



Review Article

Plant-Microbe Interactions - Insights and Views for Applications in Sustainable Agriculture

Anne Sahithi Somavarapu Thomas

School of Biosciences and Technology, Vellore Institute of Technology, Vellore, Tamilnadu, India

Wasinee Pongprayoon

Department of Biology, Faculty of Science, Burapha University, Chon Buri, Thailand

Kraipat Cheenkachorn

Department of Chemical Engineering, Faculty of Engineering, King Mongkut's University of Technology North Bangkok, Bangkok, Thailand

Malinee Sriariyanun*

Biorefinery and Process Automation Engineering Center (BPAEC), The Sirindhorn International Thai-German Graduate School of Engineering (TGGS), King Mongkut's University of Technology North Bangkok, Bangkok, Thailand

* Corresponding author. E-mail: macintous@gmail.com DOI: 10.14416/j.asep.2021.07.008

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Abstract

The term “microbiome” refers to the association of plants with various microorganisms which play an important role in the niches they occupy. These microorganisms are found in the endosphere, phyllosphere, and rhizosphere, of host plants which are involved in plant ecology and physiology. The structure and dynamics of the plant microbiome have been significant seen in the last few years. In addition, the plant microbiome enhances the host plant with gene pools, which is referred to as the second plant genome or extended genome. Interestingly, the microbiome associated with plant roots has received unique attention in recent years due to its important role in host nutrition, immunity, and development. Prospective studies of the microbiome have been coupled with the need for more sustainable production for agriculture. On the other hand, various environmental factors are associated with plant-microbiome interactions that can affect composition and diversity. This review provides insights and views of plant microbiome for sustainable agriculture. Host factors that influence the microbial community, root-associated microbial consortium, commercial application, and limitation of plant microbiome were discussed. Also, this review provides current knowledge of the plant microbiome into potential biotechnology products that can be used in agricultural systems. Regardless, microbiome innovation represents the future of sustainable agriculture.

Keywords: Agriculture, Microbial consortium, Plant-microbe interaction, Sustainability, Mutualism

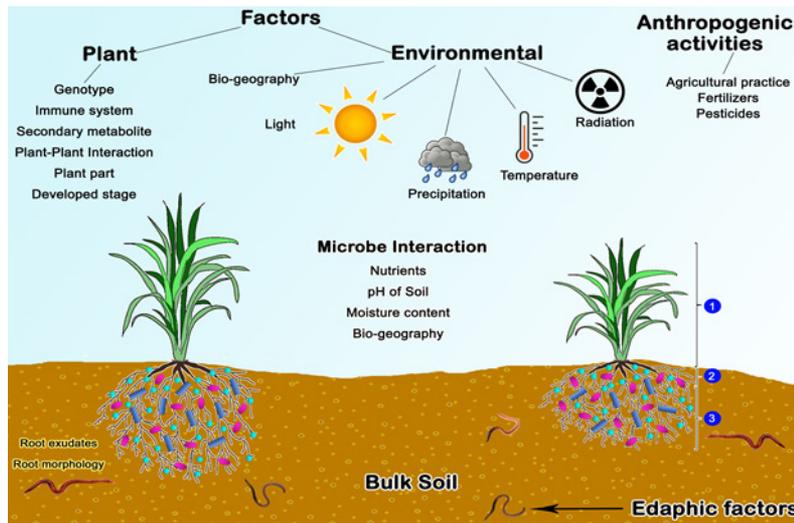


Figure 1: Plant-microbiome interactions and their associations to environmental factors ((1) Phyllosphere, (2) Endosphere, and (3) Rhizosphere).

1 Introduction

The various types of microorganisms associated with higher organisms (animals, humans, plants) are collectively defined as their microbiome [1]. To date, several studies have progressed rapidly involving humans, plants, monkeys, insects, and rats as carriers of the microbiome [2]. Recently, research has focused more on the interpretation of the function and composition of microbiomes between plants and soil. Plants are now demonstrated to live in association with a wide variety of microorganisms rather than being separate [3]. These microbes can live either in the endosphere or phyllosphere between plants and soil and are predominant in bacteria and fungi. So far, thousands of bacterial and fungal taxa from plant tissues have been reported [4]. These microbes play an important role in increasing the availability of nutrients to plants and increasing plant resistance to stress. In addition, plant growth and survival also lead to physiological functions that may be related to the microbiome known as the plant holobiont [5]. *Arbuscular mycorrhizal* fungi (AM) and legume rhizobia are considered the most prominent examples of interactions between plants and microbiota [6]. This symbiosis greatly affects the capability of the roots to absorb several nutrients from the soil [7]. It has been reported that disclosure of several types and results of plant-

microbial interactions, generating considerable interest among researchers [8]. Predicting advances in plant microbiome research is difficult. However, the future both applied and fundamental research on the plant microbiome is based on 1) improving culture methods, 2) the role of microbiomes in soil, and 3) gene transfer [9]. This review provides insights and views on recent research on plant mutualism with microbes for sustainable agriculture. Also, the overview of the microbiomes that are present above and below the soil near to the plant tissue, environmental factors, impact on plant mutualism, commercial application, and limitation studies of plant- microbiome were discussed. Various microbial communities are present in the outer surface and in the inner tissues of the plant known as ‘Plant Microbiome’. The three spheres of the plants have major parts for the plant microbiome interactions namely endosphere, rhizosphere and phyllosphere. Plant microbiome interactions and factors are shown in the Figure 1.

1.1 Endosphere microbiome

Microorganisms near the endosphere can invade the inner layer tissues of the plant’s roots and occupy them, forming an endophytic microbiome. AM and other endophytes are the predominant colony-forming bacteria of the inner sphere [10]. It has been reported

that bacteria and to some extent archaea are significant members of the endosphere plant-microbiome, that can be beneficial to the plants [11]. On the other hand, like the rhizosphere, the endospheres are also very specific to the microbial consortium. In general, the mutualism of the plant microbiome is higher outside the host than in the community of endophytic microbes [12]. In addition, the physiological characteristics and diversity of the host's endophytic microbiome (aboveground and underground tissue) may also differ [13].

1.2 Rhizosphere microbiome

The rhizosphere soil zone (1–10 mm) surrounding the roots, which consists of deposition by the root exudates, mucus, and dead plant cells [14]. The rhizosphere is diverse, including bacteria, oomycetes, fungi, algae, nematodes, viruses, protozoa, and archaea [15]. It has been reported that beneficial rhizosphere microbiome such as bacteria, plant growth-promoting rhizobacteria (PGPR), mycorrhizae, and biocontrol microbes was frequently studied [16]. Gans, Wolinsky reported that one gram of soil contains more than one million of different micro-bacterial genomes [17]. On the other hand, İnceoğlu, Al-Soud reported that in a potato rhizosphere around 55 thousand operational taxonomic units (OTUs) are present [16]. It has been reported that the relationship of the microbial community between soil is not associated with the host root (bulk soil) and the soil of the rhizosphere is irrelevant [18]. *Xanthomonadaceae* and *Actinomycetes* have been reported to be groups of bacteria present in the rhizosphere, and they are less abundant than those living in bulk soil [3]. On the other hand, *Mycorrhizal* fungi are rich in rhizosphere communities and have also been found in over 200,000 plant species. It is also associated with more than 80% of the entire plant microbiome community [18]. In addition, it is a plant nutrient and plays a vital role in plant carbon cycling in the soil ecosystems to which this *Mycorrhizal* root is associated [18]. Also, it has been reported that mycorrhiza maintains nitrogen and phosphorus at about 80% of plant requirements. In profit, they receive celluloses and phospholipids from the host plant [8]. Recently, it has been reported using sequencing techniques that AM exhibits a combination of species and intraspecific diversity [19].

1.3 Phyllosphere microbiome

The areas where flowers, leaves, stems, and fruits grow are known as the “phyllosphere” and they are also relatively poor in nutrients than the rhizosphere and endosphere. Due to environmental factors such as temperature, rain, wind, radiation, and humidity, this microbial community is subjected to seasonal fluctuations. These factors directly affect the physiological standards of the host plant, such as (water intake, photosynthesis, respiration, etc.), and indirectly affect the population structures of the microbiomes [19]. The species of microbial communities that are rich in the natural phyllosphere region were reported. The diversity of fungal communities in the phyllosphere in temperate regions is more diverse than in tropical ones [20]. In addition, it has been reported that 10^{26} cells of the bacterial phyllosphere population are present on earth and about 10^7 cells are present on the leaf surface of the host plant per cm^2 [21]. On the other hand, the numbers of the fungal community population are smaller [22]. Microbes in the phyllosphere of different plants are comparatively similar to higher-level taxa, while lower taxa in the same region remain substantially different. This indicates that microorganisms may need to adapt their metabolism to survive in the phyllosphere [21].

2 Plant-Microbiome Interactions

Agriculture productivity is affected by microorganisms, for example by helping and controlling the availability/absorption of nutrients and increasing plant resistance to stress [23]. Recently, several studies have focused on niches in specific plant regions and regulation in their specific microbiome [24]. It has been reported that the factors that influence this assembly were varied in various parts of the plant-based on the studies of phylogenetic and functional analysis [25]. Even though the plant microbiome is recognized as a huge treasure of microbial diversity, some types of crops, their functions, and composition have not yet been studied for their bacterial communities [26]. The significance of plant-microbiome interaction can be studied to be applied in the prevention of plant-pathogen [27]. The mechanisms of interactions of the plant-microbiome are unknown due to the lack of proper methodologies [28]. On the other hand, the ability of soil microbes

can be understood by relieving stress in crops for plant-microbiome interactions [29]. Archaea and nematodes have been reported to contribute significantly to the diversity of the microbiome and they interact with other microorganisms to control ecosystem functions and soil-plant processes [30]. In addition, it has been reported that there is an important relationship between soil microbial-based plants-microbiome-insect interactions by the release of volatiles from terrestrial plants after modulation [31]. These studies are more holistic in the interaction of nutrients to understand which dietary and biological factors determine the structure and, therefore, the function of the structures of soil and plant microbiome. The bacterial community is influenced by antagonistic, commensal interactions, and competitive. The general modes of plant-microbial interaction are competition, exchange, inter-dependence between nutrients, and the exchange of metabolites [32]. Therefore, direct cooperative or competitive interactions between community members may depend on interactions under certain conditions.

3 Environmental Factors- Impact on Mutualism

Environmental factors such as heat, drought, cold, salt, and pathogen infections can have devastating effects on plant growth and yield in the field [33]. Recently, there have been reports that global crop production is under the influence of environmental factor, mainly due to abiotic and biotic stresses [34], which can lead to the loss of more than millions of dollars. According to Lesk, global warming and drought have reduced the production of grains such as wheat, corn, and rice by about 10% over a 50-year lifespan, raising serious concerns for various governments [35]. The impact of global warming on the bio-phenology of spring plants is demonstrated [36]. Longer growing seasons can increase carbon absorption and potentially reduce leaf emergence, climate change, germination, and fruiting [37]. Some of the key findings and effects of factors affecting the plant-microbial interaction are shown in Table 1.

3.1 Abiotic factor

Abiotic factors include extreme drought, temperature,

light, waterlogging, and salinity as the main parameters affecting plant growth [38]. Plant Growth Promoting Rhizobacteria (PGPR) were found to be essential for the growth of plants. It has been reported that PGPR helps plant growth by stimulating root and shoot by producing Amino-Cyclopropane-1-Carboxylate (ACC), solubilizing phosphate, and indole acetic acid. In addition, they also help in the resistance to adverse environmental factors.

3.2 Biotic factor

Biotic factors, such as interactions between organisms, pathogen infestation, and plant growth-promoting bacteria have been used as biocontrol agents against plant pathogens [39]. Biological stress induced by PGPR has been reported to affect plant growth in two different ways; by producing phytohormones or promoting the absorption of certain nutrients. In addition, phyto-anticipants are used as protective compounds against plant pathogens that cause biotic stress.

3.3 Agriculture practice

Cultivation practices and the use of land are the most important causes of biodiversity loss, leading to undesirable consequences for the environment [40]. The effects of soil management practices depend on soil type, microbiome, and plant species, and approximately 10% of the imbalance in microbial diversity can be attributed to agricultural practices used [41]. Vegetation affects changes in the structure of soil and the diversity of microbiomes. For example, excess land use affects the pattern of microbial communities [42]. On the other hand, no effect of land use on microbial diversity in the rhizosphere was found, indicating that plant species have an impact on the rhizosphere community than soil properties [43]. Meanwhile, plants may have resilient core microbiome compositions that are less susceptible to change due to differences in land use and soil type [44]. The microbiome of deciduous forests is relatively intact, and differences were seen in soil and vegetation properties. Incessant cultivation can cause changes in soil properties, which in turn affects microbiome communities [45].

Table 1: Biotic and abiotic factors affecting the plant-microbial interactions

Type of Factor	Effect of Factor	Studies Associated and Key Findings	Reference
Biotic factor	Plant genotype	Root structure in the border cells varied between cotton cultivators. Therefore, plants of different genotypes have different compositions and may promote growths of certain microorganisms.	[46]
		In the <i>Arabidopsis</i> phyllosphere, four out of nine genotypes were tested with different microbial compositions. This is due to the genetic factors of the host plant associated with the microbiota.	[47]
		Inoculation of rhizosphere soil from a tomato plant resistant to <i>Ralstonia solanacearum</i> suppressed disease symptoms in susceptible plants. This shows that the role of the local microbiota is to protect plants from microbial pathogens.	[48]
	Bio-inoculants (beneficial interactions)	Potato plants were inoculated with <i>Methylobacterium</i> spp., structural changes in the endogenous microbial community were observed. This bacterial inoculant increased the relative abundance of <i>Massilia</i> sp., <i>Acinetobacter</i> sp., <i>Entyloma</i> sp., and <i>Phoma</i> sp.,	[49]
		After inoculating wheat seeds with <i>Paraburkholderia phytofirmans</i> (PsJN) in the spring, the effect of microbial inoculum on the seed microbial flora was observed. An important finding is that it reduced the population of <i>Proteobacteria</i> and stimulated <i>Flavobacterium</i> .	[50]
		<i>Metarhizium</i> fungus inoculated in beans increased microbiome that promotes plant development growth such as <i>Bradyrhizobium</i> , <i>Flavobacterium</i> , <i>Chaetomium</i> , and <i>Trichoderma</i> . This inoculation can suppress the activity of the pathogen <i>Fusarium solani</i> .	[51]
		<i>Herbaspirillum seropedicae</i> and bacteria combined with humic acid were inoculated in the root maize seeds resulted in a variety of nitrogen compounds.	[52]
	Effect of pathogen	Phytopathogenic fungi presence in <i>Arabidopsis thaliana</i> resulted in the alteration of epiphytic and endophytic bacterial colonization of the phyllosphere.	[53]
		<i>Rhizoctonia solani</i> inoculation in the lettuce resulted in increased diversity of Gammaproteobacteria.	[54]
		Banana trees that were infected with <i>Fusarium oxysporum</i> were colonized with bacteria from the Enterobacteriaceae family, while in healthy plants, populations of <i>Pseudomonas</i> and <i>Stenotrophomonas</i> were found to be increased.	[55]
		In kiwifruit, <i>Pseudomonas syringae</i> causes a disease called canker disease, which affects the microbial community of <i>Actinidia deliciosa</i> in the phyllosphere, where it resulted in the reduction of the microbial community.	[56]
	Effect of agricultural practice	Green fertilizers are used to alter the composition of the yerba mate bacterial microbiome, and cultivation in monoculture leads to the development of an abundant fungal microbiome.	[57]
Long-term cultivated soil was compared in both traditional and organic systems. It was concluded that these soils contained different microbial flora.		[58]	
Single crops of black pepper alter the composition of soil microbial communities and their physicochemical properties over a long period (12-38 years). As a result, the reproduction of the <i>Fusarium</i> pathogen is significantly reduced.		[59]	
Abiotic factors	pH	Significant structural difference of 57% in taxon abundance were observed due to pH of environments.	[60]
	Drought	In rice, <i>Actinomycetes</i> and <i>Chloroflexi</i> phylum increased and the root system was reconstructed under drought conditions.	[61]
		Drought conditions altered the composition of microbiomes present in the root, and also increased the richness of <i>Actinobacteria</i> .	[62]
	Temperature	Treating the soil at different temperatures (50–80°C) alters and reduces the bacterial community and reduces the ability to fight diseases.	[63]
Salinity	Evaluations of salinity on soil microbiome and the spinach rhizosphere were studied. The outcome was an increase in water absorption by plants (transpiration)	[64]	

4 Root Associated Microbial Consortium

The plant microbiome provides the host plant with additional gene pools, which is why it is often referred to as the secondary plant genome or extended genome [65]. Interestingly, the root-associated microbiome has received unique attention in recent years due to its important role in development, nutrition, and immunity [62]. The microbial community in the soil is closely related to the plant root system, so the root system functions according to microbial interactions. Plant Growth-Promoting Microorganisms (PGPMs) have been reported to be beneficial for root line growth [66].

Plants inoculated with PGPM were reported to show higher root biomass and faster root growth [67]. Kaur *et al.* reported that *Penicillium simplicissimum* GP17-2 was inoculated into a cucumber plant under barley grain soil conditions resulting in the rapid growth of both (longer and larger root systems) after 3 weeks of planting [66]. It can improve the plant's ability to absorb nutrients and water, and also helps in the interaction between the plant and the rhizosphere [68]. Root system architecture (RSA) is associated with two main physiological consequences, namely the growth of the main and lateral root (LR) and root hairs (RH) [69]. However, LR and RH develop a major characteristic root structure that promotes the absorption of water and minerals. Contreras-Cornejo *et al.* reported that high efficiency was shown in LR production after inducing *Trichoderma* in *Arabidopsis thaliana* [70]. Similarly, Lee *et al.* reported that rapid growth was observed in *Arabidopsis thaliana* and Chinese cabbage after induction of *Brassica rapa L.* in RH. List of Root associated microbiome studies and

key findings are shown in Table 2.

On the other hand, phenolic and amino acids in watermelon root exudates significantly increase sporulation and germination of *Fusarium oxysporum* f. sp. *niveum* [71]. In the tomato plant, root exudates are stimulated and germinated microconidia of pathogens *F. oxysporum* f. sp. *lycopersici* and *F. oxysporum* f. sp. *radicis-lycopersici* which is affected by plant age [72]. Moreover, root exudates can be detected by fungal pathogens, which allow the fungal hyphae to orient themselves in the direction of their growths towards the root.

Dong *et al.* reported that colonization of *Piriformospora indica* in the root system was increased in the diameter of the extension zone by 2 times, biomass by 1.4 times, and the thickness of the epidermis and cortical layer LR by 1.5 times compared with the group of untreated plants [73]. This LR stimulation appears to be an early interaction phase in phytopathogenic root colonizing fungi [74]. Martínez-Medina *et al.* reported that a reduction in cytokinin content was seen after the induction of *Trichoderma*, and it promoted the root growth of melon plants [75]. Also, similar results were obtained by Sofo *et al.*, when *Trichoderma harzianum* T-22 was inoculated into plants, showed a significant decrease in cytokinins (dihydrozeatin and trans-zeatin) in the root system [76]. However, the root tips are considered the main site synthesis of cytokinins, the above results indicate that cytokinins play a negative role in root growth [77]. Overexpression of cytokinin oxidase/dehydrogenase (CKX) genes in transgenic plants results in elongation of the root meristem, improved root branching, LR origin closer to the apical root meristem, and root formation [78].

Table 2: Models of the root-associated microbiome and host plants

Plant Host	Microbiome	Key Findings	Reference
Rice	<i>Actinobacteria</i> and <i>Chloroflexi</i>	Drought stress is responsible for taxa that is specific to the compartment. This shows that drought affects plant physiology and re-builds root microbial communities. In addition, this contributes to the survival of plants in extreme environmental conditions.	[61]
Wheat	<i>Triticum aestivum L.</i>	Soil organic and activated carbon increased with long-term nitrogen fertilization but changed during the growth phase. This provides a link between increased nitrogen fertilizer inputs, carbon changes, and migrations of root microbial communities.	[79]
Barely	<i>Phyllobacterium</i> , <i>Paenibacillus</i> , and <i>Trabusiella</i>	In all seed and root samples, resulted in an association with OTUs indicates a significant relationship between seed and root-related microbiome. Phytohormones from seeds and roots play an important role in seedling germination and colonization.	[80]
Potato	<i>Flavobacterium</i> , <i>Pseudomonas</i> , and <i>Acinetobacter</i>	In potatoes, the rhizosphere was significantly rich in the genera of fungi. Analysis of the bacterial and fungal community microbiota showed that the structure formation of bacterial microbiota in the rhizosphere was dependent on the host plant.	[81]

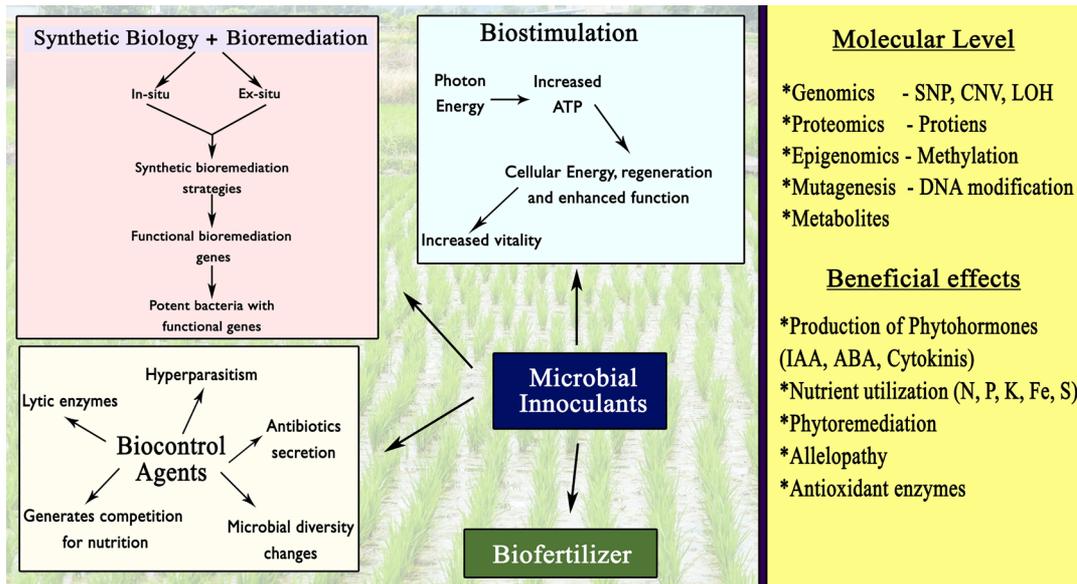


Figure 2: Applications of microbial inoculants and beneficial effects in sustainable agricultural activities.

5 Commercial Applications of a Microbial Consortium

The consortium of microbes can be used as a biological tool to stimulate plant growth [29]. The consortium of soil microorganisms has been reported to have beneficial effects on plant growth, and various other microorganisms have been commercialized for agricultural use [82]. On the other hand, a consortium that promotes plant growth may be feasible to enhance the activity of fungi and rhizobacteria [83]. The commercial application used for sustainable agricultural and beneficial effects are shown in Figure 2. Global demand for microbial inoculants has increased by 12% due to rising costs of fertilizers and the efficiency for environmentally friendly technologies in society [84]. A commercial product for growing wheat and canola is (JumpStart®) which contains *Penicillium bilaii*. Using this commercial product in one study reported a high yield (66%) of wheat. However, several studies have reported less beneficial properties [85]. Modifiers and bio-fertilizers, which are supplied to farmers under various schemes with subsidies from 25 to 75%. Moreover, the acceptability of biofertilizers for farmers remains inconsistent due to 1) pest inoculants, 2) temperature sensitivity, and 3) environmental factors [86].

5.1 Biostimulation

Biostimulants are factors that can be separated from phytonutrients for the insemination of plant development and growth. [87]. By using these biostimulants it can increase around 10% of the yield of crops and it could reach 3.68 billion dollars by 2022 with an annual growth of 45% in the world market [83]. Biostimulants are of five different types namely, humic acids, microbial inoculants, flavic acids, amino acids, protein hydrolysates, and seaweed extracts [88]. It has been reported that AMF is a local microbial consortium of three species [89]. Recently, studies have reported that seeds consisting of 10^8 microbial cells were inoculated and coated with an adhesive, which showed that they were affected by temperature and humidity, and their effectiveness [90]. In addition to the traditional delivery approach, new methods have been developed. For example, flower spray inoculation has been reported to continue to produce next-generation endophytic colonized seeds and regulated seed microbiomes. It resulted in colonization of germinated plants was effectively carried out with the inoculated strain. This indicates that using a different approach may lead to increased efficiency of microbial inoculation in the field [91]. Further research is needed on the development of biostimulants to compare with conventional chemical inputs in field trials with a variety

of fruit crops and over varying climates and conditions before farmers will be willing to accept them.

5.2 Biocontrol agents

The biocontrol agents (BCA) have major functions of such as, *B. popilliae*, *B. thuringiensis*, and *P. fluorescens* is to suppress or control plant diseases by acting as antimicrobial and antifungal agents [92]. Biocontrol agents that are used to control disease after harvesting mainly focus on isolating microorganisms with pathogen resistance. It has previously been found to be an indispensable biocontrol agent when used against soil and foliar diseases and is a potent antagonist [93]. Wilson and Wisniewski discovered many antagonist models, and this became the basis for several other biocontrol research programs in the early and recent years [94]. PGPRs of species such as *Azotobacter*, *Azospirillum*, *Bacillus Burkholderia*, *Pseudomonas*, *Serratia*, *Rhizobium*, are currently produced commercially on a large scale, but for the use of these biofertilizers and microbial bio-pesticides for agricultural purposes. The main obstacles are the stability, reliability, and shelf life of microbial inoculum in the field [95]. In addition, antagonists that produce secondary metabolites suppress target pathogens, which means that antibiotic production is difficult during the process [94]. 2-hexyl-5-propyl resorcinol (HPR) has been reported as a key role in biofilm formation [96] On the other hand, the essential feature that was well-defined is that the level of growth and plant's survival rate after application of a biocontrol agent on injured fruit's surface to prevent pathogen intact.

5.3 Bioremediation

Bioremediation is a collective phenomenon that involves the process of using a biological system to restore or clean up contaminated sites [95], [96]. Due to anthropogenic activities and population growth, the ecosystem has been affected by contaminations [97], [98]. Bioremediation characterization is the most important step [99], [100]. This helps establish the most accurate and viable bioremediation techniques [101]. High concentrations of contaminated heavy metal in the environment cause deteriorating water quality [102]. Increasing the effectiveness of bioremediation through the use of genetically engineered microorganisms

(GEMs) is a promising approach to resolve this problem [103]. This mechanism can be achieved by degrading target pollutants, including cumbersome compounds, incorporating new and efficient metabolic pathways, expanding the substrate range of existing pathways, and increasing the stability of catabolism [104]. Biological techniques that use specific microorganisms to break down various pollutants into non or low-toxic compounds are demonstrated to achieve environmentally sustainable growth and development [101]. On the other hand, the efficiency of bioremediation and biodegradation of environmental pollutants using microbial strains (single) is still low and limited [105]. The efficiency of bioremediation with the biological method in contaminated areas is varied depending on soil type, location, and characteristics of bioremediation methods, and it needs the method to incorporate these microbes into those targeted areas to allow the microbe's survival [106]. Therefore, more attention has been transferred to the microbial consortium due to their unique multiple functions, robust and adaptive properties.

6 Limitation of the Study in Plant-Microbiome Interactions

Despite the many advantages over monocultures, several problems remain when using co-culture methods for production purposes. Therefore, it is necessary to gain understanding and recognition of these limitations to motivate the development of the R&D activities to overcome these bottlenecks.

6.1 Co-cultivation compatibility

One of the key factors for the success of the co-cultivation system is strain compatibility. The spots that make up co-cultivation should be able to grow efficiently under the same growth parameters, such as environment, temperature, pH, and oxygen demand, and should not produce toxic compounds that cause significant harm to other members of the microbial community [107]. These microbial strains belong to the same species because the goal is to achieve similar growth. On the other hand, the different growth rate is an issue when different species with slightly different environmental requirements are used to create a synthetic microbial consortium. One possibility to solve this problem is

to introduce positive interactions between microbial partners during co-culture fermentation.

6.2 Reproducibility

The reproducibility and balance ratio throughout the co-cultivation of the microbial consortium for the symbiotic cultivation process is innovative. It has been reported that due to various factors, such as substrate competition, consortium toxicity, doubling times can fluctuate in the co-culture population [108]. This greatly affects the reproducibility of co-culture engineering studies. Reactor volume can also affect the viability of co-culture [109]. Changing the ratio of inoculation between co-cultivation partners has been reported to strongly affect overall production during crop cultivation [110]. Another study reported mutualistic growth of the desired population to maintain the co-culture formulation [111]. However, manipulation of growth rates and biomass of consortium are greatly affected by population's communications based on quorum sensing [112]. Therefore, these growth and metabolic pathways are thought to be regulated among co-culture members.

6.3 Exchange of metabolites

The exchange of metabolites between the different strains in microbial consortium results in the different biochemical intermediates, such as phosphorylated derivative molecules or Coenzyme A derivative species. Taking this into account, the modules of the metabolic pathway must be separated between the constituents so that the binding metabolites can be easily transported between members of the co-cultures. In addition, the membrane transporter can be genetically modified to promote the transportation of the intermediates to the desired direction [108].

6.4 Data acquisition

Comprehensive data collection for symbiotic culture is a major challenge as medical, industrial, and environmental applications require detailed data collection and description [113]. It was reported that the distribution of metabolic fluxes in the co-culture system was possible to achieve than within the cells, which gives an advantage over monoculture systems

for obtaining information about metabolism [114]. However, in an artificial consortium, metabolic interactions are difficult to decipher as microbial members can exchange interacting metabolites [115]. However, there are reports of co-culture characterization (theoretical and experimental strategies) that determine metabolic flux without any physical separation of cells.

7 Conclusions

In our world, we are facing these negative effects of food supply depletion, soil pollution, climatic conditions, and water scarcity, while global food demand will increase by 70% in 2050 [116]. Because of these impacts, natural resources, such as the plant microbiome are an alternative option to sustainable agriculture. However, the knowledge on plant microbiomes through the scientific literature is not sufficient. Advancement in research, such as sampling, extraction, and molecular techniques (amplification of DNA, bioinformatics, and sequencing) is required. On the other hand, the composition and function of the plant microbiome are essential to modulate or optimize for the growth of sustainable agriculture. Although the structure of microbiomes can be influenced by several factors discussed in this review, the underlying knowledge of the mechanisms involved in plant microbiomes is still lacking. The composition and diversity of the microbiome and their functions are the major concerns for future research on sustainable agriculture and environmental protection.

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