Chapter 8 Microbiome of Plants: The Diversity, Distribution, and Their Potential for Sustainable Agriculture



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Abstract Plants contain associated microbiomes, which facilitate the plant's productivity by supporting their healthy growth in native niche. Globally, sustainable food production is quintessential, wherein the growth-promoting abilities of plantassociated microbes become vital. Recent literatures reveal significant structure and dynamics on plant microbiome, which recognizes the regulation of plant fitness by native microbiome. Henceforth, it is essential to practice modern microbial developments for strengthening crop production. Many of the environmental factors modulate the microbiome organization. This chapter emphasizes the comprehensive characterization of different niche's microbial interactions, agricultural habits, bioinoculants, and abiotic factors to microbial diversity and sustainable plant health. Moreover, conventional and advanced approaches (omics/multi-omics) for studying plant microbiome diversity and plant microbiome interactions are also discussed, which would be helpful in developing novel microbial formulations for sustainable agriculture.

Keywords Plant microbiome \cdot Microbiome diversity \cdot Niche \cdot Agriculture \cdot Bioinoculants

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8.1 Introduction

Term "plant microbiome" describes "the microorganism's community with the potential of harboring a space in plant body as symbionts, commensal or pathogen." Plants harbor microbial hotspots along with soil as major natural microbial resource. This microbial plethora is vital in promoting plant's growth, health, and productivity. However, food productivity enhancement strategies (use of fertilizers, pesticides, and agrochemicals), industrialization, and anthropogenic interventions led to an enforced soil and microenvironment deterioration and attenuation in agriculture lands (Compant et al. 2019). These factors cumulatively exert pressure on agroecosystems and challenge the high-yielding economical and sustainable agriproducts. In this background, plant microbiomes are potential tool for enhancing agricultural productivity while maintaining sustainable ecosystem. The plant microbiomes not only promote the growth of plants but also enhance the soil fertility for facilitating sustainable agriculture. Moreover, microbiome aids in seed germination, growth, productivity, yield, adaptation, and stress resistance/tolerance of plants, which impacts the fitness of the plant leading to the sustainable agriculture (Aamir et al. 2021).

8.2 Plant Microbiome: Diversity, Composition, and Distribution

Microbiomes possess high degree of diversity and are dispersed on soil, water, and air, which can associate with the plant organs (Gupta et al. 2021). The microbiome distribution on plant is majorly categorized into phyllospheric (present on aerial parts such as stem, leaves, and flowers), endospheric (present on inner plant tissues), and rhizospheric (present on below ground components such as roots and surrounding soil) (Fig. 8.1) (Aamir et al. 2021; Santos and Olivares 2021). In addition, microbes also reside as epiphyte on plant surface (Compant et al. 2019). As endophyte microbes penetrate the epidermis and colonize inter- and intracellularly. In general, ectomycorrhizal fungi penetrate root spaces intracellularly after developing a mantle, which surrounds root tip. However, endomycorrhizal fungi develop arbuscules for intracellular colonization (Santos and Olivares 2021). Naturally, healthy plant harbors multifaceted diversity of microorganisms such as bacteria, and fungi are foremost constituent associated with plants (Trivedi et al. 2020). Some examples of plant-associated bacterial and fungal strains and their functional role in normal/stressed environment are listed in Tables 8.1 and 8.2, respectively.

Generally, microbial dynamics is associated with the types of plant species, its developmental stages, or genetic makeup. And, changes in host plant environment during the different life stages play a crucial role and arbitrate the microbial diversity by innate defense system stimulation of plant (Dastogeer et al. 2020; Gupta et al. 2021). Additionally, abiotic and biotic stresses-driven and -compromised defense



Fig. 8.1 Schematics of morphological, biochemical, and molecular characterization of plant microbiome

system can also alter microbiome diversity. Henceforth, to study the biotic/abiotic factors influencing microbial matrix at phylogenetic and functional level, it is essential to estimate the plant microbiome's heterogeneity individually and in understanding different niches (Santos and Olivares 2021).

Recent studies and advances in the knowledge of plant microbiome have demonstrated that plant-associated heterogenetic microbial consortia influence their growth, development, and productivity (Bhatt et al. 2020; Singh et al. 2019; Trivedi et al. 2020). The microbiome consists of some microorganisms, which can interact with other species/host and influence theorganization microbial community. Such microorganisms are known as "hub-microorganisms" of the microbiome (Agler et al. 2016). Microbiome diversity and composition are majorly affected by soil profile and physiochemical characteristics (texture, moisture proportion, pH, temperature, salinity, organic matter, etc.). Moreover, microbe–microbe/plant– microbe interaction, microbial/host secretome, anthropogenic factors, cultivation exercises, and environmental changes also influence at a certain extent (Bhatt et al. 2020; Li et al. 2020; Oyserman et al. 2021).

		Growth		
Strains	Host-plant	parameters	Activity and function	References
Bacillus subtilis	Zea mays, Acacia gerrardii	Nutrient deficiency and salinity stress	Solubilization of supple- ments (Mg, Ca, N, P, K) and their delivery to plant	Hashem et al. (2016), Rodrigues et al. (2016)
Pseudomonas putida	Pennisetum glaucum, Hordeum vulgare, Citrus macrophylla	Salt and salinity stress	Tolerance and enhanced phytoremediation	Jodeh et al. (2015)
Novosphingobium sp.	Glycine max	Normal	Improved nitrogen diges- tion and transport of supplement	Hara et al. (2019)
Pseudomonas fluorescens	Oryza sativa, Citrus aurantifolia	Drought stress	Enhanced phosphate solu- bilization, growth, and chlorophyll content	Shahsavar et al. (2016)
Enterobacter sp.	Pennisetum glaucum, Brassica juncea	Metal stress	Enhanced phosphate solu- bilization, growth, and phytohormones	Durán et al. (2018)
Klebsiella sp.	Avena sativa	Salt stress	Enhanced salt tolerance	Sapre et al. (2018)
Acinetobacter calcoaceticus	Agave americana	Normal	Improved growth and sugar content	De La Torre- Ruiz et al. (2016)
Streptomyces sp.	Pisum sativum	Drought stress	Improved salt tolerance, seed germination, root/ shoot length, and ROS gathering	Zahir et al. (2008)
Saccharibacteria, Verrucomicrobia Firmicutes	Triticum aestivum	Normal	Antifungal property against Microdochium, Neoascochyta, and Fusar- ium spp.	Kinnunen- Grubb et al. (2020)
Sinorhizobium and Rhizobium	Hordeum vulgare	Oils sand mining	Increased plant growth, improved resistance against biotic/abiotic stresses	Mitter et al. (2017)
Acremonium sp. Mesorhizobium Mesorhizobium ciceri	Cicer arietinum	Normal	Improved knob size, yield, and nitrogen content. Antifungal property against <i>Botrytis</i> , <i>Fusarium</i> , <i>and Rhizoctonia solani</i>	Alok et al. (2020), Qin et al. (2017)
Rhizobium daejeonense	Agave americana	Normal	Enhanced growth, sugar, and solubilization of supplements.	De La Torre- Ruiz et al. (2016)

Table 8.1 Examples of bacterial strains involved in plant microbiome assembly, their function and relevance in normal and stressed conditions

		Growth		
Strains	Host-plant	parameters	Activity and function	References
Penicillium menonorum	Cucumis sativus	Normal	Plant-growth-promotion activity via production of siderophore and indole-3 acetic acid and phosphate solubilization	Babu et al. (2015)
Acaulospora scrobiculata, Funneliformis mosseae	Morus alba	Normal	Enhanced growth due to increased chlorophyll content and rate of pho- tosynthesis. Improved conductance of stomata.	Shi et al. (2016)
Rhizophagus intraradices, R. fasciculates, Glomus mosseae, Scutellospora sp., and Gigaspora margarita	Solanum lycopersicum	Drought and salt stress	Enhanced water trans- port, water pressure, and phosphorous aggregation.	Chitarra et al. (2016), Mohumad Tahat (2012), Padmavathi et al. (2015), Viscardi et al. (2016)
Rhizophagus clarus	Sorghum bicolor, Capsicum annuum	Normal	Improved plant growth	Lee and Eom (2015)
Glomus etunicatum	Citrus aurantifolia	Drought stress	Improved plant growth, chlorophyll and photosynthesis.	Shahsavar et al. (2016)
Glomus species	Allium cepa	Normal	Improved plant growth, chlorophyll, and photosynthesis.	Shuab et al. (2014)
Funneliformis mosseae, Rhizoglomus intraradices	Lactuca sativa	Normal	Enhanced zinc absorption	Konieczny and Kowalska (2016), Zhang et al. (2020)

Table 8.2 Examples of fungal strains involved in plant microbiome assembly, their function and relevance in normal and stressed conditions

8.3 Approaches for Studying Plant Microbiome Diversity

Plant microbiome exhibits extensively wide-ranging diversity depending upon habitat and plant organs such as phyllo/endo/rhizospheric regions. Plant microbiome diversity investigation aims to unravel the structural/functional diverseness of a specific host plant-associated microbial community in a definite habitat (Bhatt et al. 2020; Dastogeer et al. 2020; Liu et al. 2019). The colonization of microbiome is facilitated by the host's secondary metabolite secretome and specialized structures such as hairs and trichomes (Gupta et al. 2021). Conventionally, identification and characterization of plant microbiomes (bacteria and fungi) consists of sequencing of universally conserved sequences and bioinformatic analysis. Briefly, this method consists of different sequential steps as: (1) microbial isolation from phyllo/endo/rhizosphere, (2) morphological characterization (for phenotypic and microscopic characteristics), (3) biochemical characterization (for biomolecules and enzymes), (4) Sanger's sequencing (for 16S rNRA/18S rRNA), and (5) Basic Local Alignment Search Tool (BLAST) analysis using National Centre for Biological Information (NCBI) database.

These conventional methods give the outlook information only, henceforth holistic approaches using modern biotechnological techniques to unwrap complete multi-dimension information to understand the mechanistic component are essential. In this context, during last few years various studies implemented advance techniques to unwrap the microbiome exclusively and understand their interaction mechanism with host (Fitzpatrick et al. 2020). It has been established that along with the host and habitat, microbiomes are also affected by their environment and developmental stages. In recent years, advanced modified Sanger's sequencing techniques including 454-pyrosequencing, Oxford nanopore, Illumina, Ion- torrent, PacBio, and hybrid-platform were used to reveal rare microbial taxa in definite niche (Bhatt et al. 2020; Gupta et al. 2021). These techniques extract complete genomic information leading to comprehensive microbial diversity study in a given population through phylogenetic and comparative genomics studies. Nevertheless, these techniques fail to differentiate dead/live cells, which raises the possibility of errors in estimation or hiked microbiome diversity, which are being addressed by managing PCR error using specifically tagged DNA (Gupta et al. 2021).

Moreover, microbiome also contains enormous diversity in uncultivable microbes, which makes it difficult to select a suitable method for their identification. However, in recent years advanced culture-independent direct-environmental DNA cloning, next generation sequencing, single strand conformation polymorphism, denaturing/temperature gradient gel-electrophoresis, terminal restriction/restriction fragment length polymorphism, and fatty acid methyl esters were reported for plant microbiome studies (Bodor et al. 2020; Gupta et al. 2021; del Orozco-Mosqueda et al. 2018).

Omics technologies (genomics/metagenomics, transcriptomics/metatranscriptomics, proteomics/meta-proteomics, and metabolomics) give a comprehensive genetic, structural, and functional information of the plant microbiomes (Sharma et al. 2020). This information, coupled with the metabolic engineering at cellular and/or molecular level, enhances the knowledge on dynamics of microbiomes.

8.4 Factors Affecting Plant Microbiome Diversity

Microbiome consists of several microbes; however, various factors including genome organization, microbial interactions, biotic/abiotic components, local agricultural practices, environmental factors, and physiochemical factors greatly affect plant microbiome organization in local habitat. Some important factors are described below:

8.4.1 Impact of Genomic Organization

Plants benefit from capacities of their microbiome, which is the reason they devote some fraction of their carbon sources toward the development and sustenance of the microbiota. Plants with different genotypes perform distinctively toward metabolism of roots, composition of root secretome, recognition system, and native defense mechanism (Santos and Olivares 2021). Plant genotype alters the root metabolism by modulating the metabolic intermediates (pyruvic acid, citric acid, malic acid, lactic acid, etc.), nitrogenase activity, and reactive oxygen species (ROS) generation (Shcherbakova et al. 2017). Genotype also modulates composition of root secretome in terms of organic acids (citric, malic, and succinic), sugars (ribose, glucose, galactose, and fructose), amino acids (glycine, serine, lysine, and histidine), isoflavones, enzymes (chitinases, proteases, phytases), and phytoalexins (Shcherbakova et al. 2017). Genotype mediates the localized/systemic immune responses of plants by transcriptional changes leading to the elaboration of physical barriers, synthesis of antimicrobial compounds, defense phytohormones, jasmonic acid, salicylic acid, and gaseous ethylene (Lebeis et al. 2015).

Studies demonstrate that varieties of this nature can modify the design and action of the plant microbiome, which thus follows up on development, sustenance, and protection from biotic and abiotic stresses (Santos and Olivares 2021). Curlango-Rivera et al. demonstrated the impact of genotype toward composition of root microbiome, wherein cotton cultivars showed structural differences in their border cells (Curlango-Rivera et al. 2013). These cells are shaped from meristematic cells and were at first thought to be "dead" and answerable for the mechanical security of the root tip. Today, it is realized that line cells are connected with colonization of the root by microorganisms. Essentially, plant roots store high and low sub-atomic weight compounds at the root-soil interface, the rhizodeposition, which might shift as per their genotype. Along these lines, plants with various genotypes can deliver compounds with various creations, advancing explicit microbial flagging and colonization. While examining the seed microbiome, various creators distinguished the effect of the plant genotype on the microbial synthesis of the seed. In the tomato phyllosphere, a review uncovered that four of the nine genotypes tried had an alternate microbial arrangement, which demonstrates that the hereditary elements of the host plant might shape the related microbiota (Morella et al. 2020). In the

rhizosphere, microorganisms from the families Solibacteraceae, Pseudomonadaceae, Cytophagaceae, and Bacillaceae were more bountiful in Fusarium-safe bean cultivars (Mendes et al. 2019). Fusarium opposition formed the microbial gathering of the rhizosphere and chose bacterial taxa with biocontrol action (Santos and Olivares 2021). In recent study, transplantation of rhizospheric soil from a *Ralstonia solanacearum*-resistant tomato plant to a prone plant genotype stifled the susceptibility (Kwak et al. 2018).

8.4.2 Impact of Agricultural Activities

Agricultural activities alter soil's nutrient and physiochemical properties. Nutrient properties act as selection pressure for selection of plant microbiome and altered nutrition influences plant's microbiome profile in negative way and reduces their productivity. Several studies reported the change in microbiome in different agricultural practices using green manure (Bergottini et al. 2017), organic manure (Lupatini et al. 2017), mulch (Qin et al. 2017), nitrogen fertilizers (Cai et al. 2017; Zhu et al. 2016), and crop rotation (Hong et al. 2020). Therefore, for achieving high agricultural productivity, it is essential to comprehend the impact of feasible practices on the design of the plant's microbiome referring native plants and vegetable/ animal residues (Santos and Olivares 2021).

8.4.3 Impact of Bioinoculants

Bioinoculant is a practical strategy to build crop efficiency while lessening the utilization of synthetic chemicals, though information on its effect on the plant microbiome is extremely scant. Subsequently, understanding the connection among inoculated and native microbial networks in plants will add to the improvement of natural products.

Microbial inoculants proficiency relies upon the inoculum characteristics and its capacity to bridge local microbial contest or its layout in the rhizosphere. Rhizospheric fitness (in terms of efficient microbial contents) is an essential factor for promising plant responses (plant-microbe interactions), however, has been explored below par. The cooperation between local miniature life forms of the plant and miniature organic entities (called "transients") can be competitive, parasitic, mutualistic, or predatory (Santos and Olivares 2021), wherein secretomes containing probiotic/antimicrobial compounds selectively stimulate/inhibit the growth of microorganisms (Pieterse et al. 2016). Taken together, the native microbial organization of the host plant is urgent for the achievement of its colonization by transient microbes. Different signalling routes between plants and microorganisms as well as among microorganisms make up the base of the microorganisms in the root area. During plant-microbe interactions the population density is managed by

releasing low atomic weight quorum sensing compounds such as acylated-homoserine-lactones (Hartmann et al. 2014).

The impact of the bioinoculant is regarded as indirect when it causes changes in the native microbiome structure and function by producing probiotic or antimicrobial compounds (Santos and Olivares 2021). Several reports stated the alteration in endophytic population's structure while using inoculants (Andreote et al. 2014; Conn and Franco 2004). In another study, changes in the phenotype of the endophytic potato were reported after *Methylobacterium* sp. inoculation to it, wherein relative proportion of biocontrol regulators (*Acinetobacter* sp., *Massilia* sp., *Phoma* sp., and *Entyloma* sp.) were also increased (Ardanov et al. 2016).

The bioinoculants effects are considered as direct if inoculum directly alters/ improves the metabolism of plant or root exudates profile, which in turn modulates microbiome's structure and function (Santos and Olivares 2021). Molecular advanced technologies permit portraying the microbiome of various plants or contrasting microbiome of plants treated with bio-inoculants. This information will be helpful in developing novel bioinoculants, or shaping it as per the agricultural need.

8.4.4 Impact of Pathogens

The endophytic plant community can harbor useful and destructive microbes in an inactive state. These microbes can be "reactivated" by extrinsic factors including pathogen's attack (Santos and Olivares 2021). The endophytic community encourages plant resistance either with the presence of resistance inducing microbes or reactivation of endophytic population by entry of a microbial biocontrol strain/ abiotic stimulus (Podolich et al. 2015). Nevertheless, reactivation of inactive endophytic microbes after pathogenic attack is more proficient (Santos and Olivares 2021). Agler et al. reported phyllosphere's reformed colonization of endophytic and endophytic bacteria by pathogenic fungi *Albugo* sp. and *Dioszegia* sp. (Agler et al. 2016). Likewise, a decrease in the number of *Bacillus* species in roots, and *Streptomyces & Flavisolibacter* in the rhizosphere of Chinese cabbage was observed with the presence of pathogenic *Plasmodiophora brassicae* (Lebreton et al. 2019). These findings show that the microbiome can protect plants against pathogenic attacks, hence it is conceivable that it can change the microbiota of the host plant.

8.4.5 Impacts of Abiotic Factors

Plants and their microbiome are naturally exposed to different environmental variations including humidity, pH, temperature, salinity, and ultraviolet rays, which straightforwardly or by implication alter the microbial composition. The microbiome profiles of soil from various climate zones shows enormous taxonomic and functional variety, although arid conditions revealed the least functional variation (Tripathi et al. 2017). Lower functional diversity in arid regions is associated with the up-regulation of sporulation/dormancy-associated genes and down-regulation of nutrient (N, P, and S) cycling and stress-associated genes (Tripathi et al. 2017). This study has significant ramifications for understanding the effects of environmental change on various microbiomes. In comparison of soil rhizospheric microbiome of eight different countries, highly significant variation was displayed and credited to difference in pH of different country's soil (Simonin et al. 2020).

Water-stress/drought has maximum impact on plant microbiome (Santos and Olivares 2021). Santos-Medellín et al. studied rice plants exposed to water pressure had their root microbiome rebuilt, which can add to the endurance of plants in this condition (Santos-Medellín et al. 2017). Soil heat (50–80 °C) exposure influences microbiome and disease resistance due to the reduction in antagonistic bacterial loads of Mycobacteriaceae, Micrococcaceae, and Streptomycetaceae (van der Voort et al. 2016). Likely, with routine exposure of plants to UV radiation due to DNA damage phyllospheric microbiome stratification occurs; however, some bacteria acquire UV protection by endospore formation, exo-polysaccharides, and pigments such as melanin, xanthomonadine (Kumar et al. 2019).

Taken together, abiotic factor greatly influences the structure and diversity of plant microbiomes.

8.5 Role of Plant Microbiome in Sustainable Agriculture

Plant microbiome influences agriculture via enhancing soil fertility and promotion of plant growth. Microbes are diverse in nature and constitute of beneficial, harmful, and pathogenic microorganisms.

Plant growth-promoting bacteria (PGPB) synthesize phytohormones (cytokinin, auxin: indole-3-acetic acid, gibberellin, jasmonic acid, and salicylic acid), which act as phytostimulant and enhances plant growth (Kaur 2020; Rastegari 2020; Santos and Olivares 2021). Moreover, ethylene (a stress hormone) is regulated by the enzyme 1-aminocyclopropane-1-carboxylate deaminase (ACC deaminase), which breaks down the molecule ACC and stimulates plant development by lowering ethylene levels (Glick 2014; Santos and Olivares 2021; Shahid et al. 2021). Some common ACC deaminase producers are Pseudomonas spp., Bacillus spp., Paraburkholderia spp., Arthrobacter spp., and Pantoea spp. (Rastegari 2020; Santos and Olivares 2021). These genera exhibit various properties including phytohormones, phosphate solubilization, and nitrogen fixation which enhances nutrient uptake and stress tolerance. In contrast, some bacteria produce phytoactive compounds, which cause disease symptoms in plants. Some common examples of pathogenic bacteria are Pseudomonas syringae (infects tomato, tobacco, olive, and green bean), Xylella fastidiosa (infects potato and banana), Erwinia amylovora (infects ornamental plants), Xanthomonas spp. (infects banana), Ralstonia solanacearum (infects banana and potato) (Gupta et al. 2021; Rastegari 2020).

Several bacteria directly facilitate essential nutrients (iron, nitrogen, phosphorus, etc.) acquisition and promote plant development (del Orozco-Mosqueda et al. 2018).

Plant resistance is influenced by microorganisms which are present above and below the soil due to alteration in plant defense system or commensal interactions (Igiehon and Babalola 2018). Various biocontrol mechanism are involved in plant resistance induction such as production of siderophores (chelating agents with potential of insoluble ferric-ions sequestration), antibiotics (2,4-diacetylphloroglucinol), enzymes (proteases, chitinases, phytases), lipopeptides (bacillomycin-D, mycosubtilin, and iturin-A), volatile organic compounds, and bacteriocins (del Orozco-Mosqueda et al. 2018; Santos and Olivares 2021).

Of note, microbiome not only induces plant growth by these biocontrol mechanisms, but also these perform bio-fertilization (by controlled availability and attainment of nutrients for plants) for regulating plant growth. Some typical examples of biofertilization are symbiotic associations between *Rhizobium* (nitrogen-fixing bacteria), arbuscular-mycorrhizal fungi, and phosphate solubilizing bacteria to deliver nitrogen and phosphorus, to plant, respectively (Santos and Olivares 2021). Some examples of phosphate solubilizing bacteria are *Rhizobium*, *Bacillus*, *Microbacterium*, *Azotobacter*, *Erwinia*, *Serratia*, *Burkholderia*, *Enterobacter*, *Beijerinckia*, *Flavobacterium*, and *Pseudomonas* (Chhabra 2019; Chhabra et al. 2013; Chhabra and Dowling 2017; Kumar et al. 2019).

Rhizobium evolves with leguminous plants and has potential of directly fixing atmospheric nitrogen, hence facilitates self-establishment of plants in low nitrogen soils (Santos and Olivares 2021). Notably, along with *Rhizobium*, leguminous plants also contain some nitrogen-fixing endophytic bacteria such as *Azospirillum*, *Azotobacter*, *Gluconacetobacter*, and cyanobacteria (*Calothrix*, *Nostoc*, *Anabena*) (Kumar et al. 2019). Moreover, there are some nitrogen-fixing microorganisms (*Bacillus*, *Beijerinckia* and *Klebsiella*), which can fix nitrogen in non-leguminous plant in their free form (Santos and Olivares 2021).

Taken together, above-mentioned characteristics of microbiome justify their importance toward sustainable agriculture in terms of inducing crop's nutrient intake, disease resistance, harsh environment tolerance, growth, yield, and productivity.

8.6 Current Trends and Future Perspectives

Continuously increasing global demand of food is challenging for the farmers, wherein they have to tackle with various stresses such as changing hostile climate, nutrient, water scarcity, and pollution. In this background, plant growth-promoting potential natural resources such as plant microbiome become a viable alternative tool for supporting plant health and sustainable agriculture. In plant microbiome establishment microbial diversity, their inter/intra generic interactions and environmental factor are critical. Despite extensive microbiome knowledge to scientists, still advances are needed for comprehensive information. In recent years, advanced

biotechnological tools, bioinformatics, and meta-omics approaches together have established pipelines for structural, genomic, and functional organization of plant microbiomes and their interaction with plants. With such all-inclusive information, it would be easy to improve native microorganisms at cellular or molecular level leading to the more efficient bioinoculants development for improving crop's yield and productivity.

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