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Host Microbe Interaction in Soil

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Abstract: Soil is a dynamic and complex environment, comprising of myriad of microbes which contribute towards maintaining soil health and promoting plant growth. The microbe-microbe or plant-microbe interactions happen in the soil which can be positive or negative. Positive interactions include mutualism, syntrophism, commensalism and proto-cooperation whereas negative interactions include predation, parasitism, competition and ammensalism. Majority of plant-microbe interactions occur in rhizosphere because of the high concentration of root exudates. Root exudates help to establish host and microbe communication. Root exudates contain flakes of root cells, mucilage, carbon compounds, amino acids, phenols etc. The primary step in establishing an interaction is recognition of the host cell by the microbe. Microbe recognizes host-signaling molecules like secondary metabolites, siderophores, etc. Additional mechanism includes transduction signaling, biofilm production and transference of molecules and genetic information. The interactions are prone to environmental factors like temperature, moisture, circadian clock and nutritional status of soil. To study the plant-microbe-environmental interaction, a mathematical expression called metabolic modeling is used. It supports stoichiometry analysis of metabolic reactions. Efficient agro-climatic ecosystem and bioremediation of pesticide polluted soil can be achieved by exploiting plant-host interactions for realizing agriculture sustainability.

Keywords: Environment, Metabolic modeling, Plant-microbe interaction, Root exudates, Secondary metabolites

Soil impacts the above ground and below ground factors which support the growth of plants. The zone of soil extending few mm from the surface of root is known as the rhizosphere. It is this space where all interactions occur (Zhang et al 2020). There are many different types of microbial interactions that occur between various organisms in the rhizospheric soil. Microbial interactions are vital for their development, colonization and infection. A wide range of interactions that promote associations, such as mutualistic and endosymbiotic relationships, as well as competitive, antagonistic, pathogenic, and parasitic relationships, have developed as a result of the long history of co-evolution among many species (Faust and Raes 2012). These relationships have also led to adaptation and specialization among various organisms. All ecological components of the interactions include physiochemical changes, metabolite conversion and exchange, signaling, chemotaxis, and genetic exchange leading to genotypic selection. The release of root exudates causes the principal plant-microbe interactions to take place in the rhizosphere. Root cell flakes, mucus, carbon compounds, amino acids, phenols and other substances are found in root exudates. Microbes can identify these host signaling molecules in addition to secondary metabolites and siderophores. Microbial interactions in the rhizosphere also result in the production of biofilms, the transfer of chemicals and genetic information, and the transduction of signals. These interactions are sensitive to environmental factors like soil nutrition, temperature, moisture and circadian rhythm. They can be analyzed and even predicted by metabolic modeling to get greater information about relationship between environment, microbes and plants. Exploiting the interactions between plants and their hosts can result in a conducive environment which promotes agriculture sustainability.

Host Microbe Interaction in Rhizosphere

One of the most complicated ecosystems is the rhizosphere, which consists of the small, limited area where soil meets plant roots. It is home to a variety of microorganisms and invertebrates that have an impact on biogeochemical processes, plant growth and stress reduction (Bano et al 2021, Philippot et al 2013). Notably, the rhizosphere offers a rich environment in which numerous microbial communities, including some that are beneficial to plants flourish. These communities, also found residing endophytically in plants, help the plant adapt to its surroundings more effectively. The two primary phases in establishing the rhizomicrobiome in the rhizosphere are chemotaxis and colonization. Root exudates play an important function in the chemotactic migration of rhizospheric bacteria to roots and early colonisation because they are both a vital source of nutrition and signaling molecules for them. Also, root exudates secreted in the rhizospheric zone influence the relationship between plants and microbes by attracting particular rhizobacteria, beneficial fungi, mutualistic arbuscular mycorrhizal fungus (AMF) *etc.* that promote plant growth. Root microbiome constructed from rhizospheric microbial communities benefit plants through the formation of biofilm (mediated by quorum sensing), the synthesis of plant hormones (Indole Acetic Acid), nitrogen fixation and antibiosis (Jain et al 2020). Root exudates containing flavonoids are known to attract phytopathogens including *Fusarium solani* and *Phytophthora sojae* as well as symbiotic nitrogen-fixing *Rhizobium* and Arbuscular Mycorrhizal Fungi (AMF) (Del Carmen Orozco-Mosqueda et al 2022). Root exudates, in addition to acting as signaling molecules, chemo-attractants and stimulants, can also occasionally function as repellents and inhibitors in the multipartite interactions with rhizospheric microbial soil associations. Root exudates are continuously modified in response to the immediate changing environment. They have a reputation for moderating the early conversation between soil microbes and roots (Gamalero et al 2022). Root exudates have recently been found to be highly effective at luring soil microbes, according to a research using $_{13}$C labeling method (Lange et al 2015).

The synergistic relationships that plants have with rhizospheric microorganisms, such as rhizobia and AM fungus are well documented. These relationships enhance plant nutrition by facilitating the acquisition of nitrogen and phosphorus, in exchange for fixed carbon from plants (Oldroyd 2013). Application of VAM @ 10 ml per plant increased the germination and vigour of *Anthocephalus cadamba* seedlings (Chauhan et al 2023). Rhizobia are recognized as forming symbiotic relationships with legumes and *Parasponia* species whereas AM fungi are recognized as interacting with more than 80% of vascular plants. Bio-inoculation of *Neobacillus niacini* increased seed germination by 23.2% in *Vigna mung* L grown in high salinity stress (John et al 2023). The foliar application of water soluble fertilizers and PGPR significantly increased nodule count in black gram (Babu et al 2023). Along with siderophores and volatile substances like hydrogen cyanide fluorescent *Pseudomonas* in the rhizosphere is known to produce a wide range of other chemicals as siderophores. Organic acids, significant fraction of roots exudates, are known to control plant-microbe interactions (Chen et al 2012). It is recognized that organic acids, particularly those from the tricarboxylic acid cycle, serve as carbon sources and signaling molecules (Yuan et al 2015)

Several plant species use chemical signaling from root exudates to control other plant members, insects, nematodes, soil bacteria, and fungus. Rhizosphere-based chemical warfare occurs when a plant pathogen repeatedly attacks the plant and the plant responds by secreting defense proteins, phytoalexins and phenols to meet the threat. Comprehensive sequencing is used by a variety of plants, including *Arabidoposis thaliana, Medicago truncatula*, rice, maize, and others to find abundant supplies of antimicrobials, indoles, terpenoids, flavonoids and other natural compounds (Singh et al 2023). Phytoalexin generated by *Arabidopsis* root exudates provide resistance to *Phytophthora capsici*. Similarly, resistance to *F. graminearum* was afforded by the secretion of derivatives of cinnamic acid in barley (Wang et al 2013). The non-protein amino acid canavanine and other compounds have been shown to interfere with quorum sensing (QS), nodulation and the formation of EPS II, acting as suppressors of N-fixing bacteria (D'Mello 2015). The ability of some rhizobial strains to detoxify canavanine makes them favorable to other rhizospheric microorganisms found in legume roots (Vukanti 2020). Strong external antibacterial properties of phenols and terpenoids have long been recognized. They increase tolerance to biotic and/or abiotic stimuli by fostering metabolic flexibility inside the plants (Jain et al 2020).

Mechanism of Host-Microbe Cross Talk

Plant exudates in the soil are recognized by microbes as the initial stage of plant-microbe interaction. The exudates from plants, which are made up of organic acids, amino acids, and carbohydrates can change depending on the plant and its biotic or abiotic environment (Haldar and Sengupta 2015). The variety of processes, including secondary metabolites, siderophores, quorum sensing systems, biofilm formation, and cellular transduction signaling are involved in the exchange of molecular and genetic information. The expression of genes of each organism in response to environmental (biotic or abiotic) stimuli is the fundamental unit of interaction and generates the molecules that are a part of these interactions. Microorganisms grow into a community through these mechanisms. They may exhibit great variations depending on the multitrophic interactions. Cells may communicate and act in accordance with their surroundings through the synthesis of signaling molecules (also known as auto-inducers). Microbial-Associated Molecular Patterns, also known as PAMP (Pathogen Associated Molecular Patterns) are conserved at generic level (Phelan et al 2012). These facilitate cell to cell communication.

Signal Transduction

All biochemical procedures known as "signal transduction" are used by cells to convert environmental cues into targeted responses. It is now believed that signal transduction occurs through highly organized networks where a small number of modular domains regulate protein-protein interactions and the reversible construction of signaling complexes. Cell signaling can be divided into three stages *viz.,* reception, transduction and response. A signaling molecule is picked up by a cell from the extracellular environment. Signal is recognized when a signal interacts to a receptor protein either inside the cell or on its surface. Then, a change in the receptor protein occurs. Transduction is started with this modification. The pathway for signal transduction involves many steps. Each relay molecule modifies the subsequent molecule in the signal transduction pathway. Later, certain cellular responses are prompted by the signal (Zschiedrich et al 2016).

Quorum Sensing

Bacterial cells communicate with one another using quorum sensing (QS). In order for bacterial communities to express their genes collectively, this procedure involves the creation and detection of signaling molecules (known as auto-inducers) (Hawver et al 2016). Gram-negatives and Gram-positives express QS genes in different ways. The signaling molecules acyl-homoserine-lactones (AHLs) in Proteobacteria or cis-11-methyl-2-dodecanoic acid (also called diffusible signal factor-DSF) are present in Gram negatives like *in Xanthomonas* and *Xylella* and gamma-butyro lactones in *Streptomyces* and peptides are found in Gram positives (Rai and Bai 2020)**.** The first QS system was identified in the *Vibrio fischeri* (formerly known as *Photobacterium fischeri*) bacterium in the 1980s. It has a low population density in the sea and does not glow. It glows when it is in a symbiotic relationship with fish and squid. The transcriptional regulator *R* and the autoinducer synthase *I*, also known as *LuxR* and *LuxI*, are two proteins that are involved in the QS system in Gram-negative bacteria. Thus, QS can play a variety of roles, such as fluorescence emission, virulence, sporulation, competence, antibiotic production and biofilm formation (Hawver et al 2016). It can also act during the interaction of various organisms, such as bacteria-bacteria, fungal-bacteria, and bacteria-host (animals or plants). About 6–10% of the microbial genomeis regulated by Quorum sensing (Braga et al 2016).

Biofilm Formation

Bacterial pathogens typically go through five main stages while forming biofilms on every substrate or layer (Srinivasan et al 2021). These stages include attachment, colonisation, proliferation, maturation and dispersion. Initially, free-swimming planktonic cells reversibly bind to biotic or abiotic surfaces by weak interactions like acid-base, hydrophobic, Van der Waals and electrostatic forces. Stronger connections, such as those involving lipopolysaccharide, flagella, and pili allow pathogenic bacteria to permanently attach to surfaces and form colonies. Then large amount of EPS is produced and the multilayered bacterial cells get accumulated. In maturation and dispersion stage, the coupled multilayered bacterial cells developed into a mature biofilm with a typical 3D biofilm structure. After biofilm has fully developed, it is broken down or dispersed *via* mechanical and active procedures (Srinivasan et al 2021).

Siderophore

Small chemical molecules known as siderophores are created by microbes when there is shortage of iron. They help the microorganisms absorb iron more effectively. Bacteria release siderophores into the surrounding environment, which are detected by cell surface receptors and carried inside the microbial cell (Khasheii et al 2021). Thus, they are related to both cooperative and antagonistic microbial interactions. In addition, many siderophores serve other functions, such as those of signaling molecules, oxidative stress-reduction tools, antibiotics and metal sequestration agents, including those for heavy metal toxins (Johnstone and Nolan 2015). Some *Pseudomonas* species are dependent on a group of siderophores called pyoverdines, which are helpful in regulating bacterial growth for the formation of biofilm and infection (Ghssein and Ezzeddine 2022). Exotoxin A, Prp Leudoprotease and pyoverdine among other virulence factors are said to be produced as a result of a cascade that is allegedly initiated by pyoverdines (Lamont et al 2002).

Secondary Metabolites

Microorganisms often react by exchanging metabolic products which triggers complicated regulatory reactions involving the formation of secondary metabolites. Secondary metabolites include nitrogenous compounds, phenolic compounds, glycosides, tannins, terpene compounds, and flavonoids which are produced by microorganisms. They do not play a crucial role in the growth, development and reproduction of the producing organism. But these substances can play crucial roles in ecological interactions and are typically bioactive (Yin and Keller 2011). The roles of secondary molecules are extensively researched in endophyte-phytopathogen-plant interactions, parasite interactions, and symbiotic interactions.

There is still a great deal of diversity regarding the metabolites and mechanisms behind the interactions between the host plant, phytopathogen and endophyte. Endophytic fungi are known to produce a wide range of bioactive secondary metabolites that are connected to the endophyte complex interactions with the host and phytopathogens. These compounds carry out significant ecological functions such as promoting plant growth and acting as phytopathogen defense agents (Narayanan and Glick 2022). These interactions have been researched in co-cultures of the endophyte *Trichoderma harzianum* and phytopathogen *Moniliophthora roreri,* which live together in cacao plants. *Moniliophthora roreri*, a phytopathogen, and

Trichoderma harzianum, an endophyte, which coexist in cacao plants, have been co-cultured to study this relationship. *M roreri* is known to be antagonistic to *T harzianum*, which is widely used as a biocontrol agent (Tata et al 2015). Four secondary metabolites (T39 butenolide, harzianolide, sorbicillinol and an unidentified chemical), whose formation was reliant on the presence of phytopathogens were spatially localized in the interaction zone (Tata et al 2015). There have been reports of antifungal activity for harzianolide and T39 butenolide. Bisorbicillinoids, a family of secondary metabolites with a variety of functions, are produced *via* sorbicillinol as an intermediary (Bouthillette et al 2022).

Bacteria were used in other co-cultured research studies. The citrus variegated chlorosis phytopathogen *Xylella fastidiosa* was shown to be inhibited by *Methylobacterium mesophilicum* SR1.6/6 and *Curtobacterium* ER1.6/6 isolated from healthy and asymptomatic plants by Lacava et al (2004). *In vitro* co-cultivation with a citrus endophytic strain of *Methylobacterium mesophilicum* also allowed for the evaluation of *Xylella fastidiosa's* transcriptional profile (Lacava et al 2004). It was discovered that growth-related genes including those responsible for DNA replication and protein synthesis were down-regulated. Acriflavin resistance, toluene tolerance, *pilY* transporter, and dihydrolipoamide dehydrogenase were up-regulated, whereas genes involved in energy synthesis, stress, transport and motility were down-regulated (Dourado et al 2015). The genome sequencing and transposon mutagenesis of an endophyte strain of *Burkholderia seminalis*, which suppresses *Burkholdia riagladioli's* orchid leaf necrosis, provided another method for studying the relationship between endophytes, phytopathogens and plants. This method identified eight loci that are involved in biological regulation (Araújo et al 2016).

Cell membrane of few bacteria is composed of hopanoids, which serve the same purpose as cholesterol in eukaryotes (Hoshino and Gaucher 2021). They stabilize the membrane in addition to controlling the membrane's fluidity and permeability. Studies using biosynthesis genes knockouts, such as *hnpF* (squa-lene hopene cyclase-shc), reveal that the absence of hopanoids affects bacterial tolerance to a variety of stress conditions, including toxic compounds like dichloromethane (DCM), extremely acidic environments, and other environmental stresses (Ali and Mir 2020). It also affects bacterial resistance to antibiotics and antimicrobial lipopeptides as well as multidrug transport and bacterial motility. Hopanoids thus play a role in the interaction between bacteria and plants, influencing how bacteria adapt to an aerobic microenvironment and a low pH growth medium as well as how *Frankia spp.* metabolizes nitrogen (Schmerk et al 2015). For instance, the nitrogen-fixing bacterium *Bradyrhizobium diazoefficiens* needs a certain form of hopanol to co-exist with its host, the tropical legume *Aeschynomene afraspera* (Kulkarni et al 2015).

Numerous secondary metabolites that were differently expressed during the mycoparasitic interaction between *Stachybotrys elegans* and *Rhizoctonia solani* have been discovered (Chamoun et al 2015). In response, *R. solani* produces more of the gene encoding pyridoxal reductase than *S. elegans* does throughout the encounter. *S. elegans* also expresses genes linked to parasitism and synthesizes enzymes that break down cell walls. Induced secondary metabolite profiles during the interaction were revealed by a metabolomic investigation (Guan et al 2021). The mycoparasite had a considerable impact on metabolism of *R. solani* in that only a few Diketopiperazines were produced. Biosynthesis of many antimicrobial chemicals was down-regulated as a result of the interaction. Among other biological functions, diketopiperazines have antibacterial qualities that are well-documented. Trichothecenes and atranones are the major mycotoxins that the mycoparasite *S. elegans* produced. The alteration in growth and development metabolism of *R. solani* was thought to have been caused by the trichothecenes. An important class of mycotoxins called trichothecenes has been linked to oxidative stress and the inhibition of eukaryotic protein production (McCormick et al 2011).

The symbiotic association between the bacterial species *Burkholderia* and the phytopathogenic fungal genus *Rhizopus*, which causes rice seedling blight, is a complex inter-kingdom interaction (Mir and Hamid 2023). According to a report, *Rhizopus* cannot develop spores in the absence of the endosymbiont, proving that the fungus depends on the production of certain substances by the symbiont for completion of its life cycle. Studies on the metabolites and mechanisms involved in the communication and interaction in this complex symbiont-pathogen-plant connection are intriguing and ongoing work.

Environmental Factors Effecting Host Microbe Interactions

Plant relationships with beneficial microorganisms can be hampered by environmental stressors. Plant signaling pathways linked to defense hormones and reactive oxygen species are induced during stress which explains why environmental factors interfere with plant-microbe interactions. Environmental stressors frequently have an impact on a plant metabolism and physiology which can stunt its growth and ability to reproduce. Stressors also frequently interfere with plants' relationships with useful microorganisms. These microorganisms trigger host mechanisms that effectively reduce the adverse consequences of stressors. Abiotic environmental stressors such as soil nutrition, temperature, moisture and circadian rhythm are a threat to plant microbe interactions.

Temperature: Temperature is an important factor impacting plant microbe interaction as demonstrated that an increase in temperature prevents the development of type IV secretion-associated pilus and the expression of virulence (vir) genes in *Agrobacterium* infections (Velasquez et al 2018). *Pectobacterium atrosepticum*, exhibits greater virulence at higher temperatures. It is linked to increased synthesis of enzymes that break down plant cell walls, quorum-sensing signals and quicker development of illness.

Positive plant-microbe interactions are impacted by a higher temperature as well. Arbuscular mycorrhizal fungi (AMF) typically benefits from higher temperature impact. Plant colonization and hyphal growth are both positively impacted. This is possible because plants are able to allot carbon to the rhizosphere where AMF thrives quickly (Khaliq et al 2022). *Curvularia protuberate*-mediated heat tolerance has been reported in tomatoes. It indicates that the underlying process may be universally relevant to support a variety of plants' ability to withstand high temperatures. Even plants can benefit from some microorganisms' assistance in overcoming various conditions. An example *Burkholderia phytofirmans* strain *PsJN*, is reported to increase plant tolerance to heat in tomato crop, cold in grapevine crop, drought in wheat crop, and salt and freezing in *Arabidopsis* (Issa et al 2018). It has direct antifungal effects which improve plant defense. *PsJN* confers multi-stress tolerance.

Detrimental effects of temperature stress on plants may be reduced by some native rhizospheric bacteria and endophytes. Certain plants tolerate higher temperature while they live in association with other organisms. A mutualistic relationship between a fungal endophyte *Curvularia protuberate* and tropical panic grass *Dichanthelium lanuginosum* allow both species to grow at high soil temperatures. The mutualistic contact is facilitated by a double-stranded RNA (dsRNA) virus from this fungus (Márquez et al 2007). However, this plant and the fungus when present alone are unable to survive at high soil temperatures.

Circadian clock: The relationship between the internal and external circadian clocks and several elements of plant biology is extensive. Transcriptional and translational feedback loops work together to control the circadian clock. *Circadian Clock-Associated1* (*CCA1*) and *Late Elongated Hypocotyl* (*LHY*) are two important morning-phased transcription factors (Karapetyan and Dong 2018). It is generally held that the circadian clock is a self-sustaining system. However, recent studies have revealed that light, temperature and humidity can change some aspects of its operation. Studies have revealed that effector-triggered immunity (ETI) at night is enhanced by humidity implying that at night there's an increase in pathogenic infection (Karapetyan and Dong 2018).

Circadian clock regulates the temporal regulation of PAMP triggered immunity (PTI) against *P syringae* infecting *Arabidopsis* plants (Bhardwaj et al 2011). It has also been demonstrated that *Glycine-rich RNA-binding protein7* (*GRP7*, an RNA-binding protein) binds to the transcripts of the pattern-recognition receptor (*PRR*) genes *Flagellin Sensitive2* (*FLS2*) and *EFTu receptor* (*EFR*) (Nicaise et al 2013). The stomata of plants serve as entry points for a large number of pathogenic and non-pathogenic microorganisms. In response to pathogen invasion, stomatal closure is one of many downstream immunological outputs that PRRs regulate (Melotto et al 2017). *CCA1* and *LHY* may have an impact on the stomata's receptivity to pathogen invasion in a diurnal cycle by controlling the synthesis of PRRs via *GRP7* (Zhang et al 2013).

Microbes also respond or behave differently depending on the time of day. At particular times of the day, fungi and oomycete pathogens produce hyphae, produce spores and spread those spores. However, circadian-modulated pathogenicity is relatively poorly studied. The first instance of a microbial clock influenced plant-pathogen interaction was demonstrated by Hevia et al (2015). Pathogens utilize exposure to light stimulus to start an illness (Hevia et al 2015). For instance, the blue light receptor *Cercospora* regulator of Pathogenesis1 (*Crp1*) in *Cercospora zeae-maydis*, is essential for sensing plant stomata. It possibly mediates the biosynthesis of the light-activated toxin cercosporin. This cercosporin disrupts stomatal guard cell membranes. It facilitates fungal infection through stomata (Kim et al 2011). The pathogenicity of *P. syringae* is impacted by light. Red light inhibits bacterial entry through stomata by down regulating the expression of genes involved in the biosynthesis of coronatine toxin because *P. syringae* needs coronatine to open the stomata to promote bacterial entry. Together, light and circadian rhythm influence plant-microbe interaction alike temperature stress.

Moisture: Water is indispensible to sustain life. Numerous elements of plant and microbial biology can be significantly impacted by low amount of water and too much of water as well. Plants respond to water shortage by a signaling cascade initiated by an increase in ABA and leading to extensive transcriptional reprogramming, physiological modifications, including stomata closure to lessen transpiration (Zhu 2016). FLS2 in *Arabidopsis* recognizes bacterial pathogens like *P. syringae* or PAMPs like flg22 (a 22-amino-acid epitope of *Pseudomonas flagellum*). It causes stomatal closure resulting in lowering of pathogen infiltration (Melotto et al 2006). ABA-induces stomatal closure under drought stress. The mesophyll cells inside the leaf's mesophyll experience inhibition of the SA signaling pathway as a result of elevated ABA, which impairs SA-mediated resistance to invasion (Jiang et al 2010).

Plant-microbe interactions are impacted by drought as well. Researchers discovered that while the composition of microbial communities was influenced by drought in all examined sections (bulk soil, rhizosphere and root endosphere), in drought stressed rice plants tendency of composition change is more when intimate community is associated with the roots (Santos-Medellin et al 2017). Similar findings were made when researchers looked at how soil moisture affected the microbiome of sorghum roots. They discovered that while the richness of the bacterial communities in the soil around the roots remained mostly unaffected, the rhizosphere and the root endosphere were much less diverse during droughts (Xu et al 2018). Actinobacteria and Firmicutes are more prevalent under drought. The root endosphere exhibits the severe decrease in community diversity and increase in abundance of Actinobacteria and Firmicutes. The change in root metabolites results from drought stress on the host side. It is unknown if and mechanism by which drought triggered metabolites "modulate" the root microbiome to support plant stress responses. In times of drought, there are molecular interactions between plants and their associated microbiome. These interactions modify the root microbiota to adapt to drought stress. The basic understanding required to use microbiota to improve drought tolerance in crop plants can be understood by deciphering this molecular conversation (Ali et al 2022).

Many plant disease outbreaks are known to require precipitation and/or high air humidity. The hypersensitive response (HR), phenomena that frequently occurs in plants during ETI, is characterized by cell death at the site of pathogen infection. The HR is hypothesized to stimulate secondary immune responses and inhibit the growth of biotrophic infections. High atmospheric humidity reduces HR cell death in a number of plant-pathogen interactions (Leisner et al 2022). High humidity usually promotes pathogen virulence in contrast to suppressing host immune function. Water and high humidity play in boosting spore germination and bacterial motility before entry into the plant. Additionally, high humidity is essential for promoting bacterial virulence and survival post-invasion (Dechesne et al 2010) An early sign of many foliar diseases is water-soaked lesions, which develop when liquid builds up abnormally inside the leaf cells. Water soaking produces a disease-friendly micro-environment for bacteria, dilution of defense chemicals derived from plants, and/or facilitation of bacterial spread from the original infection sites (Xin et al 2016).

Root disease development is influenced by moisture. The bacterial wilt in ginger plants caused by the soil-borne *Ralstonia solanacearum* is more severe in high soil moisture (Jiang et al. 2018). Under low soil moisture, there is high expression of the *WAK16* and *WAK3-2 WAK* wall-associated kinase genes. *WAK1* is crucial for keeping track of the integrity of cell walls (Brutus et al 2010). The expression of *WAK16* and *WAK3-2* is suppressed by high soil moisture and plants become less resistant to *R. solanacearum*. This suggests that *WAK16* and *WAK3-2* may be crucial in detecting soil moisture and facilitating cell wall-based plant immunity (Jiang et al 2018).

Nutritional status: The pursuit of nutrients is one of the fundamental mechanisms that govern interactions between plants and microbes. Nutritional state of plants and the availability of nutrients in the environment have a big impact on how well plants and microbes get along. It is widely known that both the soil and plant phosphate levels tightly control the complex symbiotic connection between terrestrial plants and phosphate-acquiring AMF (Muller and Harrison 2019). The influence of phosphate on plant-microbe interactions is one aspect of plant-AMF interactions. For phosphorus-acquiring AMF, *Arabidopsis thaliana* is a non-host (Fernandez et al 2019). Hiruma et al (2016) discovered the endophytic fungus *Colletotrichum tofieldiae (Ct)* in wild *Arabidopsis. Ct* is capable of transferring phosphate to *Arabidopsis* where it stimulates plant growth. However, *Ct*-mediated growth promotion can only be seen in plants that have been grown in phosphate-deficient soils. Further research revealed that the stimulation of *Ct*-dependent plant growth required a healthy plant phosphate starvation response (PSR) system (Chiou and Lin 2011). Later research by Hacquard et al (2016) revealed transcriptional suppression of host defense responses in *Ct*-colonized plants during phosphate starvation, which is likely done to promote symbiotic relationship. These two studies show that the nutritional state of the host affects the course of the *Arabidopsis-Ct* interaction. Phosphate starvation of the host results in a mutualistic interaction whereas phosphate sufficiency results in a commensal (i.e., non-mutualistic) interaction between partners.

Symbiotic nodules are formed in the roots of legumes as a result of interactions with *Rhizobium* species. This unique biological mechanism allows for the conversion of atmospheric N_2 to physiologically useful NH_3 to aid in plant growth. However, the formation of nodules is an energetically expensive process for the legume host and is not economically viable when plants are cultivated in an optimum nitrogen environment (Yakha 2022). Plants have evolved auto-regulation of nodulation which maximizes the number of nodules generated in the root based on the requirement of nitrogen in the shoot to prevent high energy cost to the host. The shoot *CLAVATA1*-like *LRR* receptor kinase *Hypernodulation Aberrant Root Formation1* (*HAR1*), which senses *Rhizobium*/nitrate-induced, root-producing *CLV3/Embryo Surrounding Region* (*CLE*) peptides, is one of the main player in regulation of nodulation (Okamoto et al 2013). A root-acting *F-box* protein called *Too Much Love* (*TML*), which transmits shoot-derived inhibitory signals, prevents the growth of nodules after perception. Roots and shoots communicate to maintain a state that is receptive to symbiotic *Rhizobium* contact in nitrogen-deficient conditions (Takahara et al 2013). *MiR2111* abundance in lotus is found to be inversely linked with *M. loti* infection and nitrogen availability in a model system, using *Lotus japonicus* and *Mesorhizobium loti* (Tsikou et al 2018). *The s*hoot-produced *miR2111* is translocated through the phloem to the root to mute *TML*, a positive regulator of regulation of nodulation. To maintain the susceptibility of uninfected tissue to *Rhizobium,* Tsikou et al. (2018) postulated that shoots systemically regulate *TML* expression in roots through *miR2111.* The amount of *miR2111* is decreased in a *HAR1*-dependent manner and the course of nodulation is constrained if the plant has enough nitrogen or if a symbiotic relationship with *Rhizobium* is well established. The significance of the legume hosts in directing the symbiotic partners' beneficial interactions in response to environmental changes is highlighted by these findings (Tsikou et al 2018).

Certain mutualistic rhizosphere microorganisms can induce Induced Systemic Resistance (ISR), a type of plant protection that prepares the host for possible pathogen attacks. The *Arabidopsis* transcription factor *MYB72* was discovered as an important ISR regulator by microarray and mutant analysis (Pescador et al 2022). It is interesting to note that iron deprivation also significantly increases *MYB72* expression in roots (Panpatte et al 2020). ß-glucosidase *BGLU42* was found to be an important component of ISR and in response to iron shortage downstream of *MYB72.* When there is a lack of iron, *MYB72* activates the genes for the iron-mobilizing phenolic metabolite-producing enzymes. Another gene, *BGLU42* facilitates the release of phenolic compounds into the rhizosphere (Zamioudis et al 2014). Stringlis et al. (2018)observed that Scopoletin, a coumarin is a commonly found phenolic chemical generated and released into the *Arabidopsis* rhizosphere in iron deficit in a *MYB72*- and *BGLU42*-dependent manner. Rhizospheric microbial population of the scopoletin biosynthetic mutant *f60h1's* was discovered to be significantly different from that of wild-type plants. Scopoletin inhibits the growth of two recognized soil-borne pathogens of *Arabidopsis, Fusarium oxysporum f. sp. raphani* and *Verticillium dahliae JR2*, in a dose-dependent manner. This was demonstrated by *in vitro* antimicrobial activity assays (Zamioudis et al 2014). In iron-deficient settings, *MYB72, BGLU42*, and scopoletin seem to form a regulatory module to improve iron solubility and restructure rhizosphere microbiota to defend the host from pathogen attack by trigerring ISR (Verbon 2019).

Plant-Microbe-Environmental Interactions through Metabolic Modeling

Strategies are needed to boost plant productivity, resilience and tolerance to both abiotic and biotic stressors. Plant growth, environmental responsiveness and disease susceptibility are all supported by microorganisms in many ways. The density of natural communities, concurrent competition and cooperation, signaling interactions and environmental effects make it difficult to understand the precise mechanisms by which microbes interact with plants and with each other. The complexity of interactions between plants, microbes and environments can be understood by combining metabolic modelling with artificial communities. The use of metabolic models in community settings identifies various applications and emphasizes the value of ecological theory in assisting with data interpretation. It offers suggestions for how the fusion of metabolic modelling methods with big data may help close the gap between the complexity of natural plant-microbe systems and the simplicity of simplified artificial communities. An organism, ranging in complexity from prokaryotes to eukaryotes, can be represented mathematically by a metabolic model that depicts the stoichiometries of the metabolic reactions taking place within the organism. Models have been created from genomic data using various databases as BRENDA, MetaCyc, KEGG, JGI IMG/M to identify genes and their associated metabolic reactions. The information is then gathered into a metabolite-reaction stoichiometry matrix using software programmes as CellNetAnalyzer, Python (Von Kamp et al 2017). Creating a metabolic model is experimental because of many variables like genome completeness, accuracy of genomic data and annotations (which can lead to missing genes, reactions or pathways) and the accessibility of experimental data. A hypothesis that can be utilized to forecast physiological response under various environmental conditions is the result of building a metabolic model.

Although metabolic modelling was primarily used for single species, it is now possible to apply it to community models due to the improved accessibility of genomic data and the development of effective computer techniques. When Stolyar et al (2007) used a multi-compartment changeability balance model to predict metabolite exchange between the methanogen *Methanococcus maripaludis* and the sulphate reducer *Desulfovibrio vulgaris*; they became the first to apply this changeability balance analysis to a multispecies context. The study highlighted the critical role of hydrogen in mutualistic symbiosis between the two microbes (Stolyar et al 2007).

Plants pose a challenge for the development of high quality metabolic models because it has eukaryotic genome, distinct tissues and redundancy due to polyploidy. Current attempts to enhance databases, annotations, major and secondary pathways provide automated platforms as a starting point for plant-specific modelling as more genomic data is being gathered (Seaver et al 2018). A number of diverse plant species, including soybean seed, rapeseed, rice, potato, and maize have had specialized tissue types of their metabolisms modeled to date. For a more accurate representation of plant metabolism, multiple compartments within metabolic models have also enabled the reconstruction of multi-tissue models (Shaw and Cheung 2020). For instance, one of the most complete plant models created to date for *Arabidopsis* included six different tissues, allowing for a more precise prediction of whole-plant physiological responses (Gomes de Oliveira Dal'Molin et al 2015). Multi-scale models (e.g., incorporation of gene regulation or phenomic data) can enhance accuracy and offer experimental confirmation (Jez et al 2021) to further aid in understanding the physiological implications of elements like genomic redundancy and circadian rhythm. Despite these developments in modelling applications for both microbes and plants, few studies have examined plant-microbe interactions using a community metabolic model method i.e., combining both microbial and plant models into a single simulation. Additionally, there is still a considerable gap between laboratory-scale experimental results and field-scale outcomes, providing much possibility for advancements in this sector.

The precise source and recipient of metabolite exchanges cannot always be determined by experimental measurements. Therefore, modelling enables quicker *in silico* testing of a wide range of potential unidirectional and bidirectional interactions within a community (Ibrahim et al 2021). For instance, a methodical strategy for analyzing community relationships can start with the selection of certain organism pairings, followed by the dual member model's prediction of potential metabolite exchange-based interactions. Understanding how interactions might vary with more community members will then be made possible by comparing the pair wise interaction predictions with simulations of a larger community. The plant secretes metabolites that are necessary for the recruitment of microorganisms to a tissue, but it is still unclear how interactions between microbes and plants, as well as between microbes themselves affect this process. Understanding and predicting the assembly process will be made easier with the help of the integration of plant and microbial metabolic models in a dynamic format (e.g., the use of dynamic changeability algorithms to investigate time-resolved interaction effects. This is especially true for understanding what drives the differences in colonization between plant species as well as how pathogens may interfere with the colonization process.

Overall, combining computational and experimental approaches will expand our current understanding of the complex interactions between plants, microbes and the environment. Improvements in agriculture like the creation of microbial inoculants to encourage plant growth or resistance in the face of more frequent global climate catastrophes can be made more competent by these advancements (Lieven et al 2020). With these initiatives, maintaining high modelling standards across the scientific community will remain crucial when extending models and algorithms to more intricate plant-microbe systems (Carey et al 2020).

Plant-Microbe Interactions for Agricultural Sustainability

Plants grow, eat and are healthier when they are naturally associated with microorganisms (Ray et al 2020). Rhizospheric and phyllospheric microorganisms are important due to their applications in increased nutrient absorption, improved water sequestration, induced systemic resistance (ISR) and competitive exclusion of plant diseases and remediation of environmental contaminants. These positive characteristics have encouraged the use of plant-microbe interactions in agro-ecosystems to increase productivity. The use of commercially available plant beneficial microorganisms (CAPBM) in agro-ecosystems is largely attributed to their compatibility and complementarities with natural processes of nutrient cycling, plant protection and other associated biological activities (Adeleke et al 2019).

Abiotic stressors are a growing global threat to agricultural productivity (Etesami and Beattie 2017). These stresses include extreme heat and cold weather, flooding, drought, nutrient depletion, toxic metals and organic contaminants. Due to economic consequences, there is a need for reasonably priced, reliable and ecologically acceptable methods to lessen the negative impacts of abiotic stresses on plants. Some of these relationships involve extremely complex symbioses that confer stress tolerance including those with mycorrhizae and rhizobia that help meet the challenge of nutritional and water deficiencies. Work is being pursued on microbial strains for their capacity to offer protection against a specific stress, such as phosphate limitation and cross-protection against other stresses. This increased interest in the agricultural application of beneficial microorganisms is reflected in the literature. Many of these are enduring and have a negative impact on the ecosystem. For the repair of agricultural soils, pesticides can only be controlled by biological agents. Pesticides frequently cause an excessive amount of pollution in crop fields. When compared to physical and chemical methods, pesticide biodegradation has proven to be a more efficient, cost-efficient, and environmentally benign method (Chaudhari et al 2023)

The use of chemicals is both expensive and environmentally unfriendly. The effects of temperature changes and pH changes on biodegradation are important. Bioremediation/rhizodegradation is the process by which fungus and bacteria in the rhizosphere break down organic contaminants. If the right vegetation is used, the rhizosphere's pollution decomposers may grow in quantity and activity resulting in enhanced rhizodegradation of harmful pesticides (Saravanan et al 2020). Most of the pesticide-decomposing enzymes are created by plant-related microorganisms in the rhizosphere. They cause mineralization of pesticides (Kumar et al 2019). This rhizoremediation procedure could be a useful tool for removing pesticides from contaminated soil. The interaction between plants and microorganisms has led to the development of phytoremediation and bioremediation as substitutes for such technologies (Abhilash et al 2012). The development of agro-ecosystems and the remediation of environmental pollutants are both significantly aided by PGPR (plant growth-promoting rhizobacteria). In addition to PGPR, a number of fungi, endophytes, mycorrhizae, and algae associate with plants and aid in sustainable development (Mishra et al 2020).

CONCLUSION

Soil is a dynamic ecosystem that is inhabited by a vast array of microbes. These microorganisms play a crucial role in maintaining soil health and promoting plant growth. The interactions between microbes and plants can be both positive and negative depending on the nature of the relationship. Positive interactions, such as mutualism and commensalism, contribute to the overall health and productivity of the soil and its resident plants. On the other hand, negative interactions such as predation and competition, can have detrimental effects. Rhizosphere is a hotspot for plant-microbe interactions due to the release of root exudates. Root exudates contain various compounds that facilitate communication between plants and microbes. Recognition of host cells host signaling molecules by microbes is a crucial step in establishing these interactions. Environmental factors, such as temperature, moisture, circadian rhythms, and soil nutrient status, can influence these microbe-microbe and plant-microbe interactions. Understanding these factors is important for studying the dynamics of the soil ecosystem and developing sustainable agricultural practices. Metabolic modeling, a mathematical approach, can be used to analyze the stoichiometry of metabolic reactions and study the plant-microbe-environment interactions. This modeling helps in understanding the metabolic processes and nutrient flows within the soil ecosystem. Exploiting plant-microbe-environment interactions holds great potential for developing efficient agroclimatic ecosystems and bioremediation strategies for pesticide-contaminated soils. By harnessing these interactions, agriculture can become more sustainable. It also leads to improved soil health, enhanced plant growth and environmental conservation. By unlocking the potential of these interactions can optimize nutrient cycling, promote plant health, and reduce the environmental footprint of agriculture, leading to a more sustainable and resilient future.

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