PLANT-MICROBE INTERACTIONS: A BRIEF OVERVIEW

Abstract

Interactions between plants and microbes significantly impact how plants behave, grow, and evolve. Numerous microbial species, such as bacteria, fungi, viruses, and archaea, which colonise the rhizosphere, phyllosphere, and endosphere of the plant, are involved in these complex associations. Depending on the traits and functions of the microorganisms and how they affect the plant, these interactions may be advantageous or detrimental. Positive relationships between plants and microorganisms are crucial for nutrient uptake, stress tolerance, and disease resistance. Plant-associated microorganisms can improve nutrient availability through several methods, including nitrogen fixation, phosphate solubilization, and iron mobilisation. They may also create phytohormones, which promote the growth and development of plants. Additionally, certain beneficial microorganisms function as biocontrol agents, inhibiting pathogenic growth and safeguarding plants from illnesses. Complex molecular signalling networks, such as the flow of chemical signals between plants and microorganisms, frequently facilitate these interactions. On the other hand, certain microorganisms can infect plants, resulting in serious output losses. Plants may become infected by pathogens through wounds, holes in the environment, or direct plant tissue penetration. They create chemicals and enzymes that interfere with the plant's defences and impair its immune system. Pathogens can also hinder the intake of nutrients and interfere with regular physiological functions, which compromises the health of the plant. For sustainable agriculture and the proper operation of ecosystems, it is essential to comprehend the subtleties of plantmicrobe interactions. Utilising advantageous interactions can result in the creation of innovative techniques including biofertilizers, biocontrol agents, and bioremediation. These strategies have the potential to lessen the environmental effects of agriculture while increasing crop output and reducing chemical inputs. The study of plant-microbe interactions has been transformed by advancements in next-generation sequencing technology, omics techniques, and bioinformatics

Author

Ankan Das Palli Siksha Bhavana,

Institute of Agriculture, Visva-Bharati University, Sriniketan – 731236 rickdas.official@gmail.com *Research in Biological Sciences - Challenges and Opportunities E-ISBN: 978-93-6252-808-7 IIP Series PLANT-MICROBE INTERACTIONS: A BRIEF OVERVIEW*

tools, which have made it possible to identify and characterise complex microbial populations linked to plants. Our comprehension of these intricate linkages will be improved by more research in this area, which will also open the door to creative agricultural techniques that might help solve problems with environmental sustainability and global food security.

I. INTRODUCTION

The coexistence of plants and microbes from time immemorial has shaped the ecosystem and environmental balance. The association between these two are either positive (confers protection in biotic and abiotic stress condition) or harmful by the act of pathogenesis (Newton et al., 2010; Adeleke et al., 2019). These associations are classified into rhizosphere, endosphere and phyllosphere microbiomes based on niche (interaction of microbes with their ambient environment). The study of these three microbiomes gives us insights into the characteristics and functions of the microbial communities. Whereas, in the perspective of plants, we have a generalized concept that the root's only function is anchorage and uptake of nutrients and water from the soil. But the study of these interactions shows that roots are also involved in the secretion of several chemicals and exudates which invites microbes from different parts of soil to the rhizosphere and endosphere too.

Plant-microbe associations are influenced by several biotic and abiotic factors like host species, genotype, immunity, and climatic changes. In the recent scenario of "organics" and "natural" microbes can be utilized as a potential tool which acts as biocontrol organisms, biofertilizers, and bioremediation. All such applications are not only beneficial to humans but also help to restore the environmental balance, which has been destroyed by several anthropogenic activities and industrialization.

The recent surge in new omics technologies like genomics, transcriptomics, proteomics, metagenomics, and metabolomics paved us the way to discover more insights to determine the characteristics of the microbial community as well as its genomics and proteomics data, addressing the limitations of conventional techniques. It has also categorized microbial interactions based on their beneficiality at a very fast pace with great depths which was beyond imagination a few years back (Nadarajah et al., 2021).

This chapter discusses on the plant-microbe diversity based on niche, factors affecting these interactions (both biotic and abiotic), the mechanism behind the beneficial associations and pathogenesis, novel technologies used to analyse the microbial community and finally the applications and utilities of the plant-microbe interactions.

II. PLANT MICROBIOME DIVERSITY

Plant-microbe relationship is a very complex one and specific too. Plants secretions only signals to those microorganisms with whom the plants are suitable to make the bond and calls them to their immediate environment (Sharma et al., 2021). The soil microbes or the ones dwelling in the underground part colonizes the rhizosphere (the portion of soil regulated by roots). On the other hand, the microbes present aboveground colonizes the phyllosphere which includes microbes dwelling in seeds (spermosphere), flowers (anthosphere), fruits (carposphere), leaves (phylloplane), and stem (caulosphere) (Sivakumar et al., 2020; Hardoim et al., 2015; Nelson, 2018; Stanley and Fagan, 2002). However, there is existence of one more microbiome in addition to these two, endosphere which comprises the plant internal tissues (Sharma et al., 2021). Depending on niche, diversity among the plant-associated microbes can be seen (Trivedi et al., 2020). In general, these associations can takes place in any one of the following ways – pathogenic, parasitic or mutualistic (Newton et al., 2010).

Figure 1: Different plant-microbe interactions based on niche

2.1 Underground Plant Microbiome

A substantial element of the underground plant microbiome is the rhizosphere. Several microorganisms form a community in the rhizosphere in conjunction with plant roots (Hinsinger et al., 2009). It is physiologically active as a result. According to general estimates, each gramme of root contains roughly 10^{11} cells from 30,000 different species (Berendsen et al. 2012; Pathma et al. 2019). Exudates from the roots, such as hormones, flavones and flavonoids, amino acids, phenolic substances, and organic acids, signal soildwelling microbes to begin the process of microbial colonisation. These secretions also affect how microbial genes are expressed (Compant et al., 2021; Egamberdieva et al., 2017; Patel et al., 2015; Nadarajah et al., 2021). Pseudomonads, Actinobacteria, Proteobacteria, Bacteroidetes, Copiotrophs, and Oligotrophs are a few of the prominent communities identified in the rhizosphere (Donn et al., 2015). Protozoa, archaea, oomycetes, fungi, algae, nematodes, viruses, and arthropods are among the other creatures found in the rhizosphere in addition to bacteria (Bonkowski et al., 2009). The beneficial ones interact with the host plants in symbiotic or synergistic ways, whereas those with parasitic and pathogenic effects have adverse effects (Haldar and Sengupta, 2015). When a community has developed in tandem with the root, the root exudate concentrates on the development of biofilms that are encased in extracellular polymeric materials (Mendes et al., 2013).

Table 1: Dominant microbial communities in rhizosphere with respect to the host plant

Even the area found inside the roots, which makes up the endosphere microbiome, can be home to microbes (Hinsinger et al., 2009). An assortment of internally present bacterial and fungal endophytes colonise the plant roots. According to Sharma et al. (2022), the endophytes penetrate plant roots passively by infiltrating the cracks at the root emerging area, root tips, and lateral roots, as well as by an active process. Proteobacteria, Actinobacteria, Planctomycetes, Verrucomicrobia, and Acidobacteria make up the majority of the endophytic population. Among them, Proteobacteria forms dominant communities (Romero et al., 2014). The endosphere varies from the rhizosphere in that the host is involved in the identification and selection of microbial communities that maintain the plant's homeostasis (Compant et al., 2010). This maintains the concept of coevolution between plant and microbial symbionts. Numerous colonising endosphere bacteria have been revealed to exhibit chemotaxis pathways (Compant et al. 2010, Santoyo et al. 2016).

2.2 Aboveground Plant Microbiome

The aboveground plant microbiome is held in the phyllosphere, representing the aerial plant parts (Parasuraman et al., 2019). According to estimates, the phyllosphere has a surface area of around 10^9 km² and serves as a home for a variety of good and bad bacteria, with a density of 10^7 cells/cm² of microbes on the foliage's surface (Lindow and Brandl, 2003; Farre-Armengol et al., 2016). Temperature, precipitation, light, pH variations, O_2 concentration, availability of organic compounds, and other variables all have a large impact on the phyllosphere region (Sharma et al., 2022). It is densely populated with tiny creatures such as algae groups, bacterias like Bacteriodetes and Proteobacteria, actinomycetes, Ascomycota and Basidiomycota (fungi), viruses, and others (Sharma et al., 2022). Phyllosphere microorganisms are linked to plant development concerning biological processes like phytohormone production, biological nitrogen fixation, and defence against pathogen attacks (Cappelletti et al., 2016).

On the other hand, the aboveground endophytes which are dominant in the tissues play a variety of roles in biomass increment, stress tolerance as well as resistance, decreased intake of water, and many more by the development of symbiosis among the two (Panaccione et al., 2014; Rodriguez et al., 2009). Bacterial endophytes can be spread by several natural agents like wind, water, atmosphere, pollen, seed and insects (Frank et al., 2017). These endophytes receive their nutrition from several plant tissues like the xylem in fruits and flowers (Frank et al., 2017; Kandel et al., 2017). The location of endophytes throughout plant tissue will be heavily influenced by the food supply available within the organ to sustain their growth and development. Studies show that there exist discernible genus distinctions between endophytic and phyllosphere communities (Vishwakarma et al., 2020).

III. FACTORS INFLUENCING PLANT-MICROBE INTERACTION

3.1 Host Species

According to Sharma et al. (2021), plant species actively influence the microbiome's microbial composition. The organisation of the root-associated microbiome is more variable in plants that are phylogenetically distantly connected, exhibiting difference in phenotypic traits like root architecture, chemical secretions. The host species also influences the spatial and temporal distribution of a microbial community. Dependency on plant species was demonstrated in an experiment in which a grapevine and four species of weeds (*Stellaria media, Lepidium draba, Veronica arvensis, Lamium amplexicaule*) grown side by side in the same vineyard had substantially distinct microbial community compositions (Samad et al., 2017).

3.2 Host Genotype

Another important factor influencing interactions is the host plant's genotypic makeup, which determines phenotypic characteristics such as root hair density, nature of root exudates and rhizodeposits, root hair length, and leaf morphological features such as stomata, veins, and many others (Lindow and Brandl, 2003; Bulgarelli et al., 2012; Lundberg et al., 2012). Specific microbial species may be selectively drawn to or kept out by particular genotypes. According to Fitzpatrick et al. (2018), in flowering plants, rhizospheric microbial populations varied less as root hair length increased compared to root hair density, which increased greater variance among endophytic bacteria.

3.3 Plant-Derived Metabolites

Plant exudates nourish rhizosphere bacteria and control the variety of microorganisms (Olanrewaju et al., 2019). The effectiveness of colonisation depends on the presence of root exudates in the rhizosphere, such as amino acids, organic acids, carbohydrates, and phenolic compounds (Sundaram et al., 2015). Terpenoids, tannins, alkaloid compounds, and flavonoids are only a few examples of the secondary metabolites that the phyllosphere produces above ground and which the microorganisms use as a carbon source. Additionally, it generates volatile substances like methanol, which provides energy to the methylotrophic epiphytic bacteria and yeast as well as mediates cell wall metabolism in microorganisms (Crozier et al., 2006; Galbally and Kirstine, 2002; Vorholt, 2012).

3.4 Host Immunity

The plant's health and immunology, as indicated by its two-layered defence system, can influence microbiome composition (Sharma et al., 2021). The triggering of immunological responses and the activation of plant defence mechanisms, such as the generation of antimicrobial substances, can prevent the establishment and expansion of potentially harmful microorganisms. On the other side, certain advantageous bacteria have developed strategies to get around or decrease plant defence, enabling them to form positive relationships with plants.

3.5 Host Developmental Stages

Interactions among the microbial communities and plants are associated with the host's age and stage of development (Sharma et al., 2021). Although the chemistry of root exudates is determined by plant genotype, plant age affects their concentration, amount, and quality. Rhizodeposit secretion decline as the plant ages (Bulgarelli et al., 2013). Furthermore, the non-pathogenic endophytes are unable to mitigate the plant defence systems as it becomes more efficient as the plant ages. As a result, juvenile plants have more endophytes than older ones.

3.6 Microbe-Microbe Interaction

Apart from interactions among plants and microbes, microbe-microbe interactions are also an important factor which influences the plant microbiome (Sharma et al., 2021). The dominance of a particular species in a niche depends on the competetion that occurs among themselves for food, space, production of effectors and secondary metabolites, etc (Pathma et al., 2020). Competition, parasitism, or mutually beneficial behaviour among the bacteria are possible interactions. Keystone species are developing and revealing insight into how they coexist with other microbial species and may have regulatory effects on their environment and other microbiome members (e.g., Rhizobiales and Burkholderiales in the rhizosphere) (van der Heijden and Hartmann, 2016).

3.7 Anthropogenic Factor

Crop domestication is an example of an anthropogenic activity that seeks to enhance the qualitative and quantitative factors of output relative to their wild counterparts through continuous selection for a desired characteristic. However, the genetic variety and environmental adaptation of the domesticated crops were lost in this process. The need for artificial fertilisers and plant protection chemicals has grown as a result, which has contaminated the environment and prevented many interaction which are beneficial to the plant (Pathma et al., 2020). In contrast to the native fields having wild plant species, domesticated agriculture fields have distinct bacterial populations. Continuous nitrogen fertiliser application has been cited as having inhibited the evolution of mutualistic rhizobium bacterial strains (Weese et al., 2015). So, we can say that anthropogenic activities tend to act against the natural forces and impacts the co-evolution of plants and microbes (Pathma et al., 2020).

3.8 Edaphic Factors

The native microbial community structure is determined by the nature of the soil and physical properties, including texture, structure, colour, water-holding capability, pH levels, availability of nutrients, organic matter content, etc., as well as by geographical locations like plains or hills (Islam et al., 2020; Pathma et al., 2020). As an illustration, dark brown soil promotes the diversity of fungal communities whereas black soil supports the diversity of rhizobacteria (Xu et al., 2009; Wang et al., 2009). In contrast to fertiliser amendments, soil particle size initially dictates the corresponding microbial taxa specificity (Sessitsch et al., 2001). According to pH, acidic soils have a low variety of microbiomes, while neutral soils maintain a great diversity (Fierer and Jackson, 2006). According to studies by Davidson and Robson (1986) and Zhang et al. (2009), plants are seen to release more flavones and flavonols in nitrogen-deficient soils, which in turn triggers the rhizobia-legume symbiotic associations in the rhizosphere. The variety and biomass of microbial communities are favourably influenced, strengthened, and stabilised by conservation agriculture, which advocates minimal tillage and uses organic manuring (Wang et al., 2017).

3.9 Other Environmental Factors

According to Gupta et al. (2002), environmental changes cause variations in plant physiology, which in turn produce unique microbiomes. Additionally, a phenotypic characteristic is a result of both the plant's genotype and its environment. As a result, a plant's behaviour deviates from its usual state in a number of ways, attracting various strains of microorganisms, suitable in that environment. Limited soil moisture caused plants to produce more amino acids, which in turn impacted the rhizosphere's microbiology and decreased the growth of mycorrhizal mycelium in plant roots (Katznelson et al., 1955). While sufficient precipitation boosts the activity of soil microorganisms, increasing the carbon content of microbial biomass. Microorganisms with modified respiration may grow more quickly at a higher temperature (Sharma et al., 2022). Because of this, microbial diversity is more favourable in the tropics than in temperate regions, especially in the phyllosphere (Vorholt, 2012).

According to Bardgett (2008) and Compant et al. (2010), the altered root exudate frequently affects the interactions between plants and microbes. Radiation is a significant consideration in this scenario. In comparison to rhizospheric communities, the phyllosphere colonies are more susceptible to increasing radiation (UV) (Sharma et al., 2022). Abiotic variables affect the diversity of the plant microbiome in this manner.

IV. MECHANISM OF PLANT-MICROBE INTERACTIONS

Initially classifying all microbial infections as destructive incursions, the immune system of plants later distinguishes between pathogenic and helpful microorganisms (Pel and Pieterse 2013). Pattern recognition receptors (PRRs) found in plant plasma membranes during microbial infection detect and differentiate between MAMPs (microbe-associated molecular patterns) and PAMPs (pathogen-associated molecular patterns). Accordingly, the PRR triggers either MTI (MAMP-triggered immunity) or, PTI (PAMP-triggered immunity), which prevents infection in cases of phytopathogens but does not prevent beneficial infections. These defence responses are a result of continuous dialogues between plants and microbes, facilitated by several phytohormones. This signalling by phytohormones is crucial for the defensive reactions induced by both good and bad microorganisms. Pathogens that overcome the plant's initial line of defence produce effector molecules that interfere with the plant's defence system. Plants have developed a more noticeable defence mechanism known as ETI (effector-triggered immunity) against those effectors. Plant resistance proteins, also known as R proteins, recognise and act against the effector molecules generated by pathogens during this second stage of defence. Prior to the pathogen entering the plant, PTI offers protection, whereas R proteins step in to help once the infection has started (Pathma et al., 2020). This plant-microbe interaction mechanism, which Jones and Dangl (2006) suggested, is commonly referred to as the "zigzag" model.

V. MODERN TOOLS TO ANALYSE MICROBIAL COMMUNITY

With the development of molecular tools, it is now possible to research microbial communities connected to plant microbiomes with novel information (Pathma et al., 2020). Only less than 1% of microorganisms could be studied using culture-dependent approaches (Staley and Konopka, 1985; Pathma et al., 2020). The recent development of a variety of culture-independent methodologies yields valuable information that is now being used to evaluate the hidden microbial diversity and functional characteristics of the same (Gupta et al., 2021). Table 3 lists some molecular biology-based approaches that are cultureindependent, in contrast to the conventional methods. These techniques can be used extensively used in varied microbial diversity investigations without affecting ecosystem structure.

The above-mentioned techniques have enormous possibilities for studying the microbiomes associated with a plant, but they have some limitations, such as a lack of population dynamics data, functional data, difficulties with data analysis due to the high frequency of interspecific and intraspecific differences, and a lack of assembled microbial species genomes (Wolfe, 2018).

VI. IMPACT AND ROLE IN PLANT HEALTH AND AGROECOSYSTEM

Plant microbiomes influence entire plant health and ecological fitness by supporting plant development and avoiding abiotic and biotic stress. Plant microorganisms' effects may be generally classified into numerous roles.

6.1 Recycling of Nutrients

Microorganisms assume a pivotal role in the continuous recycling of numerous essential nutrients, including C, N, P, K, Zn, Ca, Mn and Si. Among these, nitrogen-fixing bacteria play a vital role by converting atmospheric nitrogen into a bioavailable form for plants, thereby facilitating the nitrogen cycle within ecosystems. In aquatic environments, the symbiotic interaction between bacteria and algae significantly influences the carbon and nutrient cycles. Bacteria, acting as decomposers, contribute to the breakdown of organic matter, while algae, through photosynthesis, not only harness energy from sunlight but also release oxygen into the ecosystem. Consequently, the identification and preservation of optimal densities and community compositions of these crucial microorganisms become of paramount importance for the efficient functioning of each respective nutrient cycle. Thus, meticulous management and maintenance of the microorganism population in these cycles are imperative for sustaining ecological balance and the overall health of ecosystems (Jacoby et al., 2017; Rashid et al., 2019).

6.2 Production of PGR

Plant growth-promoting chemicals such as auxin (IAA), gibberellins, cytokinins, and ACC deaminase are produced by the plant-related microbiome (Penrose and Glick, 2002; Glick, 1995). Auxins are known to be created by bacteria such as *Pseudomonas* and *Bacillus* via metabolic pathways, whereas cytokinins are produced by microorganisms such as *Agrobacterium* and some fungi. Cytokinins encourage cell division and have an impact on shoot development, leaf expansion, and nutrient absorption. Certain microbes, including bacteria like *Pseudomonas* and fungi such as *Penicillium*, can generate ethylene, a plant hormone involved in fruit ripening and senescence. Some microbes create elicitors, which cause plants to produce increased quantities of plant growth regulators and help in stress tolerance.

6.3 Role in Plant Protection

Microorganisms play an important role in plant protection by combating pests and diseases. Antimicrobial substances produced by beneficial bacteria include antibiotics, HCN, *Research in Biological Sciences - Challenges and Opportunities E-ISBN: 978-93-6252-808-7 IIP Series PLANT-MICROBE INTERACTIONS: A BRIEF OVERVIEW*

siderophores, and enzymes such as pectinase, chitinase, lipase, DNAase and others (hydrolytic in nature), which defend the host plant from invading phytopathogens and herbivores (Pathma et al., 2020). *Bacillus thuringiensis*, for example, produces toxins that are fatal to insects, making them efficient natural pesticides. Plant pathogens can be suppressed by fungi, such as *Trichoderma species*, colonising their environments, competing for resources, and creating antifungal chemicals. A varied microbial population can provide numerous ways of defence while also improving overall plant resilience.

Table 5: Examples of some microbes used in plant protection

6.4 Role as Biofertilizers

The symbiotic feature of plant-microbe interaction has proven to be an effective biofertilizer in boosting plant development. In symbiosis, bacteria use inert nitrogen from the surrounding environment to transform it into a usable form (ammonium and nitrate) for the plants while obtaining carbon from the appropriate host plant. Azorhizobium, Allorhizobium, Sinorhizobium, Bradyrhizobium, Mesorhizobium, and Rhizobium are the most effective bacterial strain genera (Singh et al., 2019).

6.5 Bioremediation/ Rhizoremediation

Bioremediation is an economic process that uses bacteria, algae, fungi, or plants to remove heavy metal ions from polluted environments by adsorption, biosorption, segregation of heavy metals into intracellular molecules, vacuolar compartmentalization, metal binding, extracellular mobilisation, or metal immobilisation (Rashid et al., 2019; Ray et al., 2020). Rhizoremediation, on the other hand, is a process of pollutant breakdown by a plant's rhizomicrobial population in a polluted location (Hao et al., 2014). Some examples are cited in table 4.

Table 4: Example of Rhizoremediation

6.6 Biocontrol Agents

The biocontrol agent effectively inhibits the growth and virulence potential of pathogenic organisms through various mechanisms including niche exclusion, nutrient competition, production of cell wall-degrading enzymes such as chitinase, synthesis of toxic secondary metabolites, and induction of induced systemic resistance in the host plant. Niche exclusion refers to the ability of the biocontrol agent to occupy and utilize specific ecological niches, thereby depriving pathogenic organisms of essential resources required for their growth and survival. By competing for nutrients, the biocontrol agent limits the availability of vital substances required by pathogens, thus impeding their ability to proliferate and cause damage. Additionally, the production of cell wall-degrading enzymes, such as chitinase, by the biocontrol agent enables it to degrade the structural integrity of pathogenic organisms' cell walls, leading to their lysis and subsequent inhibition of growth. Furthermore, the biocontrol agent synthesizes toxic secondary metabolites, which can directly or indirectly interfere with the metabolic processes of pathogens, further impeding their growth and virulence. Moreover, the biocontrol agent exhibits a remarkable ability to induce systemic resistance in the host plant. This induction triggers the plant's defense mechanisms, such as the production of antimicrobial compounds, reinforcement of physical barriers, and activation of signaling pathways, thus enhancing the plant's resistance against pathogenic attacks (Singh et al., 2019). Biocontrol agents can be used in integrated pest management (IPM) strategies, which combine multiple approaches to minimize chemical pesticide use and reduce environmental impact.

VII. FUTURE OPPORTUNITIES AND CONCLUSION

Plant-microbe interactions have a big impact on ecosystem processes such as biochemical cycling, the formation of microbial communities, and plant development. Understanding the fundamentals of the interactions between plants and microbes might help improve plant health, disease management, and risk management by revealing important biological phenomena. Even today, we still don't fully understand how these interactions work, and more research is required to pinpoint the sensors and signalling pathways involved, comprehend the molecular underpinnings of how various types of stresses and responses interact, and identify the crucial elements of such interactions. Additionally, using complete organisms, such as bacteria and fungi, to enhance plants has become a way of the past; modern techniques use molecular & sub-molecular microbial units (Bourras et al., 2015). In order to understand the disease development processes & suppression, growth and development of plants in association with microbes, immune response, nutrient cycling and absorption, and other processes, microbial ecology and molecular plant pathology must be combined with next-generation sequencing technology, multiple 'omics' tools, databases, and metabolic modelling, artificial intelligence and machine learning (Iman et al., 2016; Nadarajah et al., 2021). Given the increased attention being paid to GMOs, it is important to remember that genetically modified crops can have a significant negative influence on the native microbiomes of the plant, causing unexpected changes in the variety of related bacteria. Therefore, while developing higher-performing hybrids or GM crops, it is equally necessary to take into account the plant-associated microbiomes (Pathma et al., 2020). In conclusion, despite all odds and difficulties, we should pursue a comprehensive strategy to utilise the microbial communities related to plants in an eco-friendly and sustainable way.

REFERENCES

- [1] Newton, A. C., Fitt, B. D., Atkins, S. D., Walters, D. R., & Daniell, T. J. (2010). Pathogenesis, parasitism and mutualism in the trophic space of microbe–plant interactions. *Trends in microbiology*, *18*(8), 365-373.
- [2] Adeleke, R. A., Nunthkumar, B., Roopnarain, A., & Obi, L. (2019). Applications of plant–microbe interactions in agro-ecosystems. *Microbiome in Plant Health and Disease: Challenges and Opportunities*, 1-34.
- [3] Nadarajah, K., & Abdul Rahman, N. S. N. (2021). Plant–microbe interaction: aboveground to belowground, from the good to the bad. *International Journal of Molecular Sciences*, *22*(19), 10388.
- [4] Sharma, P., Kumar, T., Yadav, M., Gill, S. S., & Chauhan, N. S. (2021). Plant-microbe interactions for the sustainable agriculture and food security. *Plant Gene*, *28*, 100325.
- [5] Faeth, S. H., & Fagan, W. F. (2002). Fungal endophytes: common host plant symbionts but uncommon mutualists. *Integrative and Comparative Biology*, *42*(2), 360-368.
- [6] Hardoim, P. R., Van Overbeek, L. S., Berg, G., Pirttilä, A. M., Compant, S., Campisano, A., ... & Sessitsch, A. (2015). The hidden world within plants: ecological and evolutionary considerations for defining functioning of microbial endophytes. *Microbiology and molecular biology reviews*, *79*(3), 293- 320.
- [7] Nelson, E. B. (2018). The seed microbiome: origins, interactions, and impacts. *Plant and Soil*, *422*, 7-34.
- [8] Sivakumar, N., Sathishkumar, R., Selvakumar, G., Shyamkumar, R., & Arjunekumar, K. (2020). Phyllospheric microbiomes: diversity, ecological significance, and biotechnological applications. *Plant microbiomes for sustainable agriculture*, 113-172.
- [9] Trivedi, P., Leach, J. E., Tringe, S. G., Sa, T., & Singh, B. K. (2020). Plant–microbiome interactions: from community assembly to plant health. *Nature reviews microbiology*, *18*(11), 607-621.
- [10] Hinsinger, P., Bengough, A. G., Vetterlein, D., & Young, I. M. (2009). Rhizosphere: biophysics, biogeochemistry and ecological relevance.
- [11] Berendsen, R. L., Pieterse, C. M., & Bakker, P. A. (2012). The rhizosphere microbiome and plant health. *Trends in plant science*, *17*(8), 478-486.
- [12] Pathma, J., Raman, G., & Sakthivel, N. (2019). Microbiome of rhizospheric soil and vermicompost and their applications in soil fertility, pest and pathogen management for sustainable agriculture. *Soil fertility management for sustainable development*, 189-210.
- [13] Compant, S., Cambon, M. C., Vacher, C., Mitter, B., Samad, A., & Sessitsch, A. (2021). The plant endosphere world–bacterial life within plants. *Environmental Microbiology*, *23*(4), 1812-1829.
- [14] Egamberdieva, D., Wirth, S. J., Alqarawi, A. A., Abd_Allah, E. F., & Hashem, A. (2017). Phytohormones and beneficial microbes: essential components for plants to balance stress and fitness. *Frontiers in microbiology*, *8*, 2104.
- [15] Patel, J. S., Singh, A., Singh, H. B., & Sarma, B. K. (2015). Plant genotype, microbial recruitment and nutritional security. *Frontiers in plant science*, *6*, 608.
- [16] Donn, S., Kirkegaard, J. A., Perera, G., Richardson, A. E., & Watt, M. (2015). Evolution of bacterial communities in the wheat crop rhizosphere. *Environmental microbiology*, *17*(3), 610-621.
- [17] Bonkowski, M., Villenave, C., & Griffiths, B. (2009). Rhizosphere fauna: the functional and structural diversity of intimate interactions of soil fauna with plant roots.
- [18] Haldar, S., & Sengupta, S. (2015). Plant-microbe cross-talk in the rhizosphere: insight and biotechnological potential. *The open microbiology journal*, *9*, 1.
- [19] Mendes, L. W., Kuramae, E. E., Navarrete, A. A., Van Veen, J. A., & Tsai, S. M. (2014). Taxonomical and functional microbial community selection in soybean rhizosphere. *The ISME journal*, *8*(8), 1577-1587.
- [20] Roesch, L. F., Fulthorpe, R. R., Riva, A., Casella, G., Hadwin, A. K., Kent, A. D., ... & Triplett, E. W. (2007). Pyrosequencing enumerates and contrasts soil microbial diversity. *The ISME journal*, *1*(4), 283- 290.
- [21] DeAngelis, K. M., Brodie, E. L., DeSantis, T. Z., Andersen, G. L., Lindow, S. E., & Firestone, M. K. (2009). Selective progressive response of soil microbial community to wild oat roots. *The ISME journal*, *3*(2), 168-178.
- [22] Weinert, N., Piceno, Y., Ding, G. C., Meincke, R., Heuer, H., Berg, G., ... & Smalla, K. (2011). PhyloChip hybridization uncovered an enormous bacterial diversity in the rhizosphere of different potato cultivars: many common and few cultivar-dependent taxa. *FEMS microbiology ecology*, *75*(3), 497-506.
- [23] Sharma, B., Singh, B. N., Dwivedi, P., & Rajawat, M. V. S. (2022). Interference of climate change on plant-microbe interaction: Present and future prospects. *Frontiers in Agronomy*, *3*.

PLANT-MICROBE INTERACTIONS: A BRIEF OVERVIEW

- [24] Romero, F. M., Marina, M., & Pieckenstain, F. L. (2014). The communities of tomato (Solanum lycopersicum L.) leaf endophytic bacteria, analyzed by 16S-ribosomal RNA gene pyrosequencing. *FEMS microbiology letters*, *351*(2), 187-194.
- [25] Compant, S., Clément, C., & Sessitsch, A. (2010). Plant growth-promoting bacteria in the rhizo-and endosphere of plants: their role, colonization, mechanisms involved and prospects for utilization. *Soil Biology and Biochemistry*, *42*(5), 669-678.
- [26] Santoyo, G., Moreno-Hagelsieb, G., del Carmen Orozco-Mosqueda, M., & Glick, B. R. (2016). Plant growth-promoting bacterial endophytes. *Microbiological research*, *183*, 92-99.
- [27] Parasuraman, P., Pattnaik, S., & Busi, S. (2019). Phyllosphere microbiome: functional importance in sustainable agriculture. In *New and future developments in microbial biotechnology bioengineering* (pp. 135-148). Elsevier.
- [28] Lindow, S. E., & Brandl, M. T. (2003). Microbiology of the phyllosphere. *Applied and environmental microbiology*, *69*(4), 1875-1883.
- [29] Farré-Armengol, G., Filella, I., Llusia, J., & Peñuelas, J. (2016). Bidirectional interaction between phyllospheric microbiotas and plant volatile emissions. *Trends in Plant Science*, *21*(10), 854-860.
- [30] Cappelletti, M., Perazzolli, M., Antonielli, L., Nesler, A., Torboli, E., Bianchedi, P. L., ... & Pertot, I. (2016). Leaf treatments with a protein-based resistance inducer partially modify phyllosphere microbial communities of grapevine. *Frontiers in Plant Science*, *7*, 1053.
- [31] Panaccione, D. G., Beaulieu, W. T., & Cook, D. (2014). Bioactive alkaloids in vertically transmitted fungal endophytes. *Functional Ecology*, *28*(2), 299-314.
- [32] Rodriguez, R. J., White Jr, J. F., Arnold, A. E., & Redman, A. R. A. (2009). Fungal endophytes: diversity and functional roles. *New phytologist*, *182*(2), 314-330.
- [33] Frank, A. C., Saldierna Guzmán, J. P., & Shay, J. E. (2017). Transmission of bacterial endophytes. *Microorganisms*, *5*(4), 70.
- [34] Kandel, S. L., Joubert, P. M., & Doty, S. L. (2017). Bacterial endophyte colonization and distribution within plants. *Microorganisms*, *5*(4), 77.
- [35] Vishwakarma, K., Sharma, S., Kumar, V., Upadhyay, N., Kumar, N., Mishra, R., ... & Tripathi, D. K. (2017). Current scenario of root exudate–mediated plant-microbe interaction and promotion of plant growth. *Probiotics in agroecosystem*, 349-369.
- [36] Dong, C. J., Wang, L. L., Li, Q., & Shang, Q. M. (2019). Bacterial communities in the rhizosphere, phyllosphere and endosphere of tomato plants. *PLoS One*, *14*(11), e0223847.
- [37] Campisano, A., Antonielli, L., Pancher, M., Yousaf, S., Pindo, M., & Pertot, I. (2014). Bacterial endophytic communities in the grapevine depend on pest management. *PloS one*, *9*(11), e112763.
- [38] Samad, A., Trognitz, F., Compant, S., Antonielli, L., & Sessitsch, A. (2017). Shared and host‐specific microbiome diversity and functioning of grapevine and accompanying weed plants. *Environmental Microbiology*, *19*(4), 1407-1424.
- [39] Bulgarelli, D., Rott, M., Schlaeppi, K., Ver Loren van Themaat, E., Ahmadinejad, N., Assenza, F., ... & Schulze-Lefert, P. (2012). Revealing structure and assembly cues for Arabidopsis root-inhabiting bacterial microbiota. *Nature*, *488*(7409), 91-95.
- [40] Lundberg, D. S., Lebeis, S. L., Paredes, S. H., Yourstone, S., Gehring, J., Malfatti, S., ... & Dangl, J. L. (2012). Defining the core Arabidopsis thaliana root microbiome. *Nature*, *488*(7409), 86-90.
- [41] Fitzpatrick, C. R., Copeland, J., Wang, P. W., Guttman, D. S., Kotanen, P. M., & Johnson, M. T. (2018). Assembly and ecological function of the root microbiome across angiosperm plant species. *Proceedings of the National Academy of Sciences*, *115*(6), E1157-E1165.
- [42] Olanrewaju, O. S., Ayangbenro, A. S., Glick, B. R., & Babalola, O. O. (2019). Plant health: feedback effect of root exudates-rhizobiome interactions. *Applied microbiology and biotechnology*, *103*, 1155-1166.
- [43] Sundaram, B., Hiremath, A. J., & Krishnaswamy, J. (2015). Factors influencing the local scale colonisation and change in density of a widespread invasive plant species, Lantana camara, in South India. *NeoBiota*, *25*, 27-46.
- [44] Crozier, A., Jaganath, I. B., & Clifford, M. N. (2006). Phenols, polyphenols and tannins: an overview. *Plant secondary metabolites: Occurrence, structure and role in the human diet*, *1*, 1-25.
- [45] Galbally, I. E., & Kirstine, W. (2002). The production of methanol by flowering plants and the global cycle of methanol. *Journal of Atmospheric Chemistry*, *43*, 195-229.
- [46] Bulgarelli, D., Schlaeppi, K., Spaepen, S., Van Themaat, E. V. L., & Schulze-Lefert, P. (2013). Structure and functions of the bacterial microbiota of plants. *Annual review of plant biology*, *64*, 807-838.
- [47] Pathma, J., Raman, G., Kennedy, R. K., & Bhushan, L. S. (2020, June 26). *Recent Advances in Plant-Microbe Interaction*. Recent Advances in Plant-Microbe Interaction | SpringerLink. https://doi.org/10.1007/978-981-15-4099-8_2
- [48] Van Der Heijden, M. G., & Hartmann, M. (2016). Networking in the plant microbiome. *PLoS biology*, *14*(2), e1002378.
- [49] Weese, D. J., Heath, K. D., Dentinger, B. T., & Lau, J. A. (2015). Long-term nitrogen addition causes the evolution of less‐cooperative mutualists. *Evolution*, *69*(3), 631-642.
- [50] Islam, W., Noman, A., Naveed, H., Huang, Z., & Chen, H. Y. (2020). Role of environmental factors in shaping the soil microbiome. *Environmental Science and Pollution Research*, *27*, 41225-41247.
- [51] Xu, Y., Wang, G., Jin, J., Liu, J., Zhang, Q., & Liu, X. (2009). Bacterial communities in soybean rhizosphere in response to soil type, soybean genotype, and their growth stage. *Soil Biology and Biochemistry*, *41*(5), 919-925.
- [52] Wang, G., Xu, Y., Jin, J., Liu, J., Zhang, Q., & Liu, X. (2009). Effect of soil type and soybean genotype on fungal community in soybean rhizosphere during reproductive growth stages. *Plant and Soil*, *317*, 135- 144.
- [53] Sessitsch, A., Weilharter, A., Gerzabek, M. H., Kirchmann, H., & Kandeler, E. (2001). Microbial population structures in soil particle size fractions of a long-term fertilizer field experiment. *Applied and environmental microbiology*, *67*(9), 4215-4224.
- [54] Fierer, N., & Jackson, R. B. (2006). The diversity and biogeography of soil bacterial communities. *Proceedings of the National Academy of Sciences*, *103*(3), 626-631.
- [55] Davidson, I. A., & Robson, M. J. (1986). Effect of contrasting patterns of nitrate application on the nitrate uptake, N2-fixation, nodulation and growth of white clover. *Annals of Botany*, *57*(3), 331-338.
- [56] Zhang, J., Subramanian, S., Stacey, G., & Yu, O. (2009). Flavones and flavonols play distinct critical roles during nodulation of Medicago truncatula by Sinorhizobium meliloti. *The Plant Journal*, *57*(1), 171-183.
- [57] Wang, Y., Li, C., Tu, C., Hoyt, G. D., DeForest, J. L., & Hu, S. (2017). Long-term no-tillage and organic input management enhanced the diversity and stability of soil microbial community. *Science of the Total Environment*, *609*, 341-347.
- [58] Gupta, R., Anand, G., Gaur, R., & Yadav, D. (2021). Plant–microbiome interactions for sustainable agriculture: a review. *Physiology and Molecular Biology of Plants*, *27*, 165-179.
- [59] Katznelson, H., Rouatt, J. W., & Payne, T. M. B. (1955). The liberation of amino acids and reducing compounds by plant roots. *Plant and soil*, *7*, 35-48.
- [60] Vorholt, J. A. (2012). Microbial life in the phyllosphere. *Nature Reviews Microbiology*, *10*(12), 828-840.
- [61] Bardgett, R. D., Freeman, C., & Ostle, N. J. (2008). Microbial contributions to climate change through carbon cycle feedbacks. *The ISME journal*, *2*(8), 805-814.
- [62] Jones, J. D., & Dangl, J. L. (2006). The plant immune system. *nature*, *444*(7117), 323-329.
- [63] Staley, J. T., & Konopka, A. (1985). Measurement of in situ activities of nonphotosynthetic microorganisms in aquatic and terrestrial habitats. *Annual review of microbiology*, *39*(1), 321-346.
- [64] Rediers, H., Rainey, P. B., Vanderleyden, J., & De Mot, R. (2005). Unraveling the secret lives of bacteria: use of in vivo expression technology and differential fluorescence induction promoter traps as tools for exploring niche-specific gene expression. *Microbiology and Molecular Biology Reviews*, *69*(2), 217-261.
- [65] Ehrenreich, A. (2006). DNA microarray technology for the microbiologist: an overview. *Applied microbiology and biotechnology*, *73*, 255-273.
- [66] Sanguin, H., Remenant, B., Dechesne, A., Thioulouse, J., Vogel, T. M., Nesme, X., ... & Grundmann, G. L. (2006). Potential of a 16S rRNA-based taxonomic microarray for analyzing the rhizosphere effects of maize on Agrobacterium spp. and bacterial communities. *Applied and Environmental Microbiology*, *72*(6), 4302-4312.
- [67] Leveau, J. H. (2007). The magic and menace of metagenomics: prospects for the study of plant growthpromoting rhizobacteria. *European Journal of Plant Pathology*, *119*, 279-300.
- [68] Erkel, C., Kube, M., Reinhardt, R., & Liesack, W. (2006). Genome of rice cluster I archaea the key methane producers in the rice rhizosphere. *Science*, *313*(5785), 370-372.
- [69] Handelsman, J. (2004). Metagenomics: application of genomics to uncultured microorganisms. *Microbiology and molecular biology reviews*, *68*(4), 669-685.
- [70] Velicer, G. J., Raddatz, G., Keller, H., Deiss, S., Lanz, C., Dinkelacker, I., & Schuster, S. C. (2006). Comprehensive mutation identification in an evolved bacterial cooperator and its cheating ancestor. *Proceedings of the National Academy of Sciences*, *103*(21), 8107-8112.
- [71] Mark, G. L., Dow, J. M., Kiely, P. D., Higgins, H., Haynes, J., Baysse, C., ... & O'Gara, F. (2005). Transcriptome profiling of bacterial responses to root exudates identifies genes involved in microbe-plant interactions. *Proceedings of the National Academy of Sciences*, *102*(48), 17454-17459.
- [72] Yuan, Z. C., Liu, P., Saenkham, P., Kerr, K., & Nester, E. W. (2008). Transcriptome profiling and functional analysis of Agrobacterium tumefaciens reveals a general conserved response to acidic

conditions (pH 5.5) and a complex acid-mediated signaling involved in Agrobacterium-plant interactions. *Journal of Bacteriology*, *190*(2), 494-507.

- [73] de Werra, P., Baehler, E., Huser, A., Keel, C., & Maurhofer, M. (2008). Detection of plant-modulated alterations in antifungal gene expression in Pseudomonas fluorescens CHA0 on roots by flow cytometry. *Applied and Environmental Microbiology*, *74*(5), 1339-1349.
- [74] Haichar, F. E. Z., Marol, C., Berge, O., Rangel-Castro, J. I., Prosser, J. I., Balesdent, J., ... & Achouak, W. (2008). Plant host habitat and root exudates shape soil bacterial community structure. *The ISME journal*, *2*(12), 1221-1230.
- [75] Wu, C. H., Bernard, S. M., Andersen, G. L., & Chen, W. (2009). Developing microbe–plant interactions for applications in plant‐growth promotion and disease control, production of useful compounds, remediation and carbon sequestration. *Microbial biotechnology*, *2*(4), 428-440.
- [76] Walder, F., Schlaeppi, K., Wittwer, R., Held, A. Y., Vogelgsang, S., & van der Heijden, M. G. (2017). Community profiling of Fusarium in combination with other plant-associated fungi in different crop species using SMRT sequencing. *Frontiers in plant science*, *8*, 2019.
- [77] Gupta, R., Singh, A., Srivastava, M., Shanker, K., & Pandey, R. (2019). Plant-microbe interactions endorse growth by uplifting microbial community structure of Bacopa monnieri rhizosphere under nematode stress. *Microbiological research*, *218*, 87-96.
- [78] Bodor, A., Bounedjoum, N., Vincze, G. E., Erdeiné Kis, Á., Laczi, K., Bende, G., ... & Rákhely, G. (2020). Challenges of unculturable bacteria: environmental perspectives. *Reviews in Environmental Science and Bio/Technology*, *19*, 1-22.
- [79] Wolfe, B. E. (2018). Using cultivated microbial communities to dissect microbiome assembly: challenges, limitations, and the path ahead. *Msystems*, *3*(2), e00161-17.
- [80] Jacoby, R., Peukert, M., Succurro, A., Koprivova, A., & Kopriva, S. (2017). The role of soil microorganisms in plant mineral nutrition—current knowledge and future directions. *Frontiers in plant science*, *8*, 1617.
- [81] Penrose, D. M., & Glick, B. R. (2003). Methods for isolating and characterizing ACC deaminase‐containing plant growth‐promoting rhizobacteria. *Physiologia plantarum*, *118*(1), 10-15.
- [82] Glick, B. R. (1995). The enhancement of plant growth by free-living bacteria. *Canadian journal of microbiology*, *41*(2), 109-117.
- [83] Ho, Y. N., Mathew, D. C., & Huang, C. C. (2017). Plant-microbe ecology: interactions of plants and symbiotic microbial communities. *Plant ecology-traditional approaches to recent trends*, 93-119.
- [84] Pathma, J., Raman, G., & Sakthivel, N. (2019). Microbiome of rhizospheric soil and vermicompost and their applications in soil fertility, pest and pathogen management for sustainable agriculture. *Soil fertility management for sustainable development*, 189-210.
- [85] Van Peer, R., Niemann, G. J., & Schippers, B. (1991). Induced resistance and phytoalexin accumulation in biological control of Fusarium wilt of carnation by Pseudomonas sp. strain WCS 417 r. *Phytopathology*, *81*(7), 728-734.
- [86] Stout, M. J., Zehnder, G. W., & Baur, M. E. (2002). Potential for the use of elicitors of plant resistance in arthropod management programs. *Archives of Insect Biochemistry and Physiology: Published in Collaboration with the Entomological Society of America*, *51*(4), 222-235.
- [87] Kempster, V. N., Scott, E. S., & Davies, K. A. (2002). Evidence for systemic, cross-resistance in white clover (Trifolium repens) and annual medic (Medicago truncatula var truncatula) induced by biological and chemical agents. *Biocontrol Science and Technology*, *12*(5), 615-623.
- [88] Boughton, A. J., Hoover, K., & Felton, G. W. (2006). Impact of chemical elicitor applications on greenhouse tomato plants and population growth of the green peach aphid, Myzus persicae. *Entomologia Experimentalis et Applicata*, *120*(3), 175-188.
- [89] Sindhu, S. S., Rakshiya, Y. S., & Verma, M. K. (2011). Biological control of termites by antagonistic soil microorganisms. *Bioaugmentation, Biostimulation and Biocontrol*, 261-309.
- [90] Rashid, M. H., Kamruzzaman, M., Haque, A. N. A., & Krehenbrink, M. (2019). Soil microbes for sustainable agriculture. *Sustainable management of soil and environment*, 339-382.
- [91] Ray, P., Lakshmanan, V., Labbé, J. L., & Craven, K. D. (2020). Microbe to microbiome: A paradigm shift in the application of microorganisms for sustainable agriculture. *Frontiers in Microbiology*, *11*, 622926.
- [92] Hao, K., Liu, J. Y., Ling, F., Liu, X. L., Lu, L., Xia, L., & Wang, G. X. (2014). Effects of dietary administration of Shewanella haliotis D4, Bacillus cereus D7 and Aeromonas bivalvium D15, single or combined, on the growth, innate immunity and disease resistance of shrimp, Litopenaeus vannamei. *Aquaculture*, *428*, 141-149.
- [93] Kavita, B., Shukla, S., Naresh Kumar, G., & Archana, G. (2008). Amelioration of phytotoxic effects of Cd on mung bean seedlings by gluconic acid secreting rhizobacterium Enterobacter asburiae PSI3 and implication of role of organic acid. *World Journal of Microbiology and Biotechnology*, *24*, 2965-2972.
- [94] Kuiper, I., Bloemberg, G. V., & Lugtenberg, B. J. (2001). Selection of a plant-bacterium pair as a novel tool for rhizostimulation of polycyclic aromatic hydrocarbon-degrading bacteria. *Molecular Plant-Microbe Interactions*, *14*(10), 1197-1205.
- [95] Singh, P. P., Kujur, A., Yadav, A., Kumar, A., Singh, S. K., & Prakash, B. (2019). Mechanisms of plantmicrobe interactions and its significance for sustainable agriculture. In *PGPR amelioration in sustainable agriculture* (pp. 17-39). Woodhead Publishing.
- [96] Bourras, S., Rouxel, T., & Meyer, M. (2015). Agrobacterium tumefaciens gene transfer: how a plant pathogen hacks the nuclei of plant and nonplant organisms. *Phytopathology*, *105*(10), 1288-1301.
- [97] Imam, J., Singh, P. K., & Shukla, P. (2016). Plant microbe interactions in post genomic era: perspectives and applications. *Frontiers in microbiology*, *7*, 1488.