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Plant-Microbe Ecology: Interactions of Plants and Symbiotic Microbial Communities

Ying-Ning Ho, Dony Chacko Mathew and
Chieh-Chen Huang

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Abstract

Plant community dynamics are driven by the microbial mediation of soil resource partitioning and sharing by the inhibition of other host symbionts or sharing the broadly specific symbiotic fungi. The plant phenotype and ecology can be affected by the impact of the symbiotic microbes on the environment and competition for soil resources.

The advent of modern biotechnology has made it easy to study plant-microbe interactions further. Current genomic technologies applied to natural and artificial systems have shown that the plant genotype has a small but significant effect on the microbial community composition of the phyllosphere, the rhizosphere, and endophytic microbes. In this chapter, we discuss the relationship between the host and its symbiotic microbial community and the role of plant metabolites and root exudates such as organic acids, amino acids, sugars and antimicrobial compounds in shaping a specific rhizosphere community, attracting plant growth promoting rhizobacteria (PGPR) colonization on the plant roots and inhibiting or attracting soil-borne pathogens. In addition, we also review and introduce the functionality of plant symbiotic microbes for increasing the abiotic and biotic stress tolerance of the host. An understanding of the ecosystem function of plant and symbiotic microbes will guide efforts to improve agriculture practices.

Keywords: plant-microbe ecology, symbiotic microbial communities, interactions of host and symbiotic microbes

1. Introduction

Plants have recently been recognized as a metaorganism that possesses a distinct microbiome and close symbiotic relationships with associated microorganisms [1]. Plant ecology is

affected by complex interactions with plant-associated microbes. The roles of both plant-associated microbes and the host in ecosystem function have been recognized, but the detailed mechanisms are unclear. Since plants are immobile, they have coevolved with microbes and acquired a number of mechanisms that modulate the outcome of their interactions [2]. Roots can continuously synthesize, accumulate, and secrete a wide range of compounds into the soil [3], which are known as the root exudates. Root exudates contain enzymes, water, H+ ions, mucilage, and carbon-containing primary and secondary compounds [4, 5]. Campbell and Greaves [6, 7] observed that the density of microbes in the rhizosphere was 100 times greater than that in the bulk soil. Recent studies have showed that plant root exudates shape the soil bacterial community [8, 9]. According to a study by Ciccazzo [10], a plant species selects a specific rhizosphere bacterial community. The change in the microbial composition generates feedback on the plant relative performance that defines the long-term effects of the soil microbes on their coexistence with that plant species [11, 12]. The feedback can be of two types; positive plant-soil microbial feedback reinforces the spatial separation of the microbial communities [13], while negative feedback results in plant replacement, which necessitates recolonization of locally specific roots [14–16]. Systematic methods such as genome-wide association studies have enabled us to explore the relationships of plant loci and symbiotic communities [17, 18]. How does the microbiome diversity and function potentially affect host plant performance? The presence of microbial hubs in plant microbiome networks plays an important role between a plant and its microbial community [19]. Plant growth–promoting rhizobacteria (PGPR) can produce a complex blend of volatile substances, which are distinct between bacterial species and other closely related species [20–22]. Some of these bacterial volatiles can stimulate plant growth [23, 24], suppress disease stimulating ISR [25], or antagonize phytopathogens [26, 27], nematodes, or insects [28, 29].

Worldwide crop production is affected by biotic and abiotic stress factors [30–32], which cause millions of dollars in losses. The beginning of the industrial revolution in 1750 and the human activities such as burning fossil fuels and deforestation have altered the global climate. An increase in carbon dioxide and temperature is speeding up the life cycle of grain and oilseed crops [33]. According to Lesk [34], extreme heat waves and droughts have reduced global harvests of cereals such as maize, wheat, and rice by 10% in a span of 50 years, which has become a grave concern of various governments. The impact of a warming climate on spring plant phenology is evident [35, 36]. A longer growing season may increase carbon uptake and potentially mitigate climate change [37, 38], leaf emergence [39], fruiting [40], and germination [41]. Abiotic stress factors include extreme temperature [42], drought, water logging, light, and salinity as major parameters that affect plant growth. Plant-associated microbes or PGPR were found to benefit plants by enhancing nutrient uptake, stimulating root, and shoot growth by producing indole acetic acid [43, 44], 1-aminocyclopropane-1-carboxylate (ACC) deaminases [45], solubilizing phosphate [46], and enhancing the uptake of nutrients from the environment [47, 48]. They also assist and enhance plant resistance to adverse environmental stresses such as drought, heavy metals, salts, and nutrient deficiency [49]. Biotic stress factors include interaction with other organisms and infection by pathogens or damage by insect pests, and some plant growth–promoting bacteria have been used as biocontrol agents against plant pathogens [50, 51]. This chapter explores the relationships between plant hosts and their

symbiotic microbial communities. We discuss and review current reports of how the plant-associated microbial community might be shaped by the host and how the plant microbiome affects plant growth, productivity, and host survival in various symbiotic associations. This knowledge will guide efforts to improve agricultural practices and predict how environmental factors will affect the microbial community and plant diversity.

2. Plant community ecology and soil symbiont interactions

Plant ecology can be affected by global climate change in terms of above- and below-ground ecological diversity in a terrestrial ecosystem. The terrestrial plant community drives dynamic changes in the soil microbial ecology that may result in alterations in ecosystem function. The ecologist Dr. Peter Chesson postulated that stabilizing mechanisms are essential for maintenance of species diversity and coexistence [52]. Bever et al. have found evidence that microbially mediated positive and negative feedback might play a crucial role in the entire plant ecosystem and contribute to these mechanisms of plant-plant interactions [16]. Traditionally, competing plant species have been thought to have strong negative intraspecific interactions for the high overlap in resource usage [53]. However, success in finding a mechanism to explain the coexistence of competing plant species in maintaining local diversity [54]. Neglecting soil microbial community feedback might be one reason.

2.1. Soil resources and microbial interactions

Soil resources can govern the coexistence of plant species by resource partitioning and sharing. Studies have found root symbionts that increase the efficiency of nutrient uptake and allow the host to persist in a low nutrient environment, thereby directly contributing to the competitive exclusion of other plants [55]. Rhizosphere microbes can alter the availability of different forms of nitrogen or phosphorus in the soil and affect plant-plant interactions via the mediation of resource partitioning [56]. Soil resources can also be transferred by shared symbiotic fungi called common mycorrhizal networks (CMNs) [57]. In nature, different plant species commonly share the broadly specific mycorrhizal fungi. Simard and Durall demonstrated the direct transfer of resources from one plant to another via CMNs with labeled carbon, nitrogen, and phosphorus [57]. Plant community dynamics are driven by the microbial mediation of soil resource partitioning and sharing.

2.2. Host response to microbes and soil community feedback

The dynamic density and composition of the rhizospheric microbes can affect the coexistence of plant species via indirect feedback (i.e., the competition or inhibition of symbionts) in the plant population [58]. Ecologists have proposed three hypotheses to explain the mechanism that produces low diversity plant communities. The *empty niche* hypothesis suggests that novel symbionts inhabit the areas invaded by invasive plants [59]. These symbionts are more efficient at resource acquisition and preferentially associated with invasive plants than with other plants. The *degraded mutualist* hypothesis suggests that invasive plants and

their symbionts inhibit the ability of the native symbiotic community to acquire resources, indirectly reducing the performance of native plants [60, 61] (**Figure 1**). Positive feedback might be exemplified by the enhanced growth and survival of exotic seedlings near native established symbionts [62, 63]. Plant monodominance, coexistence, and invasion ecology have high relation to symbiotic microbial interactions.
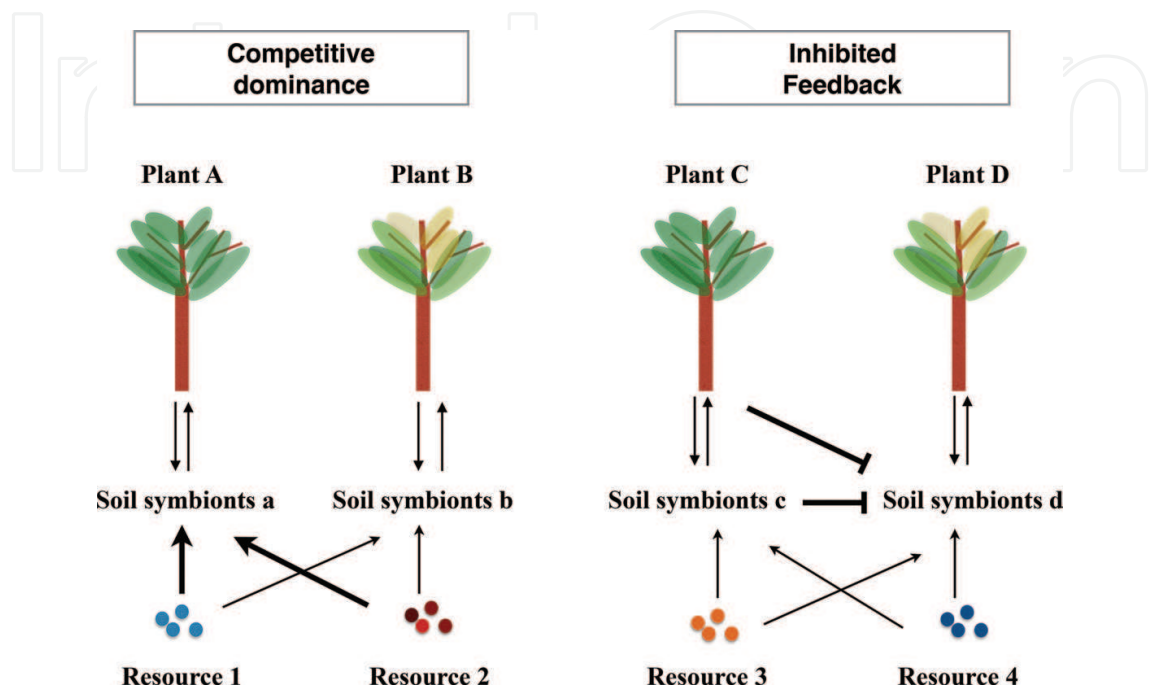
Figure 1. Plant soil community feedback in low diversity communities (modified after Bever et al. [16]).

3. Plants shape the microbial community

Microbial interactions play a crucial role in plant community ecology and performance. How do plants harbor unique microbial communities? How do plants shape a unique rhizosphere microbial community? These are the questions that must be addressed. Modern genomic technologies (e.g., high throughput sequencing) can provide clues to the answer. Lundberg et al. attempted to define the core *Arabidopsis thaliana* root microbiome [64]. They collected more than 600 *A. thaliana* plants and compared the bacterial communities using 16S rRNA gene sequencing. They observed that the root microbial communities of plants are sufficiently dependent on the host genotype to vary between inbred *A.* accessions. However, the mechanisms were not clear but included differences in the host physiology and immune responses.

3.1. Plant genes responsible for defense affect the variation of the microbial community

Several studies showed that plant genotype has a small but significant effect on the composition of the endophytic, rhizosphere, or phyllosphere microbial communities [17, 64–67]. A quantitative trait locus (QTL) analysis and a genome-wide association study (GWAS) were

used to identify taxa linked to host genes in humans, mice, plants, and flies [17, 68–70]. A GWAS of the *A. thaliana* leaf microbial community suggested that the *A. thaliana* loci are responsible for defense and that cell wall integrity affected the composition of this community [17]. Furthermore, host genetic variation shaped species richness in the bacterial community. Horton et al. showed that defense response associated genes against pathogens shaped this microbial ecosystem. In Matthew's study, 196 accessions of *A. thaliana* were sown in a greenhouse and transferred to a field site. The field experiment data suggested that the plant tissue structure (i.e., the cell wall integrity) might affect the leaf microbial community. To understand the plant host genetic factors that affect the associated microbial population, Bodenhausen et al. used a candidate gene approach to investigate the host effects on the composition and abundance of the *A. thaliana* phyllosphere community [67]. A panel of 55 *A. thaliana* mutants with alterations in the cell wall, surface structure, defense signaling, secondary metabolism, and pathogen recognition was constructed to reveal the effect on the microbiota composition and/or abundance in a small number of single host mutations. The results showed that *lacs* and *pec1* mutants affected cuticle formation, which led to an increased bacterial abundance and community composition. Moreover, the ethylene signaling gene *ein2* was observed to be a host factor that modulated the community composition. Peiffer et al. also noted that approximately 19% of the interline variation in species richness could be attributed to the host genotype in different maize lines grown in the same geographical regions [65].

3.2. Role of root exudates in shaping rhizosphere microbial community

More than a century ago, Lorenz Hiltner defined the term "rhizosphere" as the soil compartment affected by plant roots [71]. Soil microbes are chemotactically attracted to plant root exudates, volatile organic carbon, and rhizodeposition, and then proliferate in this carbon-rich environment [72]. Plant root exudates differ between plant species, so differences in rhizosphere microbiomes of different plant species are expected [73]. More recent studies have provided strong evidence for plant species-specific microbiomes [74, 75]. Plants can also shape the microbial community via root exudates. Root exudates can be categorized as sugars, amino acids, organic acids, nucleotides, flavonoids, antimicrobial compounds, and enzymes [4, 73].

3.2.1. The types of root exudate

3.2.1.1. Organic acids and amino acids

The composition of root exudates from different cultivars affects the growth of soil-borne pathogens. The susceptible peanut cultivar Ganhua-5 (GH) and the mid-resistant cultivar Quanhua-7 (QH) were chosen for a root exudate analysis and evaluated for the responses of the soil-borne pathogens *Fusarium oxysporum* and *Fusarium solani* [76]. The contents of total amino acids, alanine, and sugars in the root exudate of susceptible cultivars were significantly higher than in the mid-resistant cultivar, whereas the contents of total phenolic acids, p-hydroxybenzoic acid, benzoic acid, and p-coumaric acid were significantly lower than in mid-resistant cultivars. These differences in the root exudate composition of susceptible and resistant cultivars might be assumed to regulate the resistance mechanism in the

peanut rhizosphere. However, the spore germination and mycelial growth of the soil-borne pathogens *F. oxysporum* and *F. solani* were significantly enhanced by treatment with the root exudates from both the susceptible and mid-resistant cultivars compared with a control. If root exudates do not directly inhibit the growth of pathogens, the effects of other factors must be considered. A previous report showed that organic acids modulated the colonization and enhanced the biofilm formation of the root microbiome. Yuan et al. demonstrated that organic acids from banana root exudates facilitated the root colonization by *Bacillus amylo-liquefaciens* [77]. Fumaric acid significantly induced biofilm formation, whereas malic acid evoked the greatest chemotactic response. The results showed that organic acids from banana root exudates played a crucial role in attracting and initiating PGPR colonization on the plant roots. Rice exudates that primarily contained the amino acid residues of histidine, proline, valine, alanine, and glycine, and the carbohydrates glucose, arabinose, mannose, galactose, and glucuronic acid may induce a higher chemotactic response by the endophytic bacteria *Corynebacterium flavescens* and *Bacillus pumilus* [78].

3.2.1.2. Sugars

The amount of sugar secretion might affect infection by plant pathogens. Gou et al. showed that the *Arabidopsis* vacuolar sugar transporter SWEET2 limited the Glc-derived carbon efflux from roots and inhibited *Pythium* infection [79]. They proposed that the expression of SWEET2 modulated sugar secretion, limiting the carbon loss to the rhizosphere. The reduction of available substrates in the rhizosphere contributed to the resistance to *Pythium*.

3.2.1.3. Antimicrobial compounds

Root exudates can also participate in belowground plant defense. Low-molecular-weight antimicrobial chemicals can be divided into "phytoanticipins" and "phytoalexins" [80]. Phytoanticipins are defensive compounds that are constitutively produced and released by the plant root prior to a biotic stress such as pathogen infection. In a recent study, *Arabidopsis* roots deficient in diterpene rhizathalene A production were found to be more susceptible to insect herbivory [81]. Therefore, rhizathalene A was considered as a part of a constitutive direct defense system of the roots. Phytoalexins were defined as inducible defensive compounds that are not detected in healthy plants [80]. Five phenylpropanoid root-derived aromatic root exudates were induced by the attack of the soil-borne pathogen *Fusarium graminearum* and exhibited antifungal activity [82]. In general, root-secreted terpenoid and phenolic defensive compounds have strong antibacterial and antifungal activity [83, 84]. The largest class of plant defensive chemicals above- and below ground is terpenoids. Nonvolatile terpenoids can be secreted into the rhizosphere [85], and volatile organic compounds (VOCs) can be emitted from the roots as plant defensive compounds. Phenylpropanoids are a group of plant defensive phenolic root exudates. After a Fusarium graminearum infection, barley rapidly accumulated and secreted phenylpropanoids, which are cinnamic acid derivatives to resist a fungal attack [82]. Phenolic root exudates not only have antimicrobial activity but also beneficially attract soil-borne microorganisms that affect the native soil microbial community [86]. We have found that the same chemical compound, for example, the amino acid canavanine,

can stimulate a specific group of microbes but suppress many other soil microbes. Plants can shape the specific rhizosphere microbial community via root exudates.

3.2.2. Environmental factors effects on root exudates

Plants with different genotypes produce root exudates with different compositions. Abiotic and biotic factors also affect root exudates. Physico-chemical soil properties such as nutrient availability, organic matter content, pH, structure, and texture can affect the availability of root exudates and microbial recruitment by the plant roots. Some biotic factors such as soil microbial secondary metabolism can also affect the exudates.

3.2.2.1. Temperature

Since the onset of climate change and global warming, the resultant extreme heat and cold have affected the harvest of several crops. To elucidate the effects of temperature on root exudates, Husain and McKeen grew strawberry plants at 5–10°C and compared them with plants grown at 20–30°C. They found more amino acids in exudates in plants grown at a low soil temperature that markedly affected the pathogenicity of *Rhizoctonia fragariae* [87]. Pramanik demonstrated that in Japanese cucumber grown hydroponically in a growth chamber at high and low temperatures, the organic acid content increased with the elevation of temperature, and some of the compounds identified significantly inhibited plant root growth and/or germination of cucumber.

3.2.2.2. Soil moisture

Flood and drought have reduced global cereal harvests. Several reports have demonstrated that the soil moisture affects the release of root exudates. The temporarily wilting of plants increased the release of amino acids from the plant roots, which might be related to the incidence of pathogens in the rhizosphere [88]. Plants such as peas, soybeans, wheat, barley, and tomatoes were grown in normal moist sand and dried, remoistened sand for the liberation of amino acids. The total amount of amino nitrogen in the temporarily dried sand was many times higher than in the normal moist sand.

3.2.2.3. Soil pH and nutrition

The soil pH status and the availability of nutrients such as carbon, nitrogen, and phosphate have been found to affect the release of plant root exudates and the creation of specific chemical niches in the soil, as well as the abundance of plant pathogens and beneficial microbes [89–91]. Bowen first demonstrated a marked effect of nutrient status on the exudation of amides and amino acids from roots of *Pinus radiate* seedlings [89]. The results indicated a doubling of amides/amino acids in exudates from phosphate deficient plants. Toljander et al. analyzed the community of arbuscular mycorrhizal (AM) fungi in maize in a long-term fertilization trial and indicated the composition of AM fungi and bacteria was significantly affected and correlated with changes in pH, phosphate, and the soil carbon content [90]. Dumbrell et al. surveyed the AM fungal community of 425 individual plants from 28 plant species. The

results showed the strong support for the hypothesis that niche differentiation was based on the structuring of the AM fungal community by soil pH [91]. Root secretion of phenolics was induced in Fe-deficient soil and altered the microbial community in the rhizosphere [92].

3.2.2.4. Microorganisms

Soil microorganisms play a crucial role in plant growth and plant exudates. Microorganisms can affect exudation by affecting the permeability of root cells and root metabolism. Microorganisms can also absorb certain compounds in root exudates and excrete other compounds. Soil microbes can produce secondary metabolites that affect plant signaling and metabolism and can be considered as a "plant secondary genome" that provides plant hosts with microbe-derived compounds [93]. Some microbes and also some antibiotics (e.g., penicillin and polymyxin) increased the exudation of organic materials, altered cell permeability, and increased leakage [94, 95]. Soil microbes can also induce the exudation of phenolic compounds for enhancing plant Fe absorption in low-Fe availability soil [96].

4. Microbial community diversity and plant performances

4.1. Variation of microbial community in plant life cycle

Plant and rhizosphere microbial diversity varies throughout the plant life cycle. The factors influencing the composition and diversity of the microbial community can be classified as four processes: dispersal, drift, speciation, and selection [97]. For seed plants, the life cycle begins with a seed. Seed dispersal is an important ecological process. Seeds carry associated microbes that originate from their parent and the environment, thereby increasing the microbial diversity in a new environment. Recent studies have suggested that bacterial seed coatings can protect against pathogens [98]. Microbial seed epiphytes have an advantage over soil bacteria during plant colonization. Seed coating methods are a major area of research, and numerous patents have been filed (i.e., approximately 4000 results were found by a Google patent search for the key word "microbial seed coating" [99]. After seed dispersal, during seed germination, seed-bone microbes might gain a competitive advantage over other microbes to colonize after germination, and opportunistic microbes from the surrounding soil might have access to a novel niche as the plant develops. Microbial diversity and the community dynamically change throughout the plant life cycle.

4.2. Networking of plant-microbes (hub and edge microbes)

Plant microbiota forms a complex network. A wide range of studies has demonstrated that plant-associated microbes live either inside plant tissue or on the surface of plant organs such as the leaves and roots [100, 101]. Agler et al. characterized the microbiome of *A. thaliana* leaves [102]. Field experiments showed that both plant genotype and abiotic factors affected the microbiome composition. In addition, they observed that specific species (e.g., the plant pathogen *Albugo* and the fungus *Dioszegia*) significantly affected the microbial community structure. Agler used the term "microbial hubs" for the presence of these specific species, which were strongly interconnected with other species in the microbial network of the plants.

Microbial hubs might be responsible for mediating defense signals among plants and the effectiveness of biological control agents [19]. The term "keystone species" has been proposed for the presence of a kind of hub species that would be a determinant of colonization of widely microbial taxa. These microbial hubs and keystone species have a large impact on plant performance. A number of hypothetical relationships between plant performance and microbial diversity and composition have been proposed [19].

Microbial hubs might indirectly affect other taxa by changing host performance, response, or metabolites without directly interacting with other microbes. How can the microbial hubs be identified and how can the interaction of plants and microbes be understood? The requirement of new techniques to analyze whether a microbe has successfully entered a plant, and the observation of changes in the genotypic and phenotypic expression will be an added advantage in the study of plant-microbe interactions.

5. Plant growth–promoting microbes

The soil constitutes a pool of microscopic life forms including bacteria, fungi, actinomycetes, protozoa, and algae, and of these, bacteria are by far the most common. The highest numbers of bacteria are found in the rhizosphere, the region around the plant roots, as differentiated from the bulk soil [103]. Regardless of the concentration of bacteria in the soil, the bacteria may affect a plant in one of three ways. From the perspective of the plant, the interaction between the soil bacteria and a plant may be beneficial, harmful, or neutral [104]. Plant growth-promoting bacteria (PGPB) include those that are free living, those that form specific symbiotic relationships with plants (e.g., *Rhizobia* spp. and *Frankia* spp.), bacterial endophytes that can colonize some, or a portion of a plant's interior tissues and cyanobacteria. PGPB can promote plant growth directly by facilitating the acquisition of compounds or modulating plant hormone levels and indirectly by reducing the inhibitory effect of pathogenicity and plant growth by acting as biocontrol agents [105].

5.1. PGPB and abiotic stress

In nature, all living organisms are affected by environmental factors such as abiotic stress. Some plants have internal mechanisms to cope up with such stress, while others overcome. Abiotic stress factors include water deficit, excessive water, extreme temperatures, and salinity. The association of PGPB with certain plants can help the plants combat certain abiotic stresses and prevent the plants from dying. In the past decade, bacteria belonging to different genera including *Rhizobium*, *Bacillus*, *Pseudomonas*, *Pantoea*, *Paenibacillus*, *Burkholderia*, *Achromobacter*, *Azospirillum*, *Microbacterium*, *Methylobacterium*, *Variovorax*, and *Enterobacter* have been reported to endow host plants under different abiotic stress environments [106].

5.1.1. Cold stress

Maize plants exposed to low temperatures show reduced shoot and root growth that has been attributed to severe oxidative damage induced by cold stress [107, 108]. Treatment with *Pseudomonas* sp. DSMZ 13134, *B. amyloliquefaciens* subsp. *plantarum*, *Bacillus* simplex strain

R41 with micronutrients (Zn/Mn), or seaweed extracts proved to be beneficial cold stress protectant [109]. Inoculation of tomato seeds with plant growth–promoting psychrotolerant bacteria from the genera *Arthrobacter*, *Flavobacterium*, *Flavimonas*, *Pedobacter*, and *Pseudomonas* significantly improved plant height, root length, and membrane damage in leaf tissues as evidenced by electrolyte leakage and the malondialdehyde content [110]. A cold-tolerant PGPB *Methylobacterium phyllosphaerae* strain IARI-HHS2-67, isolated using a leaf imprinting method from phyllosphere of wheat (*Triticum aestivum* L.), showed improved survival, growth, and nutrient uptake compared to a noninoculated control at 60 days under low-temperature conditions [111]. The chilling resistance of grapevine plantlets was enhanced when inoculated with a plant growth–promoting rhizobacteria, *Burkholderia phytofirmans* strain PsJN. The root growth increased by 11.8- and 10.7-fold at 26 and 4°C, respectively, and plantlet biomass increased by 6- and 2.2-fold at 26 and 4°C, respectively [112].

5.1.2. Heat stress

The effects of global warming in recent years can be felt with the increase in global temperature. A thermo tolerant plant growth–promoting *Pseudomonas putida* strain AKMP7 was proven to be beneficial for the growth of wheat (*Triticum* spp.) under heat stress [113]. The bacterium significantly increased the root and shoot length and dry biomass of wheat as compared to uninoculated plants. Inoculation improved the level of cellular metabolites and reduced the activity of several antioxidant enzymes and membrane injury. Sorghum seedlings showed enhanced tolerance to increased temperature with the association of *Pseudomonas* sp. strain AKM-P6 [114]. Inoculation induced the biosynthesis of high-molecular-weight proteins in the leaves at elevated temperatures, reduced membrane injury, and improved the levels of cellular metabolites such as proline, chlorophyll, sugars, amino acids, and proteins.

5.1.3. Salinity

Approximately 20–50% of crop yields are lost to drought and high soil salinity [115]. The United Nations Population Fund estimates that the global human population may well reach 10 billion by 2050 (www.unfpa.org). Crop plants are very sensitive to soil salinity, and it is one of the harshest environmental factors that limits the productivity of crops. Plant-microbe associations have been found to be beneficial against abiotic salt stress in *Zea mays* upon coinoculation with Rhizobium, while Pseudomonas was correlated with decreased electrolyte leakage and the maintenance of leaf water content [116]. Salinity resistant *Pseudomonas fluorescens*, *P. aeruginosa*, and *P. stutzeri* ameliorated sodium chloride stress in tomato plants, and an increase in roots and length were observed [117]. Jha et al. demonstrated that the endophytic bacteria *Pseudomonas pseudoalcaligenes* induced the accumulation of higher concentrations of glycine betain-like compounds, leading to improved salinity stress tolerance in rice [118]. *Dietzia natronolimnaea,* a plant growth–promoting rhizobacteria, was seen to modulate a stress response gene, which led to the protection of wheat from salinity stress [119]. *Staphylococcus saprophyticus* ST1 and *Oceanobacillus profundus* Pmt2 inoculants were able to produce a biofilm and an extracellular EPS, thus helping *Lens esculenta* Var. Masoor-93 to cope with salt stress [120]. Salt-stressed *Arabidopsis* plants treated with volatile organic compounds (VOCs) from *B. amyloliquefaciens* GB03 showed higher biomass production and less Na^+ accumulation compared to salt-stressed plants without VOC treatment [121].

5.1.4. Water stress resistance

Water scarcity constrains plant productivity, and more crop productivity is lost due to water scarcity than any other abiotic stresses [122]. *Achromobacter piechaudii* ARV8 reduced the production of ethylene by tomato seedlings following water stress, and ARV8 did not affect the reduction of the relative water content during water deprivation. ARV8 significantly improved the recovery of plants when watering was resumed [123]. Water stress resistance was enhanced in green gram when treated with *P. fluorescens* Pf1 compared to untreated plants. *P. fluorescens* Pf1 was also found to produce the enzyme catalase under stress conditions, which helped to detoxify the compounds accumulated in green gram during adverse conditions [124].

Heavy metals are defined as metals with a density higher than 5 g/cm^3 [125]. Heavy metals cause a significant decrease in plant growth and protein content at high concentrations. The most common heavy metal contaminants are Hg, Cd, Cr, Cu, Pb, and Zn [126]. All of these elements are toxic to crop plants at high tissue concentrations. Heavy metal toxicity in plants leads to the production of reactive oxygen species that block essential functional groups of biomolecules. This reaction has been noted in Hg and Cd toxicity and causes oxidative injury in plants. Increasing concentrations of Hg (5–20 mg/kg soil) in tomato plant showed deleterious effects on survival percentage, germination, flowering, pollen viability, and reduced plant height. *P. putida* enhanced the Cd uptake potential of *Eruca sativa* and favored healthy growth under Cd stress by increasing the shoot length up to 27%, the root length up to 32%, the wet weight up to 40%, the dry weight up to 22%, and the chlorophyll content up to 26% [127]. Canola seeds inoculated with *Kluyvera ascorbata* SUD165 and grown under gnotobiotic conditions in the presence of high concentrations of nickel chloride were partially protected against nickel toxicity because the bacteria could lower ethylene-induced stress due to nickel toxicity [128]. *Photobacterium halotolerans* MELD1 facilitated the phytoprotection of *Vigna Unguiculata Sesquipedalis* against Hg at a concentration of 25 ppm, thus increasing productivity as well as reducing the translocation of Hg to the bean pods [121]. A plant-microbe phytoremediation system was created with the combination of vetiver grass and the functional endophytic bacterium *Achromobacter xylosoxidans* F3B for the removal of toluene in Ho et al. [129]. It was observed that *A. xylosoxidans* F3B improved the degradation of toluene in vetiver, resulting in a decrease in phytotoxicity and a 30% reduction of evapotranspiration through the leaves. Another study conducted by Ho et al. [130] observed that when *A. xylosoxidans* strain F3B was inoculated in *A. thaliana*, it helped the plant tolerate a lethal concentration of catechol and phenol and enhanced the phytoremediation and phytoprotection of the plant.

5.2. PGPB against biotic stress

Plants must withstand adverse abiotic and biotic stresses when they are sessile (**Figure. 2**). Biotic stress in plants mainly includes damage caused by other living organisms such as insects, bacteria, fungi, nematodes, viruses, viroids, and protists. Biotic stress by PGPR can affect plant growth in two different ways; by the direct promotion of plant growth by the production of phytohormones or by facilitating the uptake of certain nutrients [45]. The indirect promotion of plant growth occurs when PGPR lessens or prevents the deleterious effects of phytopathogens. *P. fluorescens* produces 2,4-diacetyl phloroglucinol, which inhibits the growth of phytopathogenic fungi [131]. Extracellular chitinase and laminarinase were
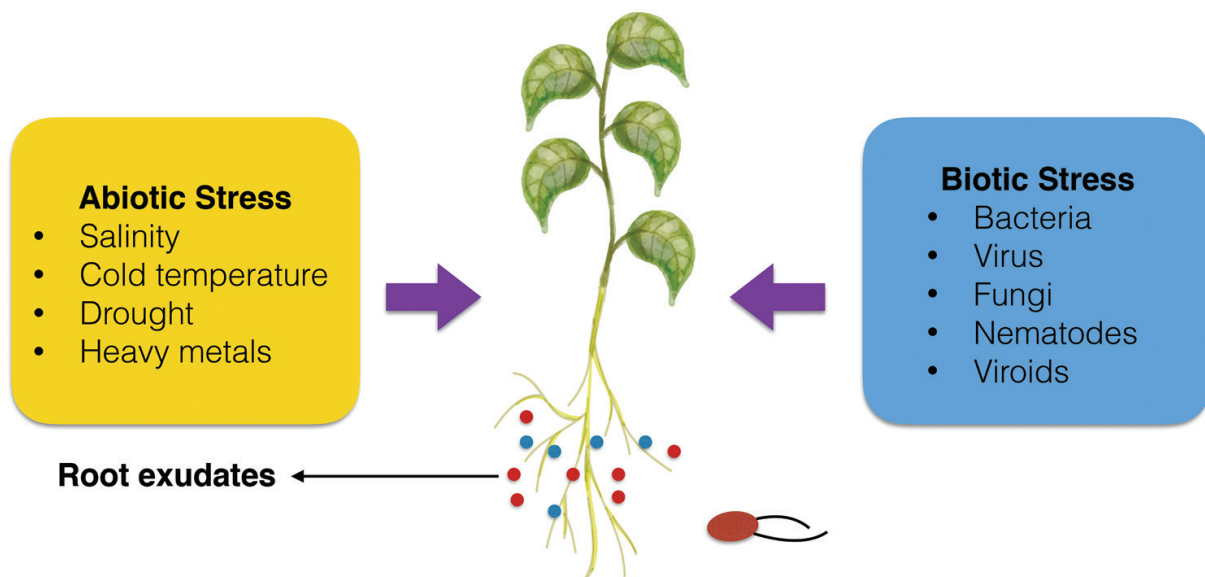
Figure 2. Factors affecting plant-microbe interactions.

produced by *P. stutzeri,* which caused the lysis of mycelia of *F. solani*, which causes root rot [132]. The endophytic *B. cenocepacia* 869T2 decreased the disease incidence of Fusarium wilt in treated banana plants to 3.4%, compared to 24.5% in noninoculated plants infected in a field test during a 7-month period [50]. The antibiotic Pyrrolnitrin, produced by *P. fluorescens* BL915 could prevent the damage from *Rhizoctonia solani* during the damping off of cotton plants [133].

Van Peer et al. [134] described a mechanism called "Induced Systemic Resistance" in carnation plants that were systematically protected by *P. fluorescens* strain WCS417r against *F. oxysporum* f. sp. *Dianthi* and by Ardebili et al. in tomato plants, in which *P. fluorescens* CHA0 protected against *F. oxysporum f.* sp. Lycopersici acted as a bio agent that induced resistance in tomato [135]. *B. amyloliquefaciens* strain FZB42, a plant root colonizing isolate, was seen to have the ability to stimulate plant growth and suppress plant pathogens [136]. In another study, endophytes were seen to protect cucumber plants against cucumber anthracnose induced by *P. fluorescens* strain 89B-61 [137] and *Achromobacter* sp. F2feb.44. *Streptomyces* sp. Zapt10, and *Bacillus licheniformis* AE6 were exploited to induce systemic resistance in cucumber against the foliar disease of downy mildew caused by the phytopathogen *Pseudoperonospora cubensis*, which enhanced yield [138].

Pest management has become an issue over time because more and more pests are becoming immune to pesticides. The global pesticide market is growing at a pace of 3.6% per year and is valued around $47 billion [139]. Development of entomopathogenic bacteria for pest management has been a new approach to handle resilient pests. Species belonging to the genera *Aschersonia, Agerata, Verticillium, Sphaerostilbe, Podonectria, Myriangium, Hirsutella,* and *Metarhizium* [140] are fungal species involved in the biological control of pests. *Bacillus thuringiensis* is the most well-known *Bacillus* species on which the efforts of the scientific community and industry have been focused [141]. *Brevibacillus laterosporus* Laubach action has

been reported to be effective against insects such as Coleoptera [142], Lepidoptera [143], nematodes [144, 145], and phytopathogenic fungi [146].

6. Future development of application

6.1. Techniques used to understand plant microbe interaction

Plants have been an integral part of our diet since humans began to farm and were no longer nomads. Since then, the world has faced a continuous challenge to feed the ever-growing population. The excess use of fertilizer is causing eutrophication [147], and genetic engineering of plants is an expensive and tedious process. The role of microbes in plant-microbe interactions has been studied in detail during the past decade [148, 149]. The results of extensive studies suggest that the exploitation of beneficial microbes is a better strategy in the long run to increase crop yield, which will play an important role in disease dissemination and control [150]. Three types of plant-microbe interactions have been studied–symbiosis between plants and mycorrhizae [151], between plants and rhizobacteria [152], and pathogenesis [153]. Omics technologies such as transcriptomics, proteomics, and metabolomics coupled with bioinformatics have been extensively applied in plant abiotic stress studies [154]. The proteomics approach has been largely adopted to investigate the protein profiles in plants in response to abiotic stresses that might lead to the development of new strategies for improving stress tolerance [155]. Microbial metabolomics is another technique that has been used to study the set of metabolites present in microbial communities [156]. A rhizosphere metabolomics–driven approach was used in the study of plant-microbe interactions for the removal of polychlorinated biphenyls as demonstrated by Lee et al. [157].

Pathogens and their emergence have been a great threat to food security, agricultural practices, and the conservation of food species, and it has become a significant task to understand the emergence of new pathogens and their role [158]. In the past, plant pathosystems were best studied one gene at a time or one protein at a time; however, the genomic era marked the beginning of the in-depth study of plant-pathogen associations [159]. Commonly known pathogen genomes have been sequenced, and the analysis of these sequences has revealed the forces that have shaped pathogen evolution and has brought to light the unexpected aspects of pathogen biology [160, 161]. The genome scale reconstruction model (GSRM) is based on metabolic reconstructions on a genomic scale for the analysis and interpretation of metabolite concentrations under specific conditions [162]. GSRM has been successfully developed for many organisms including plants, bacteria, fungi, and animals [163–165].

Various techniques to study plant-microbe interactions are sequencing, chromatography, mass spectrometry, phospholipid fatty acid (PLFA), microscopy, Fourier transform infrared spectroscopy (FTIR), nuclear magnetic resonance, and real-time PCR (RT-PCR) [166]. Further advances in the postgenomic era will pave the way for a better understanding of the interactions of endophytes, plant-pathogen, and plant immunity. Genomic tools to understand major units of the host-microbiota ecology are shown in **Figure 3**.
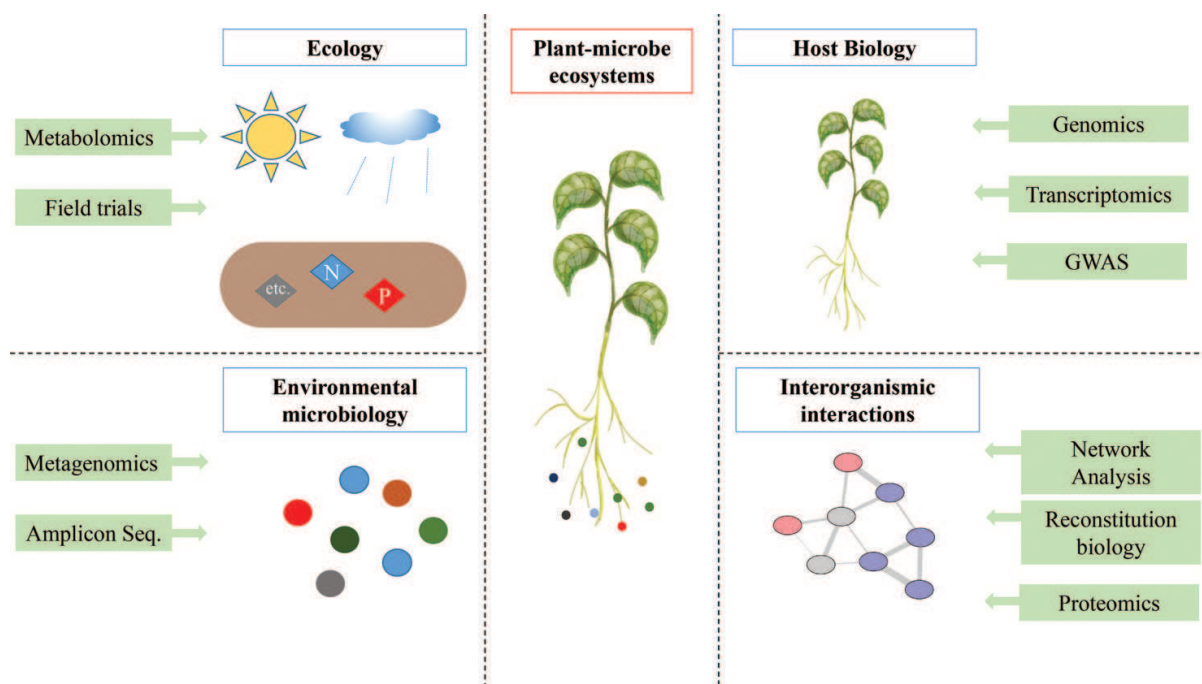
Figure 3. Genomic tools to understand major units of the plant-microbe ecological system. Colored boxes indicate technique tools that can be used to characterize key factors for the corresponding unit. (modified after Kroll et al. [167]).

7. Conclusions

In the face of pressure from climate change, contaminated environments, and crop pathogens, agricultural material and food production are currently at risk. Plant-associated microorganisms have important consequences for host health and performance. However, efforts to utilize beneficial microbes in the field have failed to consistently improve crops. The current understanding of interactions between plants and symbiotic microbial communities, the ecological consequences of plant-associated microorganisms and plant-microbial metabolic dynamics are limited. The advent of genomic approaches has helped a great deal in the understanding of the plant-bacterial interactions, but genomic approaches are still insufficient to clearly explain the interactions between plants and pathogens [168]. Approaches using metagenomics and amplicon sequencing coupled with other omics technologies [169] and the development of databases (PHI-based) [170], and metabolomics have enhanced our understanding of plant-bacterial interactions. Plant-microbe ecological communities are affected by plant genotype and environmental factors. The difference between genotypes causes different physiological and immune responses and leads to host-specific microbial communities. Plant root exudates (i.e., sugars, amino acids, organic acids, nucleotides, flavonoids, antimicrobial compounds, and enzymes) shape specific communities, attract plant growth-promoting colonization, and pathogen infections.

In the complex microbial community, we found that specific species could significantly affect the microbial community structure. Via a systems' framework of microbial network analysis, we could identify the "hub species" and "milestone species", which are candidate microbial assemblages for disease management. Network models of plant-associated microbiomes provide new opportunities for enhancing disease management.

7.1. Future perspective

The understanding of plant-microbe and microbe-microbe interactions will provide a helpful future perspective as a modulating microbiome for minimizing disease incidence and enhancing gross plant productivity. Further, beneficial plant-associated bacteria could act as counterparts against pathogens within the microbial ecosystem, as well as stabilize the ecosystem, enhance biodiversity, avoid pathogen outbreaks, and increase plant productivity. A well-studied plant-microbe partnership in the future will also help increase crop productivity at little expense and could, in turn, lead to another "Green Revolution".

Acknowledgements

Author details

Ying-Ning Ho[1], Dony Chacko Mathew[2] and Chieh-Chen Huang[2]*

*Address all correspondence to: cchuang@nchu.edu.tw

1 Agricultural Biotechnology Research Center, Academia Sinica, Taipei, Taiwan

2 Department of Life Sciences, National Chung Hsing University, Taichung, Taiwan

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