Microbiol. Rep.* 8, 896–904.
- Marihal, A. K., and Jagadeesh, K. S. 2013. “Plant–Microbe interaction: a potential tool for enhanced bioremediation,” in *Plant Microbe Symbiosis: Fundamentals and Advances*, ed. N. K. Arora (New Delhi: Springer), 395–410.
- Martínez, M.T., San-José, M.D.C., Arrillaga, I., Cano, V., Morcillo, M., Cernadas, M.J., and Corredoira, E. 2019. Holm oak somatic embryogenesis: Current status and future perspectives. *Front. Plant Sci.*, 10, 239.
- Mathesius, U., Mulders, S., Gao, M., Teplitski, M., Caetano-Anoliés, G., and Rolfe, B. G. 2003. Extensive and specific responses of a eukaryote to bacterial quorum sensing signals. *Proc. Natl. Acad. Sci. U.S.A* 100, 1444–1449.
- Nadeem, S., Naveed, M., Zahir, Z., and Asghar, H. 2013. “Plant–microbe interactions for sustainable agriculture: fundamentals and recent advances,” in *Plant Microbe Symbiosis: Fundamentals and Advances*, ed. N. K. Arora (New Delhi: Springer), 51–103.
- Numan, M., Bashir, S., Khan, Y., Mumtaz, R., Shinwari, Z. K., and Khan, A. L. 2018. Plant growth promoting bacteria as an alternative strategy for salt tolerance in plants: a review. *Microbiol. Res.* 209, 21–32.
- Rorison, I.H. The response of plants to acid soils. *Experientia* 1986. 42, 357-362.
- Schlaeppli, K., Dombrowski, N., Oter, R.G., Van Themaat, E.V.L., and Schulze-Lefert, P. 2013. Quantitative divergence of the bacterial root microbiota in *Arabidopsis thaliana* relatives. *Proc. Natl. Acad. Sci. USA.* 111, 585–592
- Schenk, P. M., Carvalhais, L. C., and Kazan, K. 2012. Unraveling plant–microbe interactions: can multi-species transcriptomics help? *Trends Biotechnol.* 30, 177–184.

- Schuhegger R., Ihring A., Gantner S., Bahnweg G., Knappe C., and Vogt G., 2006. Induction of systemic resistance in tomato plants by *N*-acyl-homoserine lactone-producing rhizosphere bacteria. *Plant Cell Environ.* 29, 909–918 10
- Smith, D.L., Subramanian, S., Lamont, J.R., and Bywater-Ekegård, M. 2015. Signaling in the phytomicrobiome: breadth and potential. *Front. Plant Sci.* 6:709.
- Smith, D.L., Gravel, V., and Yergeau, E. 2017. Editorial: Signaling in the Phytomicrobiome. *Front. Plant Sci.* 8:611.
- Taghavi, S., Garafola, C., Monchy, S., Newman, L., Hoffman, A., Weyens, N. 2009. Genome survey and characterization of endophytic bacteria exhibiting a beneficial effect on growth and development of poplar trees. *Appl. Environ. Microbiol.* 75, 748–757.
- Temme, K. 2012. Refactoring the nitrogen fixation gene cluster from *Klebsiella oxytoca*. *Proc. Natl. Acad. Sci. U. S. A.* 109, 7085–7090
- Tena, G., Boudsocq, M., and Sheen, J. 2011. Protein kinase signaling networks in plant innate immunity. *Curr. Opin. Plant Biol.* 14, 519–529.
- Vandenkoornhuyse, P., Quaiser, A., Duhamel, M., Le Van, A., and Dufresne, A. 2015. The importance of the microbiome of the plant holobiont. *New Phytol.* 206, 1196–1206.
- Yasmin, S., Hafeez, F.Y., Mirza, M.S., Rasul, M., Arshad, H.M.I., Zubair, M., and Iqbal, M. 2017. Biocontrol of bacterial leaf blight of rice and profiling of secondary metabolites produced by rhizospheric *Pseudomonas aeruginosa* BRp3. *Front. Microbiol.*, 8, 1985.
- Yergeau, E., Sanschagrin, S., Maynard, C., St-Arnaud, M., and Greer, C. W. 2014. Microbial expression profiles in the rhizosphere of willows depend on soil contamination. *ISME J.* 8, 344–358.
- Zhou, N., Zhao, S., and Tian, C. Y. 2017. Effect of halotolerant rhizobacteria isolated from halophytes on the growth of sugar beet (*Beta vulgaris* L.) under salt stress. *FEMS Microbiol. Lett.* 364:fnx091.