The Role of Plant Hormones (Salicylic acid and Jasmonic acid) in Shaping the Plant Root Microbiome

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Abstract

Plant microbiomes have important functions in promoting the growth and development of plants as well as extending plant immunity. Notably, plant hormones also show significant impacts on regulating the root microbiome. In this review, we focused on the techniques that are commonly used in the investigation of plant-microbe interactions. The way of the plant hormones salicylic acid and jasmonic acid shaping the microbiome is also discussed. With the improvement in the techniques and the deeper understanding of the communication between plants and microbiomes through plant hormones, a greater crop yield can be achieved.

Key terms: *root microbiome, plant-microbe interaction, salicylic acid, jasmonic acid*

Introduction

The term microbiome describes the cells and the collective genome of microbial communities that live in a particular habitat[1]. The microbiome includes diverse micro-organisms including bacteria, fungi, archaea, and viruses. These communities can be commensal (a relationship between two organisms where one benefits without influencing the other), mutualistic (a relationship where two organisms benefit from each other), or pathogenic (a relationship between two organisms where one causes the disease to the host)[2]. Land plants are continuously exposed to all kinds of micro-organisms including bacteria, fungi, and archaea. Microbiomes can also be found on plants tissues such as leaves, stems, and roots. Moreover, the root-related microbial communities could be further distinguished into different compartments. For example, the endophytic compartment (EC), rhizoplane, and rhizosphere are the distinct compartments of root and the soil surrounding[1].

As the microbiome in the rhizosphere is persistently studied, some important functions of the constituent microbes are revealed, including the acquisition of nutrients, disease resistance, and stress tolerance. For nutrients acquisition, the symbiotic relationship between arbuscular mycorrhizal fungi (AMF) and *rhizobium* bacteria is widely studied. Some commensal plant growth-promoting bacteria can also provide plants with insoluble minerals and improve the architecture of the root system. Moreover, in the plant defense system, the plant exudates impact micro-organisms in soil as the first defense line against soil-borne pathogens. The microbes associated with plants will alter plant evolutionary responses to environmental stress through at least three pathways that are not exclusive to each other. The pathways include changing the fitness of individual plant genotypes, expression of plant traits related to fitness, and direction of natural selection occurring within populations that experience environmental stress through the microorganisms' effects on reproductive fitness[3].

The root microbiome can be varied by different factors. For example, in the research comparing the microbiome in plants in different geographical locations, soil type is found to have a major effect on determining the composition of rhizobiomes[4]. More importantly, the root microbiome is influenced by the plant genotype. The plant exudate is one of the ways plants tune the

microbiome. The root exudates are a mix of all kinds of compounds including carbohydrates, amino acids, and organic acids. These compounds generate the gradient of carbon sources, phytochemicals, oxygen as well as pH and hence influence the root microbiome composition[5].

Besides plant exudates, plant hormones are also involved in regulating the root microbiome. Plant hormones are the chemicals in plants that are involved in cellular processes. There is a large variety of plant hormones. Table 1 summarizes the major hormones in plants and their main functions. Studies suggested that plant hormones can shape the microbiome by triggering immune pathways[6]. This review will focus on some techniques that are applied commonly to study plant-microbiome interaction and the role of jasmonic acid and salicylic acid in shaping the root microbiome on plants.

Hormone name	Primary functions
Auxin	Auxin is important to the growth and development of plants. The ability of auxin to drive the elongation of hypocotyls, epicotyls, and coleoptiles is widely studied[7].
Salicylic acid (SA)	SA has an irreplaceable role in plant immunity. This hormone is found to take part in both pathogen-associated patterns (PAMPs) triggered immunity (PTI) and induce effector-triggered immunity (ETI). In the meantime, it also has interactions with other plant hormones such as auxin, and ABA to help regulate plant growth and adaption to abiotic stress[8].
Jasmonic acid (JA)	JA is an essential hormone in plants. It is involved in multiple important biological processes in plants. For instance, it involves the plant immunity system, it also has interactions with SA which is mainly related to plant resistance. It also involves the mediation of stress and control stomatal opening and closure[9].
Ethylene	Ethylene is mainly involved in regulating the developmental process of plants. It also involves the stress response of plants. Furthermore, it also shows a response to other plant hormones[10].
Abscisic acid (ABA)	ABA is very crucial in regulating the growth and development of the plant as well as seed development. It also involves stress response and controlling the stomata opening and closure[11].
Gibberellic acid (GA)	GA involves in various biological processes. It takes part in seed dormancy and development, cell elongation, flowering initiation, sex expression as well as embryo development[12].
Cytokinin	Cytokinin is found mainly related to the growth and development of plants in all kinds of aspects such as leaf development, root development as well as vascular development[13].

Table 1. Some common hormones in plants and their main functions in plants.

Techniques of investigating plant-microbiome interaction
Arabidopsis thaliana as a model plant
Arabidopsis thaliana is a plant that is widely used as a model plant in studies about botany. This is because it has a small size and a short life cycle last (8-12 weeks). *A. thaliana* is also self-pollinating, and offspring tend to have highly homozygous gene loci. However, it can also be cross-pollinated manually. *Arabidopsis thaliana* also has a very small DNA content with only

100 Mbp per haploid genome. Therefore, its genome is easy to be edited and multiple mutants can be created[14]. Several mutants of *Arabidopsis* are already identified to detect the impact of change in host hormone production on the composition of the root microbiome. For example, *sid2* mutation reduces the accumulation of SA; *npr1* causes a deficiency in SA signaling, and *fad7/8/9* is a triple mutant deficient in JA accumulation[1]. More importantly, pathosystems can be developed in *Arabidopsis* through two ways: 1. inoculate pathogens from closely related plant species and see whether the pathogens can also cause disease in *Arabidopsis*, 2. Seek for naturally infected *Arabidopsis*. With the development of these pathosystems that show useful variation in the host response to pathogens, more problems about plant disease could be addressed[14].

Technology to determine the composition of the microbiome
There are multiple techniques used to determine the members of the root microbiome and they can be categorized into culture-dependent and culture-independent methods.

The culture-dependent method were early developed techniques. It aims to study the behavior of the microbes under defined conditions[15]. In the study of microbiome, scientists culture micro-organisms in the laboratory for the purpose of characterizing the microbial community[1]. For example, one study used transposon sequencing of *Pseudomonas* to identify genes that are related to root colonization of *Arabidopsis*. The culture-dependent techniques might not be expensive but could be time-consuming. One significant limitation of this method is that the microbiome formed in this method is incomplete and has reduced diversity compared to the actual environment[15][1]. Therefore, the microbiome might not be representative[15].

Unlike the culture-dependent method, culture-independent techniques are the molecular biology techniques that bypass the necessity of culturing microbes in the lab. Its biggest advantage is it could show the full picture of the root-associated microbiome. However, current culture-independent techniques still have limitations, as discussed below.

16s amplicon sequencing and shotgun sequencing are the two most commonly used techniques of finding out "Who is there?" in the microbiome. They are both culture-dependent techniques.

In 16s rRNA gene sequencing, the region coding for 16s rRNA is amplified with PCR using primers that recognize highly conserved regions of the genes and sequenced. The amplified sequences are then clustered into operational taxonomic units (OTUs) based on their similarities. Certain assumptions can arise from the clustering, for example, sequences of 95% identity can represent one genus, while sequences of 97% identity can represent the same species. This method shows several advantages[16]. First, it requires a relatively low cost. Second, the data analysis can be performed by established pipelines. Finally, there is also a large database for reference. However, the limitation of this technique is that the annotation is based on an assumed association of the 16s rRNA gene with taxa defined as an OTU. Also, the OTUs are generally analyzed at the phyla or genera level and are less accurate at the species level. Moreover, because only the 16s rRNA gene is sequenced, other genes are based on the predicted OTUs. Therefore, the lack of direct gene identification might limit the understanding of the microbiome because of the existence of numerous bacterial strains[17]. Also, in 16s rRNA gene sequencing, the primers targeting the 16s rRNA gene are highly conserved. Therefore, the primers might not only

target bacteria but also organelles such as mitochondria. This might influence the analysis of the microbiome that also contains plant materials[1].

For shotgun sequencing, it sequences the whole genome including the overlapping region with random primers. This method owns the strength of having reinforced ability in identifying bacteria at a species level. Due to the increase in length of reads and the assembly of contigs, the accuracy of species detection is also increased. Furthermore, shotgun sequencing has the capacity of identifying specific genes in the microbiota. It has better detection of the diversity and the prediction of genes. However, there are still disadvantages in applying shotgun sequencing: 1) It is more expensive compared to 16s rRNA sequencing, 2) it requires a much more extensive database when analyzing the data[17].

Role of plant hormones: salicylic acid and jasmonic acid in plant-microbiome interaction

Role of salicylic acid in shaping plant microbiome

Salicylic acid (SA) is a plant hormone that is universally appeared in all plants. The basal level of SA varies among different plant species[18]. For most of the plants, the SA level is relatively low during the normal growth and development process because a high level of SA may inhibit plant growth and development[19]. For example, in *Arabidopsis* the basal level of SA is around 1.a µ/M while in other species such as potato and rice the basal level of SA will be higher[20]. The changes in the surrounding environment will alter the concentration of SA in plants. These changes can be both biotic and abiotic.

When plants are under biotic stress, the SA level increases. For example, when *Arabidopsis* is infected by the fungal biotroph *Erysiphe orontii* or the bacterial necrotroph *Pseudomonas syringae pv. Maculicola,* the SA level in plants increases[21]. During this process, SA is synthesized from chorismite depend on the ICS (isochorismate synthase) genes. Some bacteria such as *Pseudomonas aeruginosa* is also found to produce SA with ICS. Studies also show that the inoculation of *Mentha x piperita* plants with different rhizobacteria strains may lead to the increase of endogenous SA production[18]. The SA level will also increase when plants are under abiotic stress. Heavy metal stress can be one of the most common stresses to plants and could impose serious effects on plants and even humans through the food chain. Research on maize showed that when a plant is exposed to Cd, the SA accumulation will increase significantly. Furthermore, other abiotic stresses such as cold will also induce the production of SA in plants[18].

The mechanism of SA influencing the root microbiome is complex. The SA can influence the root microbiome both directly and indirectly. Multiple lines of evidence suggest that SA could influence the assembly of the microbiome indirectly through an immune response. It could participate in multiple immune pathways especially systemic acquired immunity. The SAR immune response is triggered by local pathogen attack of leaves and leads to plant-wide protection including distal and uninoculated organs[22][23]. The study had shown that the activation of SAR can change the rhizobiome in *Arabidopsis*[24]. Moreover, in another research that used both SA *Arabidopsis* mutants and exogenous application of SA, the root microbiome compositions are both found to be different after applying the two methods. For instance, in the mutant *cpr5* (hyperimmune), nine members of Actinobacteria showed reduced relative abundance while 12 Proteobacteria members showed increased relative abundance. In the

experiment that used exogenous SA application, *Terracoccus sp. 273 (Actinobacteria)* was enriched in the root endophytic sample. These results showed SA influences the root microbiome by selecting different bacterial taxa (the bacteria can use SA as a carbon source or a growth-promoting factor) through its function in homeostatic control of immune system outputs[25]. These two studies suggest a general mechanism of SA can influencing the root microbiome through participating in immune activation, but a more detailed understanding of the SA-related immune signaling pathways influencing the root microbiome is still needed. The SA can also influence the root microbiome directly. For example, the growth of fungi *Fusarium oxysporum f. sp. Niveumcan* is inhibited by SA when it is released as a root exudate in watermelon[26]. Furthermore, the hormone SA is also found to be synthesized in some microbes such as beneficial root fungi *Indica* and *Mortierella hyaline*. However, the function of SA produced on plant colonization is still unknown. Studies showed that bacterial-producing SA might also support the growth of bacteria under iron limiting condition[23].

Role of Jasmonic acid in shaping the root microbiome
The hormone jasmonic acid (JA) and its derivatives can be found in higher plant species ubiquitously. They are all fatty acids that are derived from cyclopentanones and belong to the family known as oxylipids. Normally, there are high levels of JA in reproductive tissues, flowers, and seeds. It has been suggested that high levels of JA derivatives in *Zea mays* may be related to sex determination of the male reproductive structure[27]. However, the level of JA is very low in root and mature leaves[28]. As observed with SA, the concentration of JA in plants is also influenced by the surrounding environment that includes both biotic and abiotic environmental factors.

When the plant is under attack by herbivory insects, pathogens (specially necrotrophs) as well as wounding, JA can be synthesized rapidly[29]. All kinds of abiotic environmental factors could also impose changes in the concentration of JA, especially abiotic stresses. For example, when drought happens, there will be a rapid increase in endogenous content of JA and gradually decrease to basal level when drought continues. Moreover, the endogenous JA content was also found to increase to a larger extent when the plant (*Arabidopsis*, tomato, potato) is treated with salt. It is worth noting that the JA concentration increases in salt-sensitive plants but nearly has no change in salt-tolerant plants[9]. To summarize the synthesis process, JA is produced through the consistent action of enzymes in plastids, peroxisome, and cytoplasm. The stresses activate phospholipase in the plastid membrane and promote the synthesis pf linolenic acid. The linolenic acid will then be converted to 12-oxo-phytodienoic acid (12-oxo-PDA) through oxygenation with lipoxygenase (LOX), allene oxide synthase (AOS), and allene oxide cyclase (AOC). JA is then synthesized from 12-oxo-PDA by the activity of 12-oxo-phytodienoic acid reductase (OPR) and 3 cycles of beta-oxidation[9].

Similar to SA, JA can also influence the root microbiome directly or indirectly. The mechanism of JA influencing the root microbiome indirectly is also related to plant immune response, but JA participates in different pathways compare to the SA. In the research that applies exogenous JA to activate plant immune response, the rhizosphere bacterial community is influenced. The bacterial population that was enriched was found to have a close relationship with organisms that involve in plant defense. For example, a *Bacillus* population is found to be enriched upon the

activation of JA-mediated immune response. This population is close relative to the strain MHS022 that is known to produce antifungal volatiles acetamide and benzothiazole. However, the bacterial populations that were found to be related to plant growth such as *Bacillus niacini* were suppressed[30]. The tudy had suggested that with different modifications of the JA-mediated immune pathways using *Arabidopsis* mutants, both the composition of root exudates and rhizosphere bacteria and archaeal communities are affected, and the changes are found to be correlated to each other. For example, in the mutants of *Arabidopsis myc2* and *med25* (the former one has an increase in expression of defense gene but with weakened wound and insect response while the latter one has weakened herbivory and wound responsive pathway), the release of asparagine, ornithine, and tryptophan was reduced[31]. According to studies, glutamic acid and tryptophan are chemotactic to plant-associated bacteria, including *Rhizobium leguminosarum, Bacillus subtilis, Bacillus megaterium, Pseudomonas putida, Pseudomonas fluorescens*, and *Azospirillum brasilense.* These findings proposed the mechanism of JA influencing the root microbiome through changing root exudate composition by regulating immune response[31]. In the oot microbiome, some microbes are detected to synthesize JA. For instance, ectomycorrhizal fungus *Pisolithus tinctorius* can synthesize metabolize JA[23]. However, whether the hormone produced by the fungi can influence the root microbiome directly is still needed to be explored further[32].

The interactions between SA and JA

A large number of studies suggested that there are complex interactions between the hormone SA and JA. Both SA and JA mediated signaling pathways can be triggered. For instance, when plants are under attack from virulent *Pseudomonas syringae* both SA and JA signaling pathways will be activiated[33]. Under certain situations, one hormone signaling pathway will be more prioritized than the other one. For instance, the SA pathway that is induced by avirulent *P. syringae* will suppress the JA-signaling pathway. However, when the *Arabidopsis* is treated by *Pseudomonas sp. CH267*, the systemic susceptibility will be induced[33]. The SA and JA tradeoff will shift toward JA dependent pathway against herbivores while sacrificing SA-related defense against bacterial pathogens. When the surrounding environment changes, plants shift between the SA and JA mediated pathways. The change in the signaling might influence homeostatic control and secondary metabolites secreted by plant roots and hence influence the root microbiome composition[32].

Discussion/conclusion

Techniques that are used to investigate the microbiome

In this review, *Arabidopsis thaliana* is discussed as a model plant. It owns unique characteristics (e.g., short life cycle, easily edited genes, etc.) that make it suitable to be used as a model plant in a wide range of research that is related to plants. The techniques (16s rRNA gene sequencing and shotgun sequencing) of identifying the compositions of the microbiome are also introduced. Moreover, the culture-dependent and culture-independent approaches of analyzing the microbiome are also discussed. These techniques are broadly used for investigating the plant-microbiome interaction. In the studies mentioned in this review, scientists used *Arabidopsis* mutants with altered hormone production and signaling to investigate plant microbiome interactions[25][31]. Moreover, both studies used 16s rRNA gene sequencing to analyze the microbiome composition.

As mentioned in the review there are limitations on the techniques. Therefore, it is important to have multiple experiments to investigate the impact of plant hormones on the composition of root microbiome more accurately. In the paper written by Lebeis et al., both exogenous applications of plant hormones and *Arabidopsis* mutants are used in the research to find out the mechanism of SA influencing the root microbiome[25].

The role of Salicylic acid and Jasmonic acid in shaping root microbiome
Plants and microbes are interacting with each other incessantly. For plants, they are trying to build up attractive habitats for beneficial microbes to colonize. However, this will also introduce pathogenic microbes. Therefore, plants need to build up mechanisms to select and manage the members in their microbiomes[34]. In this process, plant hormones play an irreplaceable role. To study the complex interactions between plant hormones and the microbiome, multiple techniques are developed. Researchers can investigate the mechanisms of plant hormones influencing microbiomes using combinations of techniques.

This review mainly focused on the plant hormones JA and SA. In the review, the basal levels of the two hormones were discussed and both biotic and abiotic factors can trigger the change in the level of the two hormones. Both of them can influence the plant microbiome directly or indirectly: (1) The two hormones can regulate the rhizobiome through their immune signaling pathways when the plant immune response is triggered. (2) Plant hormone can also make direct chemical interactions with microbes when it is secreted as root exudate or when members of the microbiome produced them. Moreover, under different conditions, the plants will shift their immune signaling pathways toward one than the other one[26,32]. However, further understanding of the mechanisms of plant hormones influencing the root microbiome is still needed. The function of phytohormone-producing microbes shaping the root microbiome is still needed to be explored further.

Besides focusing on the role of SA and JA shaping the root microbiome, the functions of other plant hormones in shaping microbiomes on other locations of plants are also studied such as the phyllosphere (the habitat for microbes provided by the parts of plants that is above ground) is also being studied[35]. The communication between plants hormones and microbes is studied in other agricultural plants as well. For instance, plant-microbiome interactions in peanut (*Arachis hypogaea L.),* legume, wheat (*Triticum aestivum*) and, rice (*Oryza sativa)*[36,37]. With a deeper understanding of the interactions between plant hormones and microbes and the mechanism of hormones regulating the microbiome, an enhanced crop yield can be achieved. For example, understanding of the JA-signaling pathway can be used to attract and maintain beneficial microbes and breeding microbe-optimized plants as well as specific plant-optimized microbiomes which are useful inoculants[38].

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