Chemistry of Plant–Microbe Interactions in Rhizosphere and Rhizoplane

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ABSTRACT
In recent years, the great studies has been made on the the plant to plant and plant microbes interactions. It has become most interested topic for plant pathologists and other Researchers. There is the formation of biofilm that have a lot of beneficial microbes that induce the resistance in hosts in regarding to many of plant pathogens. Furthermore, the communication between plant physiological processes below-ground and above-ground induces the complexity. The main aim of metabolomics studies is to explore and annotate all exo- and endo-metabolites that are present in the biological system that work out and take part in physiological processes. Recent investigation and studies has enabled researchers to explore hundreds of compounds in one single sample over a small period of time. Regarding to these metabolomics, Plants-Microbial Interactions has been explored in this review article.

Keywords: Rhizosphere, PGPRs, Chemical communication, Metabolomes, Induced Systemic Resistance.

INTRODUCTION
It has been estimated that by end of 2020, there will be the need of about 28.8 million tons of nutrients for the obtaining and production of 321 million tons of grain food. But still the availability of nutrients is only 21.6 million tons. There is a gap of 7.2 million tons between the nutrient supply and the nutrient removal (Gupta et al., 2015). In this way, world is facing a many of concerning challenges to obtain significant food in a sustainable manner, fulfilling the needs of an increasing global population because of decreasing food resources. The production of food from the plant is reduced by a superabundance of biotic stresses caused by pathogens (Williams & Hammitt, 2001, & Matson et al., 1997).
Innate immunity of that plants is the main way to defend themselves from pathogenic microbes (Nürnberger et al., 2004). The plants rely on their natural immunity and success in fighting disease against the infections or herbivore feeding depend upon the factor that how rapid and how much strong the plant have immune system (Heese et al., 2007).

Now a days, Genetic modification has been used to combat many of infectious diseases and decrease the use of pesticides and herbivore agrochemicals, that have health hazardous effects hence, the need for new eco-friendly strategies (Dixon et al., 2001). In the case of plant pathology, use of beneficial microbes is referred as eco-friendly strategies for bringing a stimulus against the disease or treatment to improve the responses against upcoming biotic and abiotic challenges. It is done by priming i.e. colonization of plant roots with beneficial microorganisms in the rhizospheric zone (Conrath et al., 2006). This priming results in bringing positive effects on the ability of the plant to defend itself against upcoming biotic and abiotic challenges. So, this interaction results in chemical communication between plant roots and plant-beneficial rhizobacteria and fungi and plant pathogenic microbes which is an eco-friendly method to combat with pathogens and herbivores (Johansson et al., 2004).

**Natural Obstacles for Interactions with Rhizomicrobes**

The complexity of the rhizosphere is associated with an ecosystem consisting of different microorganisms that increase plant growth through different mechanisms (Shi et al., 2016). Chemical communication plays a vital role in establishment of mutual relationship between plant roots and PGPR. Plants determine the community of PGPR present in the rhizosphere (Gray et al., 2005). In order to explore the rhizosphere signalonics several metabolites have been identified as the major messengers between plant roots and PGPR. Root exudates and other metabolites including primary and secondary metabolites as well as non-volatile and volatile metabolites play important roles in establishment of mutual relationships (Bertin et al., 2003). PGPR also interfere with the signaling linked phytohormone to inhibit or limit defense responses. PGPR enhance plant growth and also prime plants against infection caused by various different phytopathogens (Tank & Saraf, 2009).

The complex rhizosphere interaction between plant roots and PGPR leads to pre-conditioning of plants for an enhanced defense response against secondary stimuli. When secondary stimuli are received, the triggered events occur in an enhanced way (Conrath et al., 2006). These native, primed and triggered physiological states are resulted in changing in the metabolomes. It is investigated through targeted and untargeted metabolomic activities.

**Chemistry of Plant Immune Responses**

Plants use innate defense mechanisms against the both entrance of pathogen and herbivore feeding. Mostly this defense mechanisms is used by plants (Muthamilarasan & Prasad, 2013). But when the pathogen is more virulent or the host is not much resistant against that virulent pathogen, this innate immunity will not work properly in this situation. This failure of innate immunity, either below the ground or above the ground, will result in activation of another immune response is known as MAMP-Triggered Immunity (MTI) (Lewis et al., 2015, Newman et al., 2013). This MTI is the immunity triggered by Microbe-Associated Molecular Pattern. This immediate immunity depends on the signals received from MAMPs through specific Pattern Recognition Receptors (PRRs). These PRRs play an important role in the proper functioning of the plant immune system. These PRRs are germline-encoded host sensors for detection of pathogens (Zipfel, 2014). Some pathogens secrete special types of effector molecules that have ability to reduce the activity of MAMP-Triggered Immunity (MTI). This mechanism produces susceptibility in the host called Effector-Triggered Susceptibility (ETS) (Faris et al., 2010). This whole situation result in activation of second layer of immunity that is Effector-Triggered Immunity (ETI) which
bring rapid and robust response in plant against pathogens and is brought by specific resistant proteins present in plant (Cui et al., 2015). This Effector-Triggered Immunity (ETI) has a great association with hypersensitive response (HR) of plant.

There is another pattern of immunity that is aroused because of damage cause by pathogens i.e. from necrotic, damaged or stressed cells. This immunity is brought by the molecules called Damage-associated molecular patterns (DAMPs) (Ferrari et al., 2013). These molecules are recognized by plants in the same way as Microbe-Associated Molecular Pattern (MAMPs) and plants respond by activating defense cascades of signals (Tena et al., 2001). Actually, this signaling defense system is not much simple as it looks like. The complexity of basic signaling defense system is because of other phytohormones including auxins, ABA, cytokinin, brassinosteroids and gibberellins (Mine et al., 2018). This activity of phytohormones interplay in the background. The chemical communication between plant and microbes is very important to establish an effective symbiotic relationship between plants and PGPR and this chemical communication between plant and microbe is done on the bases of barriers and innate immunity defenses.

**Chemical Communication With in the Rhizosphere**

The rhizospheric zone is directly associated with a large number of microorganisms. Rhizosphere community members interact with roots and this interaction is done through chemical communication (van Dam & Bouwmeester, 2016). There are diverse rhizospheric communities that are naturally occurring in soil.

The microbiologists and other scientists have declared some microbes as a model organisms for plant growth promotion which are well-studied in their mode of action and regulation. From bacteria, they are the members of the genera Bacillus, Pseudomonas, Azospirillum, Rhizobium, Stenotrophomonas, Serratia and Streptomyces and from fungi are Trichoderma, Ampelomyces and Coniothyrium (Berg, 2009). There are many other factors which are involved in plant–microbe interaction and can be identified by various Molecular Techniques.

Hence, a lot of microorganisms including nematodes, fungi, bacteria, arthropod and herbivores are present in rhizosphere. These organisms, alone and in combination, interact with the plant. This interaction is base upon the chemical communication between them (Badri et al., 2009). As the other forms of communication are not feasible below the ground, therefore, these soil microbes mostly rely on chemical communication. The roots of plant secrete the special types of root exudates which contain an array of primary and secondary plant metabolites that have ability to attract the beneficial microbes and deter, or kill insect herbivores, nematodes and other microbes including nematodes, fungi and bacteria that are competing the plants (Bais et al., 2008). The scientific study and analysis of the metabolites is metabolomic study. The metabolomic study of root exudates is very helpful in better understanding this chemical communication between microbes and plant roots. The spatial explicitation of metabolomes of root and its exudates that is relevant for the rhizospheric communities can be done by novel technologies.

**Rhizospheric microbes and Plant-roots Interactions**

The interactions of plant roots and other biotic and abiotic environment factors is done by secretion of a large number of primary and secondary plant metabolites into the rhizospheric zone. Even a small plant can secrete more then hundreds of different metabolites through the root exudates (Canarini et al., 2019). The rhizospheric zone containing nematodes, bacteria, fungi and arthropod herbivores is considered as one of the most complex ecosystems on earth. The rhizospheric zone is associated with increased microbial abundance and activity. The most commonly occurring PGPR genera present in
the rhizosphere are Pseudomonas, Bacillus, Enterobacter, Burkholderia, Acinetobacter, Paenibacillus and Arthrobacter.

Microbiologists and other scientists are working on the advancement in plant-beneficial microbe interactions to develop and commercialize beneficial microbial inoculation to improve plant health. These inoculants contain natural or synthetic communities of beneficial microbes. It can be achieved by introduction of new microbial community into the soil. The interaction of these microorganisms with each other and with the plant is achieved by chemical communication in a very sophisticated manner, established in the rhizosphere.

Plants and plant growth promoting rhizobacteria (PGPR) secrete various chemical compounds that are beneficial for establishment of mutual relationships between them. This below – ground interaction primes and produce response in plants against various environmental stimuli that may be abiotic as well as biotic stresses. On receiving the priming stimulus any of abiotic or biotic stresses leads to activation of signaling molecules, regulation of primary metabolism and activation of gene to produce enzymes involved in the production of secondary defense metabolites. In case of a secondary stimulus, the same process is occur as in the priming stage takes place but in secondary stimulus the process occur at enhanced level to reduce and minimize the impact on the plant (Berbara & García, 2014). Trans-generational priming is the ability of plants in which they pass on the induced primed state to their progeny.

**Regulatory Networks for Communication of plants with microbial world**

Agricultural use of potentially beneficial rhizosphere microbes is rapidly increasing day by day because of their multi-functional benefits including plant-protection and growth regulation. Plant growth promoting rhizobacteria (PGPR) are most commonly used (Lugtenberg & Kamilova, 2009), non-pathogenic microbes which bring direct benefits to the plants while there also some bacteria in rhizospheric zone which indirectly help the plants by inducing the defense response in plant and ameliorating the biotic and abiotic stress (Kloepper et al., 1980). These direct or indirect effect for regulation take place through highly specialized communication system that is induced in plant through multiple levels of interaction. The activation of host immune responses upon requires comprehensive and precise genetic expression for reprogramming and communication between hosts and microbes on the bacterial infection or rhizobacteria perception (Van wees et al., 2008).

During the the few last decades, potential strategies of inoculation of PGPR has emerged have been made to induce tolerance against the biotic and abiotic stress in plants; hence, it is important to explore the basis of these interactions.

Over the years, use of PGPR is becoming more trending phase and extensive studies are being made for the use of PGPR for the plant growth promotion. The use of PGPR is promising alternatives to chemical fertilization, pesticides, and herbicides. PGPRs improve beneficial properties through direct mechanisms and indirect mechanism including mineral solubilization (Ashraffuzzaman et al., 2009), nitrogen fixation (Malik et al., 1997), siderophore production (Lenin & Jayanthi, 2012), biosynthesis of phytohormone (Maheshwari et al., 2015), production of antibiotics (Fernando et al., 2005), production of hydrolytic enzymes (Hafeez et al., 2011), Production of Lipopolysaccharide (LPS) and Induced Systemic Resistance (ISR) (Bent, 2006). Major all classes of molecules secreted by PGPRs are involved in Protection of plant against soil-borne pathogens and induction of Induced Systemic Resistance (ISR).

Many of antibiotics and other related molecules are secreted by certain bacteria including Bacillus and Pseudomonas genera. These antibiotics and other related molecules are secreted by bacteria have a great ability to inhibit pathogen growth even at low concentrations. Such antibiotics and other related compounds from Bacillus and
Pseudomonas genera are the widely studied in disease management. *Pseudomonas fluorescens* produces 2, 4 diacetyl phloroglucinol (2, 4 DAPG) (Bangera & Thomashow, 1999) which is an antibiotic and have the great activity against the soil-borne pathogen *Sclerotium rolfsii* and has a 75% inhibition effectiveness. Phenazine-1-carboxylic acid is another microbial antibiotic that is produced by rhizosphere Pseudomonas species. Phenazine-1-carboxylic acid (PCA) causes oxidation-reduction and accumulation of superoxides in target cells. The wide distribution of phenazine-1-carboxylic acid also facilitates the evolution of a pathway to catabolize phenazine-1-carboxylic acid for microbes (Mavrodi et al., 2012). Phenazine-1-carboxylic acid is effective against wheat disease caused by *Gaeumannomyces graminis* var. *tritici* and stem rot in groundnut caused by *Sclerotium rolfsii*. Another novel antibiotic is zwittermicin produced by bacterium *Bacillus cereus*. Broad spectrum activity enables Zwittermicin to suppress plant disease (Stabb et al., 1994) caused by gram positive and gram negative prokaryotic micro-organisms. Some other bacteria secrete hydrolytic enzymes that have ability to degrade numerous cell wall components of oomycetes and other fungi. These hydrolytic enzymes are proteases, lipases, amylases, glucanases and chitinases.

**Metabolic Events associated with Priming ability of PGPR**

The priming ability of PGPR is associated with key metabolic events. Mainly, the metabolic events associated with activity of PGPR are modification of cell wall, primary metabolite modification, expression of defense genes and biosynthesis of secondary metabolites (Khan et al., 2019). The priming of PGPR can be divided in to three major events including perception of the priming stimulus, secondary stimulus and trans-generational priming. In early stages of priming, the signaling by phytohormones and other signaling molecules occurs. In different stages of plant defense responses or plant priming, phytohormones are very important plant metabolites. For example, major hormones in PGPR priming induction are jasmonic acid (JA) (Van der Ent et al., 2009) and ethylene (ET), while the major hormone involved in systemic acquired resistance (SAR) is SA. Other phytohormones including auxins, cytokinins, gibberellins, ABA and brassinosteroids also play a vital role in plant resistance. These hormones act as either antagonistically or synergistically to reprogram the defense mechanism (Spoel & Dong, 2008). Secondary metabolites also play a vital role in plant defense systems and environmental adaptation. PGPR stimulates the secondary metabolism through different chemical molecules.

**Mechanisms of plant growth promotion by microorganisms**

The Plant–microbe interactions involve diverse mechanisms. The direct mechanisms of plant growth promotion are similar to the disease suppression process. The success of mechanisms of plant growth promotion can vary within different pathosystems and rhizospheric atmosphere. For the successful plant–microbe interactions, the ability of microbes to colonize plant habitats is important.

Colonization of microbes requires the few steps including recognition, adherence, invasion, colonization and growth. Microbes also use several strategies to establish interactions. Plant roots initiate interactions with soil microbes by producing some chemical signals that are recognized by the microbes, which in turn produce signals that start-up the colonization of microbes. To take part in this crosstalk, motile organisms are much at benefit.

The production of phytohormones including indole-3-acetic acid (IAA), ethylene, gibberellins, and cytokinins, play an important role in process of plant growth (Jeon et al., 2003). These mechanisms of plant growth promotion involve the Production of PGP by microorganisms. Actually, a lot of mechanisms are involved in plant–microbe interaction. Even in cases of individual beneficial plant–microbe interactions, several mechanisms take part.
Direct mechanisms of plant growth promotion have great similarities with disease suppression process. For establishment of a successful plant–microbe interactions, the ability of microbes to colonize plant habitats is important. The production of phytohormones can be done by the plant themselves and by their associated microorganisms. Furthermore, bacteria which are plant-associated can influence the hormonal balance of the plant.

The plant–microbe interaction can be explained by example of IAA phytohormones which is produced by root-associated bacterium Serratia plymuthica HRO-C48 in which the production of IAA is regulated by quorum sensing (QS) (Scherwinski et al., 2007).

Other than these mechanisms, improvement of nutrient acquisition is involved in direct growth promotion. Plant-associated microorganisms can provide macronutrients and micronutrients. The most important process is bacterial nitrogen fixation. The Symbiotic relationship between rhizobia and its legume host plants is also an important example of PGPR. Bacteria involved, metabolize root exudates and produce the fixed nitrogen for plant. The ability to fix nitrogen also occurs in some other free-living bacteria including Azospirillum, Burkholderia and Stenotrophomonas. Some other bacteria provide sulfate to the plant which is produced by bacteria through oxidation.

Bacteria can also provide phosphorus to plant which is liberated from organic compounds i.e. phytates. Thus, indirectly, involve in plant growth promotion. Azospirillum treatment can increase the root growth and other activities that increases the macroelements and microelements uptake. Because of the activities of microbes, mineral supply is also increased which in turn involve in plant growth promotion and includes synthesis of siderophores and siderophore. Solubilization of bacterial siderophores and the secretion of organic acids make the poorly soluble inorganic nutrients available for the plant. Pseudomonas fluorescens have ability to acidify its environment and to solubilize mineral phosphate (de Werra et al., 2009).

Furthermore, the gluconic acid metabolism have a great association with antagonistic activity against plant pathogens. This antagonistic activity involve the inhibition of microbial growth by diffusible antibiotics and other volatile organic compounds (VOCs), biosurfactants, and toxins. Antagonistic activity can also be in the form of competition for colonization, sites and nutrients, competition for minerals, degradation of pathogenicity of pathogen and reducing the virulence of the pathogen or it can also be in the form of parasitism that involve production of extracellular cell wall-degrading enzymes. Plant-associated microbes can reduce the activity of pathogenic microorganisms through microbial antagonisms. They can also activate the plant defend system by a phenomenon termed “induced systemic resistance” (ISR). However, sometimes, the mechanism of ISR elicit the pathogen-induced systemic acquired resistance (SAR) (Mishina & Zeier, 2006).

**CONCLUSION**

In conclusion, there is a high specificity of the plant–microbe interaction. PGPR that elicit ISR in one plant species is specific for that plant only. This indicate the specificity in the interaction between plant and plant-associated microbes. The parameters involved in ISR may also be same with those involved in microbial antagonism. PGPR can also activate the defense-related gene expression which can produce stronger defense reaction.

**REFERENCES**

Ashrafuzzaman, M., Hossen, F. A., Ismail, M. R., Hoque, A., Islam, M. Z., Shahidullah, S. M., & Meon, S. (2009). Efficiency of plant growth-promoting rhizobacteria (PGPR) for the enhancement of rice growth. *African Journal of Biotechnology, 8*(7).

Badri, D. V., Weir, T. L., van der Lelie, D., & Vivanco, J. M. (2009). Rhizosphere...
chemical dialogues: plant–microbe interactions. *Current opinion in biotechnology, 20*(6), 642-650.

Bais, H. P., Broeckling, C. D., & Vivanco, J. M. (2008). Root exudates modulate plant—microbe interactions in the rhizosphere. In Secondary metabolites in soil ecology (pp. 241-252). Springer, Berlin, Heidelberg.

Bangera, M. G., & Thomashow, L. S. (1999). Identification and characterization of a gene cluster for synthesis of the polyketide antibiotic 2, 4 -diacetylphloroglucinol from Pseudomonas fluorescens Q2-87. *Journal of bacteriology, 181*(10), 3155-3163.

Bent, E. (2006). Induced systemic resistance mediated by plant growth-promoting rhizobacteria (PGPR) and fungi (PGPF). In Multigenic and induced systemic resistance in plants (pp. 225-258). Springer, Boston, MA.

Berbara, R. L., & García, A. C. (2014). Humic substances and plant defense metabolism. In Physiological mechanisms and adaptation strategies in plants under changing environment (pp. 297-319). Springer, New York, NY.

Bertin, C., Yang, X., & Weston, L. A. (2003). The role of root exudates and allelochemicals in the rhizosphere. Plant and soil, 256(1), 67-83.

Canarini, A., Kaiser, C., Merchant, A., Richter, A., & Wanek, W. (2019). Root exudation of primary metabolites: mechanisms and their roles in plant responses to environmental stimuli. *Frontiers in Plant Science, 10*, 157.

Conrath, U. (2009). Priming of induced plant defense responses. Advances in botanical research, 51, 361-395.

Conrath, U., Beckers, G. J., Flors, V., García-Agustín, P., Jakab, G., Mauch, F., & Pugin, A. (2006). Priming: getting ready for battle. *Molecular plant-microbe interactions, 19*(10), 1062-1071.

Cui, H., Tsuda, K., & Parker, J. E. (2015). Effector-triggered immunity: from pathogen perception to robust defense. *Annual review of plant biology, 66*, 487-511.

de Werra, P., Péchy-Tarr, M., Keel, C., & Maurhofer, M. (2009). Role of gluconic acid production in the regulation of biocontrol traits of Pseudomonas fluorescens CHA0. *Applied and Environmental Microbiology, 75*(12), 4162-4174.

Dixon, R. A. (2001). Natural products and plant disease resistance. *Nature, 411*(6839), 843-847.

Faris, J. D., Zhang, Z., Lu, H., Lu, S., Reddy, L., Cloutier, S., & Oliver, R. P. (2010). A unique wheat disease resistance-like gene governs effector-triggered susceptibility to necrotrophic pathogens. *Proceedings of the National Academy of Sciences, 107*(30), 13544-13549.

Fernando, W. D., Nakkeeran, S., & Zhang, Y. (2005). Biosynthesis of antibiotics by PGPR and its relation in biocontrol of plant diseases. In PGPR: biocontrol and biofertilization (pp. 67-109). Springer, Dordrecht.

Ferrari, S., Savatin, D. V., Sicilia, F., Gramegna, G., Cervone, F., & De Lorenzo, G. (2013). Oligogalacturonides: plant damage-associated molecular patterns and regulators of growth and development. *Frontiers in plant science, 4*, 49.

Gray, E. J., & Smith, D. L. (2005). Intracellular and extracellular PGPR: commonalities and distinctions in the plant–bacterium signaling processes. Soil biology and biochemistry, 37(3), 395-412.

Gupta, G., Parihar, S. S., Ahirwar, N. K., Snehi, S. K., & Singh, V. (2015). Plant growth promoting rhizobacteria (PGPR): current and future prospects for development of sustainable agriculture. *J Microb Biochem Technol, 7*(2), 096-102.
Hafeez, F. Y., HASSAN, M. N., Naureen, Z., & Yasmin, S. (2011). PGPR: Versatile tool to combat soil borne pathogens and improve plant health. *Aspects of Applied Biology, 106*, 241-245.

Heese, A., Hann, D. R., Gimenez-Ibanez, S., Jones, A. M., He, K., Li, J., & Rathjen, J. P. (2007). The receptor-like kinase SERK3/BAK1 is a central regulator of innate immunity in plants. *Proceedings of the National Academy of Sciences, 104*(29), 12217-12222.

Jeon, J. S., Lee, S. S., Kim, H. Y., Ahn, T. S., & Song, H. G. (2003). Plant growth promotion in soil by some inoculated microorganisms. *The Journal of Microbiology, 41*(4), 271-276.

Johansson, J. F., Paul, L. R., & Finlay, R. D. (2004). Microbial interactions in the mycorrhizosphere and their significance for sustainable agriculture. *FEMS microbiology ecology, 48*(1), 1-13.

Kloepper, J. W., Leong, J., Teintze, M., & Schroth, M. N. (1980). Enhanced plant growth by siderophores produced by plant growth-promoting rhizobacteria. *Nature, 286*(5776), 885-886.

Khan, N., Bano, A., Rahman, M. A., Guo, J., Kang, Z., & Babar, M. A. (2019). Comparative physiological and metabolic analysis reveals a complex mechanism involved in drought tolerance in chickpea (Cicer arietinum L.) induced by PGPR and PGRs. *Scientific reports, 9*(1), 1-19.

Lenin, G., & Jayanthi, M. (2012). Indole acetic acid, gibberellic acid and siderophore production by PGPR isolates from rhizospheric soils of Catharanthus roseus. *Int J Pharmacy Biol Arch, 3*, 933-8.

Lewis, L. A., Polanski, K., de Torres-Zabala, M., Jayaraman, S., Bowden, L., Moore, J., & Kulasekaran, S. (2015). Transcriptional dynamics driving MAMP-triggered immunity and pathogen effector-mediated immunosuppression in Arabidopsis leaves following infection with *Pseudomonas syringae pv tomato DC3000*. *The Plant Cell, 27*(11), 3038-3064.

Lugtenberg, B., & Kamilova, F. (2009). Plant-growth-promoting rhizobacteria. *Annual review of microbiology, 63*, 541-556.

Maheshwari, D. K., Dheeman, S., & Agarwal, M. (2015). Phytohormone-producing PGPR for sustainable agriculture. In *Bacterial metabolites in sustainable agroecosystem* (pp. 159-182). Springer, Cham.

Malik, K. A., Bilal, R., Mehnaz, S., Rasul, G., Mirza, M. S., & Ali, S. (1997). Association of nitrogen-fixing, plant-growth-promoting rhizobacteria (PGPR) with kallar grass and rice. In *Opportunities for Biological Nitrogen Fixation in Rice and Other Non-Legumes* (pp. 37-44). Springer, Dordrecht.

Matson, P. A., Parton, W. J., Power, A. G., & Swift, M. J. (1997). *Agricultural intensification and ecosystem properties. Science, 277*(5325), 504-509.

Mavrodi, D. V., Mavrodi, O. V., Parejko, J. A., Bonsall, R. F., Kwak, Y. S., Paulitz, T. C., & Weller, D. M. (2012). Accumulation of the antibiotic phenazine-1-carboxylic acid in the rhizosphere of dryland cereals. *Applied and Environmental Microbiology, 78*(3), 804-812.

Mine, A., Seyfferth, C., Kracher, B., Berens, M. L., Becker, D., & Tsuda, K. (2018). The defense phytohormone signaling network enables rapid, high-amplitude transcriptional reprogramming during effector-triggered immunity. *The Plant Cell, 30*(6), 1199-1219.

Mishina, T. E., & Zeier, J. (2006). The Arabidopsis flavin-dependent monooxygenase FMO1 is an essential component of biologically induced
systemic acquired resistance. *Plant physiology, 141*(4), 1666-1675.

Muthamilarasan, M., & Prasad, M. (2013). Plant innate immunity: an updated insight into defense mechanism. *Journal of biosciences, 38*(2), 433-449.

Newman, M. A., Sundelin, T., Nielsen, J. T., & Erbs, G. (2013). MAMP (microbe-associated molecular pattern) triggered immunity in plants. *Frontiers in plant science, 4*, 139.

Nürnberger, T., Brunner, F., Kemmerling, B., & Piater, L. (2004). Innate immunity in plants and animals: striking similarities and obvious differences. *Immunological reviews, 198*(1), 249-266.

Scherwinski, K., Wolf, A., & Berg, G. (2007). Assessing the risk of biological control agents on the indigenous microbial communities: *Serratia plymuthica* HRO-C48 and *Streptomyces* sp. HRO-71 as model bacteria. *BioControl, 52*(1), 87-112.

Shi, S., Nuccio, E. E., Shi, Z. J., He, Z., Zhou, J., & Firestone, M. K. (2016). The interconnected rhizosphere: high network complexity dominates rhizosphere assemblages. *Ecology letters, 19*(8), 926-936.

Spoel, S. H., & Dong, X. (2008). Making sense of hormone crosstalk during plant immune responses. *Cell host & microbe, 3*(6), 348-351.

Tank, N., & Saraf, M. (2009). Enhancement of plant growth and decontamination of nickel-spiked soil using PGPR. *Journal of Basic Microbiology, 49*(2), 195-204.

Tena, G., Asai, T., Chiu, W. L., & Sheen, J. (2001). Plant mitogen-activated protein kinase signaling cascades. *Current opinion in plant biology, 4*(5), 392-400.

van Dam, N. M., & Bouwmeester, H. J. (2016). Metabolomics in the rhizosphere: tapping into belowground chemical communication. *Trends in plant science, 21*(3), 256-265.

Van der Ent, S., Van Wees, S. C., & Pieterse, C. M. (2009). Jasmonate signaling in plant interactions with resistance-inducing beneficial microbes. *Phytochemistry, 70*(13-14), 1581-1588.

Van Wees, S. C., Van der Ent, S., & Pieterse, C. M. (2008). Plant immune responses triggered by beneficial microbes. *Current opinion in plant biology, 11*(4), 443-448.

Williams, P. R., & Hammitt, J. K. (2001). Perceived risks of conventional and organic produce: pesticides, pathogens, and natural toxins. *Risk analysis, 21*(2), 319-330.

Zipfel, C. (2014). Plant pattern-recognition receptors. *Trends in immunology, 35*(7), 345-351.