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Harnessing the plant microbiome to promote the growth of agricultural crops

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ABSTRACT

The rhizosphere microbiome is composed of diverse microbial organisms, including archaea, viruses, fungi, bacteria as well as eukaryotic microorganisms, which occupy a narrow region of soil directly associated with plant roots. The interactions between these microorganisms and the plant can be commensal, beneficial or pathogenic. These microorganisms can also interact with each other, either competitively or synergistically. Promoting plant growth by harnessing the soil microbiome holds tremendous potential for providing an environmentally friendly solution to the increasing food demands of the world's rapidly growing population, while also helping to alleviate the associated environmental and societal issues of large-scale food production. There recently have been many studies on the disease suppression and plant growth promoting abilities of the rhizosphere microbiome; however, these findings largely have not been translated into the field. Therefore, additional research into the dynamic interactions between crop plants, the rhizosphere microbiome and the environment are necessary to better guide the harnessing of the microbiome to increase crop yield and quality. This review explores the biotic and abiotic interactions that occur within the plant's rhizosphere as well as current agricultural practices, and how these biotic and abiotic factors, as well as human practices, impact the plant microbiome. Additionally, some limitations, safety considerations, and future directions to the study of the plant microbiome are discussed.

1. Introduction

The plant microbiome can be broken down into three parts: the phyllosphere, endosphere and rhizosphere (Berg et al., 2014; Bulgarelli et al., 2012; Lundberg et al., 2012). The phyllosphere is the term used for the total above ground plant surfaces (leaves, stem, flowers and fruit) that microorganisms can inhabit. The endosphere is the microbial habitat of microorganisms that live within various plant tissues. The best studied microbiome component is the plant's rhizosphere, which is a narrow region of soil directly associated with the plant's roots (Hiltner, 1904). The organisms present within the plant's rhizosphere is the primary focus of this review. Within the plant rhizosphere reside not only prokaryotic organisms (e.g. bacteria and archaea), but also unicellular (e.g. protozoa) and multicellular (e.g. nematodes, fungi) eukaryotes and viruses, which all play important roles towards plant growth and development. It is believed that the number of microbial organisms present within the plant's microbiome typically outnumbers the host cells within the living plant (Mendes et al., 2013). The microbiome of organisms is an extension of their genomes, in which the microbes associated with the hosts have far greater protein-coding and metabolomic potentials due to their diversity and number. Microorganisms within the plant's microbiome play many vital roles in the growth and maintenance of agriculturally important plants, which include the acquisition of nutrients, reduction of plant stress and suppression of plant diseases. In addition, plants and microorganisms can coordinately assist in remediating contaminants in the environment.

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There are many factors, both biotic and abiotic, that can affect the composition of organisms within the plant's microbiome. Abiotic environmental factors such as drought, salinity, heavy-metal contamination and pH can affect plant growth and the composition of the plant microbiome. Similarly, agricultural practices such as the presence of chemical fertilizers and pesticides can alter the composition of the plant microbiome, and in some cases, can select for antimicrobial resistant bacteria. In addition, biotic factors such as invading pathogens or the application of plant growth-promoting organisms can also affect the composition of the plant microbiome.

For almost a century, scientists have reported on the importance of the soil microbiome (Waksman, 1927); however, until recently the complexity of the complete microbiome of plants was underappreciated. This was likely due to the small percentage of soil microbes that can be cultured under laboratory conditions (Stewart, 2012). However, with advances in high throughput sequencing technologies and continued reductions in sequencing costs (Pettersson et al., 2009), we are now able to begin to appreciate the diversity of microorganisms present within the soil. A better understanding of the dynamic interactions of the environment-plant-microbiome axis will facilitate the knowledge-guided, precision-application of the plant microbiome to enhance plant growth under specific conditions. This review summarizes the interactions of plant rhizosphere microorganisms among themselves, as well as with the host and the environment. Finally, we discuss some limitations to current plant microbiome studies and safety considerations for applying beneficial microbial consortia in the field.

2. Factors affecting residents of the plant microbiome

For many years, we have known the consequences of both biotic and abiotic factors on plant growth, and now due to advances in next generation sequencing we are able to appreciate the effect that these stresses have on the plant's microbiome (Fig. 1). Currently, the effects that abiotic factors (e.g. salinity, drought, pH, flooding and heavy metal contamination) and the addition that bacteria have on the plant microbiome have been well studied (Ambrosini et al., 2016; Frossard et al., 2018; Lareen et al., 2016; Naylor et al., 2017; Thiem et al., 2018; Young et al., 2018). However, until recently, the effect that both viruses (bacteriophages) and fungi have on the native microbiome is less understood (Busby et al., 2016; Koskella and Taylor, 2018; Morella et al., 2018; van der Heijden and Hartmann, 2016). Finally, we are also beginning to appreciate the role that the host plants' genotype and innate immune system plays towards the shaping of its microbiome (Hacquard et al., 2017; Haney et al., 2015; Lebeis et al., 2015).

2.1. Biotic factors

2.1.1. Plant hosts

In their natural environments, plants are in constant contact with many organisms that belong to all three domains of life. All plants possess an innate immune system, which is able to recognize invading microbes and mount an effective defense against potential phytopathogens. Unsurprisingly, the plant innate immune system plays an important role in modulating the microbial species found within its microbiome (Hacquard et al., 2017). Lebeis et al. (2015) found that the biosynthesis and signalling pathway of salicylic acid (SA) is required to assemble a normal root microbiome, and that SA modulated the colonization of the root by specific bacteria. Interestingly, the aforementioned study found no significant correlation with the other two main stress phytohormones, jasmonic acid (JA) and ethylene (ET) (Lebeis et al., 2015).

Other factors that have an impact on the microbiome of plants is host genotype and age (Wagner et al., 2016). A study by Haney et al. (2015) showed that certain *Arabidopsis* accessions support the growth of *Pseudomonas fluorescens*, whereas other accessions actively inhibit *P. fluorescens* growth. For example, it was found that *Arabidospis thaliana*

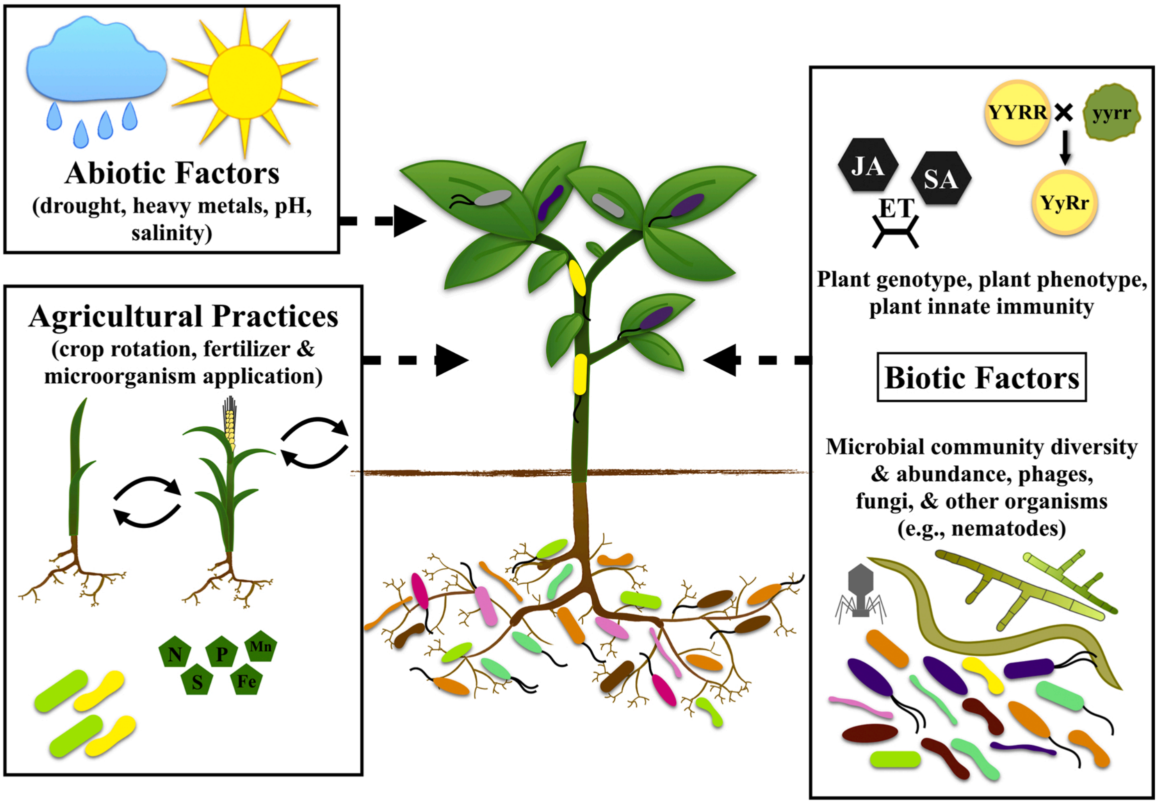

Fig. 1. Factors affecting the plant microbiome. The plant's microbiome is affected by many abiotic and biotic factors, as well as agricultural practices. These factors form a complex network of interactions that can shape and change the microbiome to the benefit or detriment of the plant.

Col-0 had reduced susceptibility to the fungal pathogen *Fusarium oxysporum* in the presence of *P. fluorescens* WCS365, while *P. fluorescens* WCS417r could trigger induced systemic resistance (ISR) and protect Col-0 from the bacterial pathogen *Pseudomonas syringae* pv. tomato DC3000 (Haney et al., 2015). Therefore, the composition of the plant microbiome can vary based on plant genotype, as well as by specific bacterial strains present.

Using metabolomic analyses (Fig. 2), Zhalnina et al. (2018) identified a consistent pattern in the chemical composition of root exudates of an annual grass that is deposited in its rhizosphere. They also demonstrated an interaction between these plant exudate profiles and genome sequence-predicted preferences of rhizosphere bacteria for consumption of aromatic organic acids exuded by the plants. This discovery shed new light on how chemical probes from plant hosts influenced the process of rhizosphere microbial community assembly and provided an attractive approach for harnessing a beneficial microbiome for plant growth promotion. However, a long-standing question in the field of plant-microbial interactions is how the plant immune system identifies potential pathogens from commensal or beneficial microbial residents, since the microbe-associated molecular patterns that are detected by plant hosts are highly conserved and present ubiquitously among almost all microbial organisms. A related question is: how does this differentiated recognition impact the components of plant-associated microbiota. A study using a combination of 16S rRNA gene profiling and shotgun metagenome analysis of root microbiota in wild and domesticated barley started to answer the above questions about how microbial functional traits contribute to host-microbial interactions (Bulgarelli et al., 2015). This study revealed that the microbial elicitors and effectors of plant immunity, among other biological functional groups including bacteriophage interactions and nutrient mobilization, were under positive selection within the barley rhizosphere (Fig. 3). The data from this study also suggested that the development of the rhizosphere microbiome appeared to be shaped by the selections amongst microorganisms in addition to their interactions with the plant hosts.

2.1.2. *Microorganisms*

2.1.2.1. Bacteria. Bacteria are the most thoroughly characterized part of the plant microbiome, due to their importance, large impact, and potential for plant growth promotion. The microbiome's bacterial composition varies vastly from differences in plant species, genotype, life cycle stage, proximity to roots, and soil type (Bulgarelli et al., 2015; Gaiero et al., 2013; İnceoğlu et al., 2011; Sasse et al., 2018). Phyla that tend to dominate the rhizosphere include Actinobacteria, Proteobacteria, Chloroflexi, and Firmicutes, as they have been seen in multiple characterization assays (Bodenhausen et al., 2013; Bulgarelli et al., 2015; Suárez-Moo et al., 2019; Veach et al., 2018). The phyllosphere typically contains more Acidobacteria and is characterized by bacteria with adapted functions like a high expression of TonB-dependant receptors, aggregate formation, production of biosurfactants, and metabolic uses for methanol, amino acids, and sugars (Delmotte et al., 2009; Vorholt, 2012).

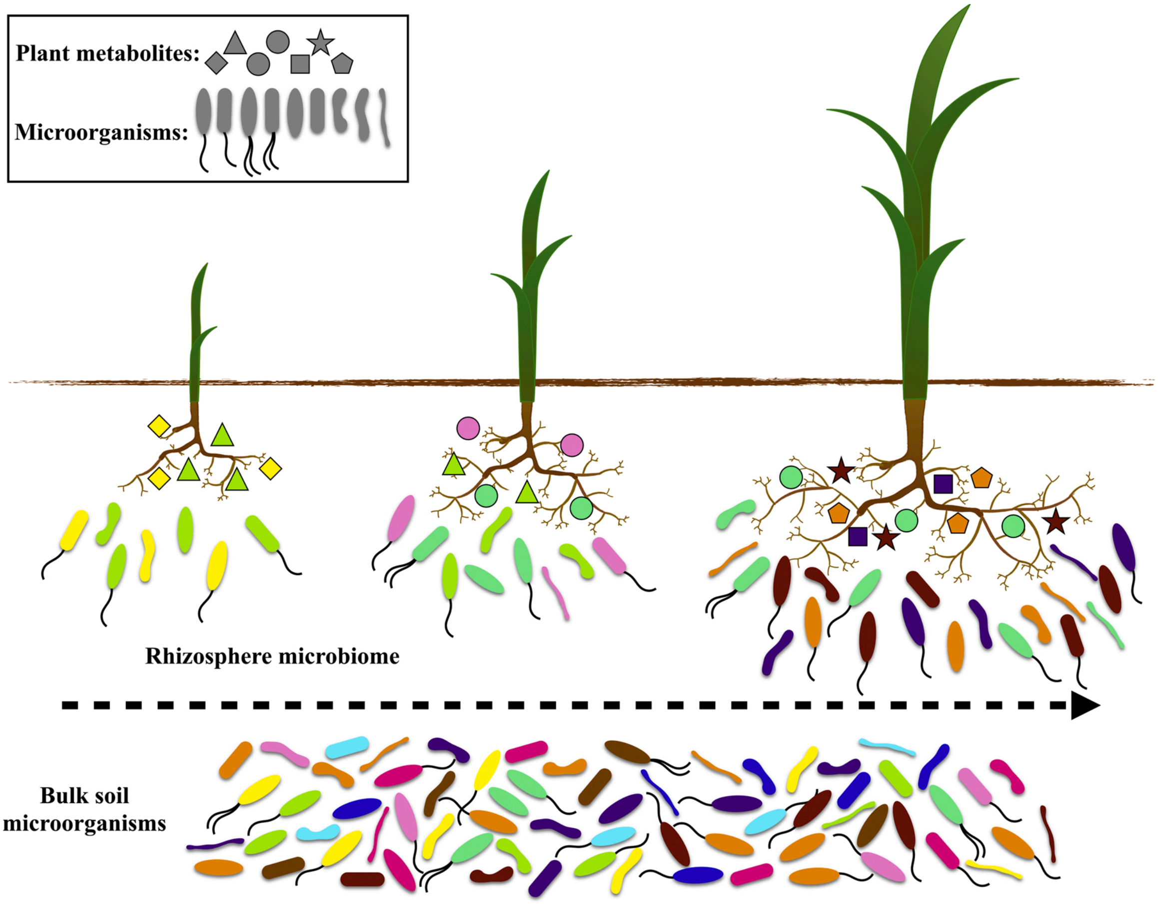

Fig. 2. Root exudates in an annual grass synchronize with microbial substrate use promoting microbial community assembly. Zhalnina et al. (2018) demonstrated that an annual grass deposited a succession of plant metabolites (distinct metabolites are indicated by separate shapes and colors) during their development (indicated by the dotted arrow moving with the growth of the plant). The bulk soil microorganisms serve as the source for the generation of the rhizosphere microbiome, where community members are selected by their genome sequence-predicted preferences for their ability to utilize the plant metabolites (microorganisms are color-matched to the preferred metabolite that attracts them to the rhizosphere microbiome). Thus, the rhizosphere microbiome assembly pattern can be predicted from analyzing plant metabolites and microbial substrate usage.

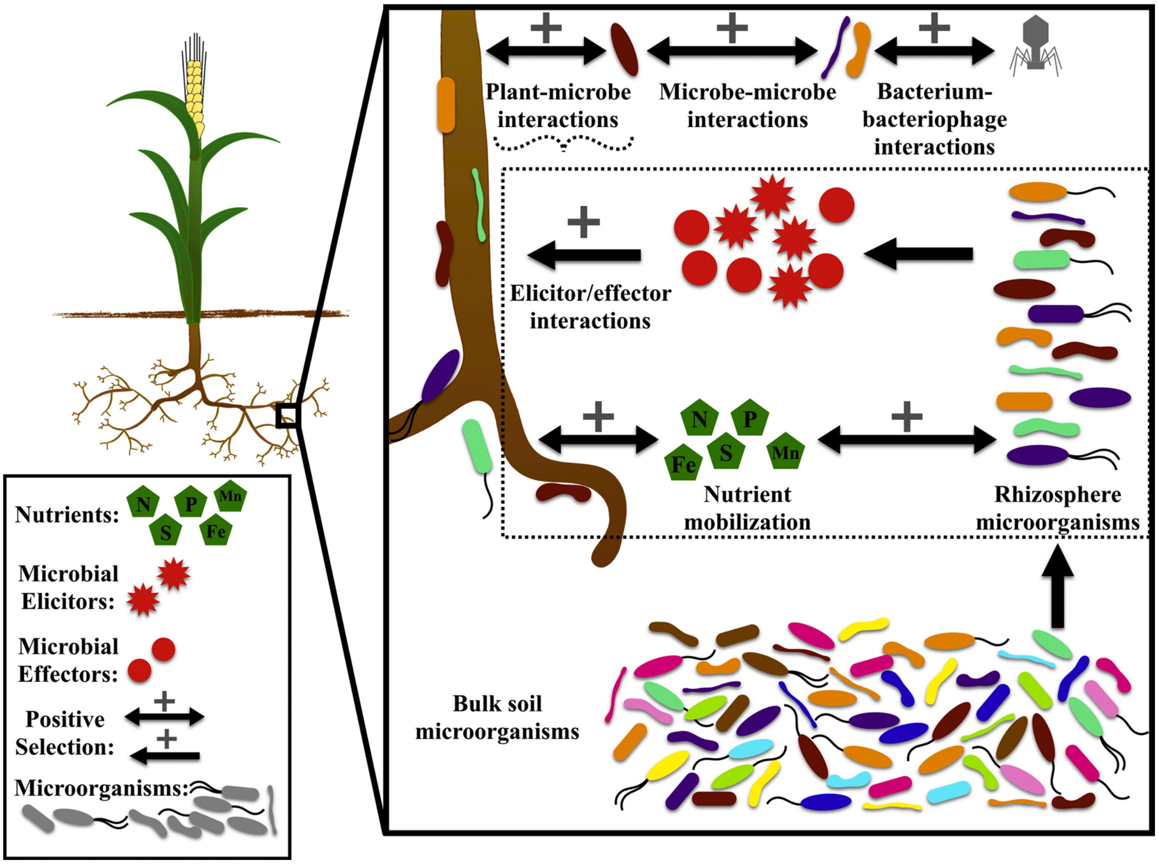

Fig. 3. The combined biological interactions occurring through positive selective forces at the root-soil interface drive rhizosphere microbiome establishment. A study by Bulgarelli et al. (2015) used 16S rRNA gene profiling and shotgun metagenome analysis of the rhizosphere microbiomes from wild and domesticated barely to discover that there was positive selection for genes facilitating interactions between host, bacteria, and bacteriophage, including genes for microbial elicitors and effectors of plant immunity and genes related to nutrient mobilization.

As bacteria are the core of the complex interconnected microbiome, they impact other inhabitants of the microbiome significantly, including other types of bacteria. These impacts may be due to synergistic effects like biofilm formation, in which bacteria can attach to a surface or each other for protection (Buonaurio et al., 2015). Adding to this, multispecies biofilms tend to be more effective than monospecies biofilms due to additive effects, which could cause mutual proliferation when a new species is introduced to the microbiome (Burmølle et al., 2006 & 2014). Other symbiotic relationships between bacterial species in the plant microbiome include quorum sensing signaling and metabolite sharing (Passos da Silva et al., 2014). An example of the beneficial relationship between bacteria in the plant microbiome is in olive trees infected with knot disease. *Pseudomonas savastanoi* pv. *savastanoi*, the pathogen responsible for olive knot, was found to be enriched by non-pathogenic bacterial species *Pantoea agglomerans* and *Erwinia toletana*, causing the disease to increase in severity (Hosni et al., 2011; Passos da Silva et al., 2014). Effects of bacteria on other bacteria in the plant microbiome can also be inhibitory. For example, a study showed that the tomato wilt disease bacterium *Ralstonia solanacearum* caused a decrease in the abundance of Actinobacteria, Bacteriodetes, Verrucomicrobia, Cyanobacteria and other phyla of bacteria in the plant microbiome during infection (Wei et al., 2018). Furthermore, *R. solanacearum* itself was also found to be inhibited by many *Pseudomonas* species, reducing pathogen density and disease prevalence (Hu et al., 2016). These inhibitory interactions may be caused by competition between species and complex long-term disease dynamics. One specific mechanism that can inhibit other bacteria is the type VI secretion system (T6SS), which is found in some bacteria and targets eukaryotic and prokaryotic cells with toxic proteins (Ho et al., 2013). *Pseudomonas putida*, using its T6SS, was found to inhibit *Xanthomonas campestris* in *Nicotiana benthamiana* leaves, decreasing the pathogenicity of *X. campestris* (Bernal et al., 2017). Another mechanism for inhibiting other bacteria is quorum quenching, which was observed in *Acinetobacter lactucae* strain QL-1 and *Acinetobacter* sp. strain XN-10, where these strains degraded the quorum sensing signaling molecules of the pathogens *Xanthomonas campestris* pv. *campestris and Pectobacterium carotovorum* subsp. *carotovorum*, respectively, thereby reducing damage to the plant hosts (Ye et al., 2019; Zhang et al., 2020). The actual mechanisms causing changes in the bacterial community of plants by other bacteria is likely influenced more by complex interplay between the plant, bacteria, and other microbes.

Bacteria have also been seen to interact extensively with fungi, impacting fungal populations and vice versa. This interaction seems to be largely plant-independent, as bacterial-mediated fungal community shifts are also seen in unplanted conditions (Durán et al., 2018). Bacteria in the plant microbiome can act in beneficial or inhibitory ways on fungi depending on the specific situation of the interactions. Keystone taxa of bacteria like members of the *Burkholderia* genus can greatly increase arbuscular mycorrhizal fungi (AMF) abundance through symbiosis, but in contrast *P. fluorescens* can suppress fungal growth (Banerjee et al., 2018). Inhibition of fungi by bacteria in the plant microbiome is commonly done through secreted metabolites. For example, *Pseudomonas piscium* was found to secrete phenazine-1-carboxamide, a compound that inhibited the pathogenic fungus *Fusarium graminearum* through targeting protein activity during infection (Chen et al., 2018). Symbiosis is also a common relationship between bacteria and fungi in the plant microbiome, especially with AMF (Braga et al., 2016; Banerjee et al., 2018; Kemen, 2014; van der Heijden et al., 2016). An interesting and complex interaction reported between *Rhizopus* spp. fungi and

Burkholderia spp. bacteria showed that they had an endosymbiotic relationship in which *Rhizopus* fungi were dependent on *Burkholderia* activity to be able to produce spores to infect rice seedlings with blight (Braga et al., 2016). These studies showed that the bacterial and fungal communities within plant microbiome have mutual effects on each other's components. Additional details of how the fungal community shapes the plant microbiome is discussed in the section below.

2.1.2.2. Fungi/Oomycetes.

Fungi, though less studied than bacteria, have many essential functions within the plant microbiome. Types of fungi in the plant microbiome vary from host to host, are impacted by nitrogen deposition (Dean et al., 2014), and are strongly dependent on soil type (Nallanchakravarthula et al., 2014). Fungi can be beneficial to plants, like *Atractiella rhizophila* which fosters plant growth (Bonito et al., 2017), or pathogenic, like *Armillaria mellea* which causes root rot disease (Aguín-Casal et al., 2004).

Though most research on fungi in relation to the plant microbiome is on the potential for plant growth promotion, there is some insight into the impact of fungi on other microbes in the plant microbiome. Most fungal interactions towards bacteria in the plant microbiome appear to be mutually beneficial. For example, one study showed that several types of AMF could produce exudates that increased bacterial abundance and changed microbiome composition, with the biggest increase observed being in Gammaproteobacteria (Lindahl et al., 2007). Another way in which fungi can affect bacteria in the plant microbiome is by facilitating bacterial root colonization through their hyphae, which promote bacterial attachment (Artursson et al., 2005). The fungal pathogen *Rhizoctonia solani* was found to produce oxalic acid and phenylacetic acid during infection, compounds that indirectly increased the abundance of *Oxalobacteraceae, Burkholderiaceae, Sphingobacteriaceae,* and *Sphingomonadaceae* bacteria in disease suppressive soils (Chapelle et al., 2016). Therefore, it appears that in disease suppressive soils, a pathogenic fungus releasing exudates may act against itself by triggering bacterial and plant stress responses to resist infection (Chapelle et al., 2016; Liang et al., 2009; Mendes et al., 2011).

Other fungal interactions in the plant microbiome are less studied. Similar to bacteria, different types of fungi also interact with each other. An *in vitro* study of interactions between two types of AMF, *Rhizophagus irregularis* and *Glomus aggregatum*, showed an intense competition between the two species, with each species' presence equally decreasing both of their abundances (Engelmoer et al., 2014). It appears that the relatedness of AMF fungi determines the amount of competition, with more distant relatives in the plant microbiome exhibiting more competition and disequilibrium in fungal populations (Roger et al., 2013). Closely related fungal species tend to exhibit more symbiosis, as seen in a study using three different fungi from a subgenus of *Glomus* where nutrient transfer was reported between the fungi and the host plant (Kiers et al., 2011; Roger et al., 2013). Overall, interactions between different fungi in the plant microbiome are difficult to predict as they depend on a multitude of factors such as soil type, the host plant, and other environmental conditions (Engelmoer et al., 2014; Verbruggen et al., 2012).

2.1.2.3. Viruses.

Bacteriophages are viruses specific for bacteria, and are extremely abundant in the biosphere (Buttimer et al., 2017). In fact, viruses are estimated to be much greater in number than prokaryotes in the plant microbiome (Parikka et al., 2017). Therefore, it is not surprising that studies have found that on average 8.9–12.1 % of bacteria in pasture soils and 23 % of bacteria in water flooded rice fields were infected with bacteriophages (Bowatte et al., 2010; Takahashi et al., 2011). Some bacteriophages naturally target pathogens found in the plant microbiome, making them of interest for use in facilitating plant growth promotion through disease prevention (Bhunchoth et al., 2015). Generally, bacteriophages tend to be much less prevalent in the phyllosphere in comparison to the rhizosphere or endosphere, likely due to the negative effect of UV light from the sun on bacteriophage survival (Iriarte et al., 2007). Characterization of bacteriophages in the plant microbiome is difficult because they do not have 16S rRNA markers like bacteria. Identification instead relies on a few conserved marker genes, and thus they are poorly understood (Koskella and Taylor, 2018; Morella et al., 2018; Steward et al., 2012; Stough et al., 2018).

Bacteriophages can alter the plant microbiome in many ways through their interactions with bacteria. Most obviously, lytic bacteriophages will impact the population size of bacteria they target, and thus cause a chain reaction in the other organisms connected with the directly targeted bacteria due to the closely interconnected nature of the plant microbiome (Buttimer et al., 2017; Koskella and Meaden, 2013; Morella et al., 2018). This effect often causes co-evolution between bacteria and bacteriophages, with bacteriophages counter adapting when their target bacteria eventually evolves to resist it (Koskella and Brockhurst, 2014; Koskella and Taylor, 2018). Bacteriophages also impact bacteria in the plant microbiome significantly through horizontal gene transfer, where they inadvertently spread bacterial genes from one host to the next. This process alters the success of bacterial colonization of the plant and thus plant health as well, as the genes transferred can benefit bacterial survival (Koskella and Taylor, 2018; Varani et al., 2013). Some bacterial plant pathogens from the genera *Pectobacterium, Pseudomonas, Ralstonia,* and *Streptomyces* have been shown to involve prophages, or genetic information from bacteriophages, in their disease symptoms (Varani et al., 2013). Thus, bacteriophages can exert negative effects on bacteria through lysis, but they may also help many pathogenic bacteria and may be important to the evolution of plant disease caused by said bacteria.

Though lesser known, viruses that target fungi also exist and are extremely pervasive (Al Rwahnih et al., 2013). These types of viruses are aptly named mycoviruses and are transferred by cell division as they lack an extracellular method of infection, and thus are transferred through spores or anastomosis (Nuss, 2005; Son et al., 2015). An example of such a mycovirus is *Sclerotinia sclerotiorum* hypovirulence-associated DNA virus 1, a single stranded DNA geminivirus that infects the fungus *Sclerotinia sclerotiorum* (Nuss, 2005). Mycoviruses have been known to induce hypovirulence in plant-pathogenic fungi, and thus have been studied for potential use in agriculture. One mechanism that may cause this hypovirulence is an alteration of fungal signalling caused by a virus, which was reported in a study on the chestnut blight causing fungus *Cryphonectria parasitica* (Choi et al., 1995).

There have also been studies focusing on the interactions of plant viruses and rhizosphere bacteria. A survey of 30 different rice fields in Africa revealed that 18.8 % of the investigated plants were co-infected by two common pathogens: rice yellow mottle virus and *Xanthomonas oryzae* (Tollenaere et al., 2017). In a laboratory study, the *Xanthomonas* load was significantly increased when co-infecting with the virus (Tollenaere et al., 2017). In another study, additional connections were made between a plant virus, bacteria and pests of the same plant host. It was shown that the zucchini yellow mosaic virus infection on cucurbit plants reduced the rates of bacterial wilt caused by the bacterial pathogen *Erwinia tracheiphila* (Shapiro et al., 2013). However, this reduced rate of bacterial wilt was likely due to the reduced visitation by cucumber beetles, the vectors for *E. tracheiphila*, rather than the direct impact on bacteria by plant viral infection (Shapiro et al., 2013).

2.1.2.4. Other microorganisms.

Archaea, though understudied in relation to the plant microbiome, are significant components of the microbiome and have great potential for use in plant growth promotion. They often have symbiotic relationships with plants through their intimate interactions with their environments and other microbial residents (Moissl-Eichinger et al., 2018). From studies of plants in a bog ecosystem, archaea were found to interact with plants and fungi affecting nutrient supply and exchange, as well as plant secondary metabolite production (Taffner et al., 2018). Plant growth promoting capabilities of archaea have not been thoroughly investigated, but other methods for potential use of archaea in agriculture have already been discovered. A study on tobacco plants using the archaeon *Methanococcoides burtonii*, which produces non-photosynthetic Rubisco (Ribulose-1,5-biphosphate carboxylase) required for the often rate-limiting carbon dioxide fixation step in photosynthesis, was found to increase photosynthesis rates and plant growth (Wilson et al., 2016). Other methods in which archaea have been found to promote plant growth include auxin biosynthesis, nutrient supply, and protection from abiotic stress (Smith-Moore and Grunden, 2018; Taffner et al., 2018). However, ammonia-oxidizing archaeal gene presence has been found to be negatively correlated with soil fertility, and more strongly positively correlated with higher pH, which could inhibit the growth of some organisms (Delgado-Baquerizo et al., 2013; Thion et al., 2016).

Another microorganism inhabiting the plant microbiome is the nematode, a common type of eukaryote, which is often parasitic to its host plant. Nematodes cause a wide range of plant disease, such as root-knot and lesion disease (Abad et al., 2003; Wuyts et al., 2007; Gamalero and Glick, 2020). Interestingly, nematodes have developed many strategies for the invasion of plants, despite the plant's innate defenses, such as injecting effectors into plant cells to reprogram the plant's basal defense signaling, and thus gene expression, to facilitate nematode infection (Ali et al., 2017 & 2018). The microbiome of the host plant has the potential to counteract nematodes to protect against disease, which has seen some success in recent research. A suppressive soil of root-knot nematodes was analyzed, and found to contain the fungus *Malassezia globosa* and multiple fungal species from the Plectosphaerellaceae family, as well the bacterium *Neorhizobium galegae*, which likely contributed to the suppression of nematodes and should be tested for plant growth promotion in further studies (Elhady et al., 2017). Another study on nematode suppressive soils also showed that fungal genera such as *Eurotium*, *Ganoderma*, and *Cylindrocarpon* were present in the most effective soils, furthering the potential usefulness of fungi against nematodes (Adam et al., 2014). Rhizobacteria also have potential for use to control plant parasitic nematodes via enzymes and metabolic by-products, that can antagonize nematodes (Castaneda-Alvarez and Aballay, 2016). A study on soybean and tomato plants showed that transplanting rhizosphere microbiomes from plants with low nematode abundances to newly grown plants infected with the root lesion nematode, *Pratylenchus penetrans*, significantly reduced the number of nematodes inside plant roots. This effect appeared not to be plant-mediated as even infected soil without plants present showed that nematodes were inhibited by the transplanted microbiome. This effect indicates a relationship between the many players in the plant microbiome and nematodes that could be harnessed in agriculture for protection against nematode infection (Elhady et al., 2018).

2.2. Abiotic factors

2.2.1. Drought

Drought is a huge environmental stressor in agriculture, which results in devastating losses yearly (Lesk et al., 2016). The effect of drought on plants has been studied extensively, however, there is not much research on the effect drought has on the plant microbiome. Obviously, drought results in a net decrease of plant and microbiome biomass (Bastida et al., 2017; Naylor and Coleman-Derr, 2018). However, some types of bacteria actually do better under drought conditions, as shown by studies on grasses and rice plants using drought treatments which resulted in a significant enrichment in bacteria in the Chloroflexi phylum (Naylor et al., 2017). Examples of drought-adapted bacteria in the microbiome that naturally dominate arid areas include members from the Proteobacteria, Bacteroidetes and Firmicutes phyla (Soussi et al., 2016).

Many facets of the plant microbiome have been studied for their ability to protect the plant against drought stress. *Acinetobacter* and *Pseudomonas* bacterial isolates were found to reduce photosynthesis inhibition induced by drought, likely through 1-aminocyclopropane-1-carboxylate (ACC) deaminase synthesis, thus alleviating root and shoot biomass decreases in drought-challenged grapevines. However, these bacterial strains did not promote growth in well-irrigated plants (Rolli et al., 2015). This suggests that there are interactions specifically between the bacteria and drought conditions, though this lack of growth promotion in control plants was not seen in other studies (Chakraborty et al., 2013; Redman et al., 2011). Another study on multiple types of plants in semiarid climates inoculated with *Bacillus thuringiensis* IAM 12077 induced positive effects on plant growth and nutrient acquisition (Armada et al., 2018). Most bacteria that promote plant drought-resistance tend to do so via metabolism and nutrient production, reducing ethylene production, and increasing root water intake (Armada et al., 2018; Gagné-Bourque et al., 2016; Marasco et al., 2013; Rolli et al., 2015).

2.2.2. Salinity

Salinity is an important factor to consider in agriculture due to its negative effect on plant health via changing osmotic forces in the plant cells causing nutrient uptake imbalances (Yaish and Kumar, 2015). It also decreases the biomass of microorganisms in the plant microbiome through drying and cells lysis, so that salinity significantly affects microbiome composition as halophytic microbes tend to dominate highly saline soils (Yan et al., 2015). Some mycorrhizal fungi can help increase sodium and calcium ion translocation in plants and increase growth, but high salinity levels also inhibit mycorrhizal association, making them less effective (Hrynkiewicz et al., 2015; Thiem et al., 2018). Further, salinity also decreases mycorrhizal colonization, hyphae growth, and germination, deterring fungal growth and, as the plant microbiome is a complex network of inter-reliant microbes, shifting many other facets that interact with fungi (Hameed et al., 2014). Another study reported that *Tomentella*, *Lactarius*, *Phialocephala* fungi became more abundant in saline areas, while *Mortierella* and *Naucoria* fungi did the opposite (Thiem et al., 2018). The effect of salinity, however, seems more impactful on bacteria when compared to fungi (Thiem et al., 2018). As expected, increased salinity in soils seems to decrease bacterial richness and diversity significantly as most bacteria are not adapted for high saline environments (Thiem et al., 2018; Yaish et al., 2016). Generally, Alphaproteobacteria tend to decrease and Actinobacteria tend to dominate in high saline soils (Kim et al., 2019; Mukhtar et al., 2016; Thiem et al., 2018; Yaish et al., 2016). Encouragingly, plant growth-promoting bacteria have been isolated from saline soils, and show promise for providing an eco-friendly option for improving plant growth in salt-stressed environments. For example, Fatima et al. (2020) showed the saline-soil isolate *Alcaligenes* sp. AF7 had various plant growth promoting characteristics (e.g., production of exopolysaccharides, indole-3-acetic, gibberellic acid and siderophores) prominent up to different salinity thresholds and the bacterium increased vegetative growth of rice more than twofold in saline soils. Additionally, *Cellulomonas pakistanensis* sp. nov. strain NCCP-11^T isolated from paddy rice was found to be moderately halotolerant (up to 12 % NaCl) (Ahmed et al., 2014) and isolates of *Cellulomonas* have shown promise as plant growth-promoting bacteria in rice, by improving nutrient availability by degrading organic matter through secreted enzymes, cellulases and hemicellulases (Duy et al., 2016). More investigation into saline-stressed soils could reveal other important halotolerant microorganisms in the microbiome, which could be utilized in agricultural practices in salt-stressed environments.

2.2.3. Heavy metal contamination

Heavy metal contamination in the plant microbiome tends to decrease microbial diversity and operational taxonomic unit (OTU) counts, as shown in multiple studies using cadmium, lead, zinc, and chromium (Gołębiewski et al., 2014; Hur et al., 2011; Jiao et al., 2019; Sheik et al., 2012). However, this does not apply to all metals as a study on copper showed that long term exposure did not change bacterial diversity and richness, but rather only shifted the abundances of some bacteria, specifically an increase in Acidobacteria and Gemmatimonadetes and a decrease in all other phyla (Berg et al., 2012). This implies that different metals have different effects on the microbiome, with zinc being the most effective in causing changes in diversity and OTU counts, followed by cadmium and lead (Gołębiewski et al., 2014; Hur et al., 2011). Though there was an initial decrease in diversity during a 90-day experiment using 50 mg/kg of cadmium chloride in water, diversity increased following this initial decrease, suggesting that the microbial community has resilience to heavy metal pollution. However, this study also used many other chemicals such as dichloromethane, so it is unclear exactly what caused the observed changes (Jiao et al., 2019). The effects of metals on the various members of the microbiome are not yet completely understood, but the use of plant growth promoting microbes to aid in heavy metal reduction through phytoextraction has the potential to become widely used in agriculture due to its demonstrated effectiveness (Chen et al., 2016; Gil-Martínez et al., 2018; Mnasri et al., 2017; Wang et al., 2016). Additionally, some plant growth promoting microbes have demonstrated high tolerance to heavy metals, including *Pantoea agglomerans* strain C1 to arsenate (Luziatelli et al., 2020), *Alcaligenes faecalis* strains Cd1−1, Ag1−1, Ag1−3 and Sn1−1 to Al^{3+}, Ag^{2+}, Cd^{2+}, Cu^{2+}, Pb^{2+} and Sn^{2+} (Abo-Amer et al., 2015), and *Alcaligenes faecalis* MG257493.1, *Alcaligenes faecalis* MG966440.1 and *Bacillus cereus* MG257494.1 to Cu^{2+}, Cd^{2+}, Pb^{2+}, and Zn^{2+} (El-Meihy et al., 2019). Thus, these strains could be used to encourage plant growth in the presence of heavy metal contamination. Further investigation into heavy metal effects on the microbiome could reveal other players of potential use to the bioremediation efforts in agricultural practices.

2.2.4. pH

The soil pH is an important factor in determining plant microbiome composition and it also affects heavy metal uptake. Soil pH is one of the largest environmental determinants of rhizobacterial composition; bacterial types were found to vary closely with small pH changes while fungal types were only weakly linked to pH changes (Deng et al., 2018; Rousk et al., 2010). Examples of this include studies that identified Acidobacteria subgroups dominating in lower pH soils and Alpha- and Gamma-proteobacteria in higher pH soils, while lower frequencies of arbuscular mycorrhiza fungi were found in lower pH soils (Qi et al., 2018; Rousk et al., 2010; Young et al., 2018). Bacterial diversity was also found to decrease with more acidic pH (Yun et al., 2016). This extreme sensitivity to pH change in bacteria is likely due to most bacteria having narrow optimal pH ranges, and to changes in nutrient availability (Fernández-Calviño and Bååth, 2010; Qi et al., 2018; Yun et al., 2016). Plant growth can be inhibited by very alkaline soils due to the reduced ability to uptake minerals, and it can be harmed by very acidic soils due to excessive uptake of toxic heavy metals (George et al., 2012; Tőzsér et al., 2017). Thus, the microbiome is also indirectly affected by pH, since the microbiome is intimately connected to the plant's health and growth. There are some plant growth-promoting bacteria that show promise in alleviating alkaline stress in plants. Dixit et al., 2020 isolated three plant growth promoting bacteria (*Alcaligenes* sp. NBRI NB2.5, *Bacillus* sp. NBRI YE1.3, and *Bacillus* sp. NBRI YN4.4) from alkaline soils and found they enhanced maize biomass and germination under alkaline conditions *in vitro* with the *Bacillus* strain NBRI YN4.4 showing the greatest enhancement of plant growth. Additionally, inoculation of the soil with NBRI NB2.5, NBRI YE1.3, and NBRI YN4.4 increased soil enzymatic activities (e.g., alkaline phosphatase, beta-glucosidase and dehydrogenase) under alkaline stress, demonstrating the value of these alkalotolerant strains on plant growth and soil fertility in alkaline conditions (Dixit et al., 2020).

2.3. Agricultural practices

2.3.1. Crop rotation

Some common agricultural practices currently used by farmers to improve yield and quality include crop rotation, application of both natural (e.g. seaweed products and manure) and chemical fertilizers, and the use of beneficial microorganisms or transgenic plants. The benefits of crop rotations have been known for some time now and include generating disease suppressive soils (Peters et al., 2003) and increasing nutrients within the soil (Stevenson and Kessel, 1996), which both boost plant growth. However, for a long time the effect of crop rotations on microbial communities within the soil has not been understood. Many recent studies are examining how crop rotations affect microbial communities within the plant's rhizosphere and bulk soil near the plants (Breidenbach et al., 2017; Maarastawi et al., 2018). For example, a study by Hamel et al. (2018) showed that using a high frequency of pulse plants within a wheat crop rotation increased soil nitrogen levels but had little effect on the rhizobacterial community composition. However, a meta-analysis by Venter et al. (2016) found that crop rotations in general do increase microbial richness and diversity, and longer rotation trials produced greater positive effects on microbial richness. Therefore, both of these studies are consistent with the benefits of crop rotation. Further studies focusing on the co-occurrence of keystone beneficial and pathogenic microbes, as well as functional gene clusters associated with these microbial communities, are required to further elucidate the underlying mechanism(s) by which crop rotation enhances disease resistance.

2.3.2. Fertilizer application

Farmers have been applying both natural and chemical fertilizers to their crops for many years. However, the effect these fertilizers have on the microbial composition in the soil was not well understood. Research to date has focused on the effect that chemical fertilizers have on a crop's microbiome due to the fertilizer's defined chemical components. A study by Yeoh et al. (2016) showed that a reduced amount of nitrogen fertilization had little effect on the sugarcane microbiome, however it resulted in both lower plant biomass and nitrogen content. Whereas, high nitrogen fertilization improved crop biomass and nitrogen content, and increased the abundance of nitrification and denitrification genes within the surrounding soil. Interestingly, a study by Lang et al. (2018) with maize showed that with increasing phosphorus fertilizer application the overall community richness of AMF and bacteria decreased, however both fungal and bacterial gene copies increased with the increasing fertilizer application. Therefore, high fertilizer application decreases microbial community diversity, but selects for microbes that are tolerant to high nitrogen and phosphorus application.

Among the limited information of the effects of natural fertilizers on microbiome, one study has shown that the application of pig manure from animals treated with Difloxacin, a fluoroquinolone antibiotic, had a significant impact on soil bacteria for over 140 days post-application compared to manure from pigs not given antibiotics. Interestingly, the application of manure from Difloxacin-treated pigs led to an increase in the presence of antibiotic resistance genes within bacteria found in the soil (Jechalke et al., 2014). Similarly, little research has been conducted on the effect that the application of seaweed extract has on the crop plant microbiome, despite the fact that many groups have reported that seaweed components and extracts boost plant innate immunity (Chandía et al., 2004; Cook et al., 2018; Mercier et al., 2001).

2.3.3. Bacteriophage application to limit phytopathogens

The application of exogenous microorganisms would inevitably have an impact on the indigenous microbiome of plants or crops and its homeostasis. The effects of the addition of the microorganisms, including bacteria, fungi, and bacteriophage on native microbiomes, have been summarized in section 2.1.2 above. Therefore, the focus of this section is to expand on the more recent development of bacteriophage application in limiting phytopathogens.

Bacteriophages can be used as an environmentally friendly approach to indirectly boost plant growth by eliminating bacterial pathogens from crop plants. Antibiotic application can generate resistant bacteria, while bacteriophages are a good alternative to antibiotics as they have biological mechanisms and may adapt to the changing resistances of their target bacteria. The use of a cocktail of several bacteriophages makes it less likely that bacteriophage-resistant mutants of the targeted pathogen will develop since each of the different bacteriophages will likely bind to a different site on the bacterial surface. Bacteriophages also have the advantage when compared to typically used compounds like copper in that they can be engineered to target a specific pathogenic bacterium (Buttimer et al., 2017). Furthermore, recent laboratory assays and field studies have generated successful results in use of bacteriophages against common problematic plant diseases in agriculture. Multiple studies on tomato plants using bacteriophage therapy against *Ralstonia solanacearum*, a pathogenic bacterium that causes bacterial wilt, and on potato plants to protect against soft rot cause by *Dickeya solani* showed success in reducing the severity of disease and thus improved plant health (Adriaenssens et al., 2012; Bae et al., 2012; Bhunchoth et al., 2015; Czajkowski et al., 2017). Other plants that have demonstrated benefits from bacteriophage therapy include citrus for citrus bacterial spot and canker (Balogh et al., 2008), leek for bacterial blight (Rombouts et al., 2016), rice for bacterial browning (Azegami, 2013), and broccoli for black rot (Nagai et al., 2017).

Bacteriophage therapy can be applied in multiple ways but this is usually done through soil application. Success in reducing *R. solanacearum* prevalence was demonstrated in planta through soil application of a bacteriophage suspension, which tended to be most effective prior to pathogen infection, and became less effective the longer after infection the bacteriophages were applied (Bhunchoth et al., 2015; Iriarte et al., 2012). Czjakowski et al. demonstrated potential for additional research in leaf application as well through an assay on bacteriophage persistence on potato leaves (Czajkowski et al., 2017). Bacteriophage effectiveness may be enhanced by introducing the bacteriophage mixture along with a nonpathogenic version of its bacterial host, thus increasing the proliferation of the bacteriophage (Buttimer et al., 2017; Nagai et al., 2017). Since a downside of bacteriophage therapy is the reduction of infectivity due to UV light exposure, researchers have sought molecules that protect bacteriophages (Buttimer et al., 2017; Jones et al., 2012). This approach may explain the success of soil-based applications, as the soil may act as a filter for the UV light. Born et al. demonstrated success in increasing the half-life of UV-irradiated bacteriophages through treatment with molecules such as astaxanthin, a light-absorbing natural product (Born et al., 2015). Adjusting the phase at which bacteriophages are introduced also has a significant effect on the successfulness of treatment and can be optimized (Wei et al., 2017). In the field, as a consequence of the UV light sensitivity of most bacteriophages, the application of this type of biocontrol agent is often done at dusk when the UV light intensity is low (Fujiwara et al., 2011; Kurtböke et al., 2016). Finally, a combinational treatment of a mixture of bacteriophage types and plant immunity boosting molecules can also increase effectiveness and is an interest of further research. For example, it was demonstrated that the combinational use of bacteriophages and acibenzolar-s-methyl to activate systemic acquired resistance was effective in combatting Asiatic citrus canker in both greenhouse and field trials (Ibrahim et al., 2017).

2.3.4. Transgenic plants

The use of transgenic plants has demonstrated great potentials in generating crops with superior traits in disease resistance, nutrient compositions and growth (Glick, 2020). Scientists started pursuing the application of bioengineered plants from the beginning of the molecular cloning age (Ausubel, 2014 & 2018). Recently, a group of researchers successfully cloned the biosynthetic pathway of bacteria-derived rhizopine into barrelclover and barley (Geddes et al., 2019). These transgenic plants were able to produce and exude rhizopine into their root milieu to recruit the rhizopine biosensor-carrying *Rhizobium leguminosarum*, which is a natural nitrogen fixer for legumes (Fig. 4). There are many other advantageous traits of transgenic plants other than facilitating nitrogen fixation. Depending on the types of transgenic plants, including the ones that produce *Bacillus thuringiensis* insecticidal toxins, or are resistant to bacterial or fungal pathogens or herbicides, or express traits for nutritional and health benefits, they may directly or indirectly impact the residents of rhizosphere microbial communities and their associated functions, which in turn make key contributions to shaping the ecological niche to enhance plant growth (Turrini et al., 2015). For a detailed review on how transgenic crops affect the soil microbial community see Turrini et al. (2015).

3. Limitations to studying the plant microbiome

Studying the microbiome has become an important area of research as a result of advances in DNA sequencing technologies. These advances have now allowed us to gain in-depth views of complex microbial communities without the need for culturing (Kuczynski et al., 2010). By examining the community of microbes that are both culturable and unculturable in their natural settings scientists have uncovered a vast amount of information on the micro-ecosystems that exist within soil (Fierer, 2017). Investigation of these communities through DNA sequencing are generally done either through targeted amplicon gene sequencing or metagenomic shotgun sequencing (Knight et al., 2018). Each of these approaches have both shared and unique limitations that are both non-specific and specific to the soil environment.

Targeted amplicon gene sequencing is one of the most common ways to study the microbial inhabitants of a complex environment such as soil. This approach provides an inexpensive method for investigating the types of microbes within a sample. Common gene targets for this type of sequencing include the 16S rRNA gene which is highly conserved in both bacteria and archaea (DeSantis et al., 2006), the 18S rRNA gene which is found in all eukaryotes (Smit et al., 1999), and finally other regions such as internal transcribed spacers (ITS) that have been shown to be effective in surveying fungi (Turenne et al., 1999). One large limitation of these approaches is the ability to correctly assign taxonomy to these types of samples (Liu et al., 2008). This is due to most short-read technologies only providing 150–400 base pairs of information making it difficult to assign species classifications. It should be noted however that long read technologies have begun to significantly improve on this issue (Johnson et al., 2019). Soil presents a particularly difficult case of taxonomic classification as it contains highly diverse microbial communities that are often difficult to culture (Handelsman et al., 1998). A recent analysis on taxonomy classification accuracy showed that soil samples contain large numbers of amplicon sequences that belong to new taxonomic groups not contained within the 16S rRNA or ITS sequence databases (Edgar, 2018). Furthermore, current taxonomic classifications tend to be biased toward microbes relevant to human health due to their historic overrepresentation within various sequence databases (Edgar, 2018).

Not only is taxonomy classification difficult for amplicon sequencing within soil communities, but it also presents challenges in studies using metagenomic shotgun sequencing. The availability of well annotated genomes for microbes found within the soil is limited with most reference genomes coming from microbes connected to human disease. This creates issues for metagenomic read mapping and taxonomic assignment as many reads can be left unclassified at lower taxonomic ranks. Further issues are created when assigning functional contributions as many genes from unculturable organisms will be missing high-confidence functional annotations due to the inability to experimentally test gene function (Pham and Kim, 2012). Without these high-quality annotations, the relative abundance of many functional pathways is difficult to determine.

The soil contains a vast number of microbes other than bacteria (Fierer, 2017), information about these organisms is critical, however,

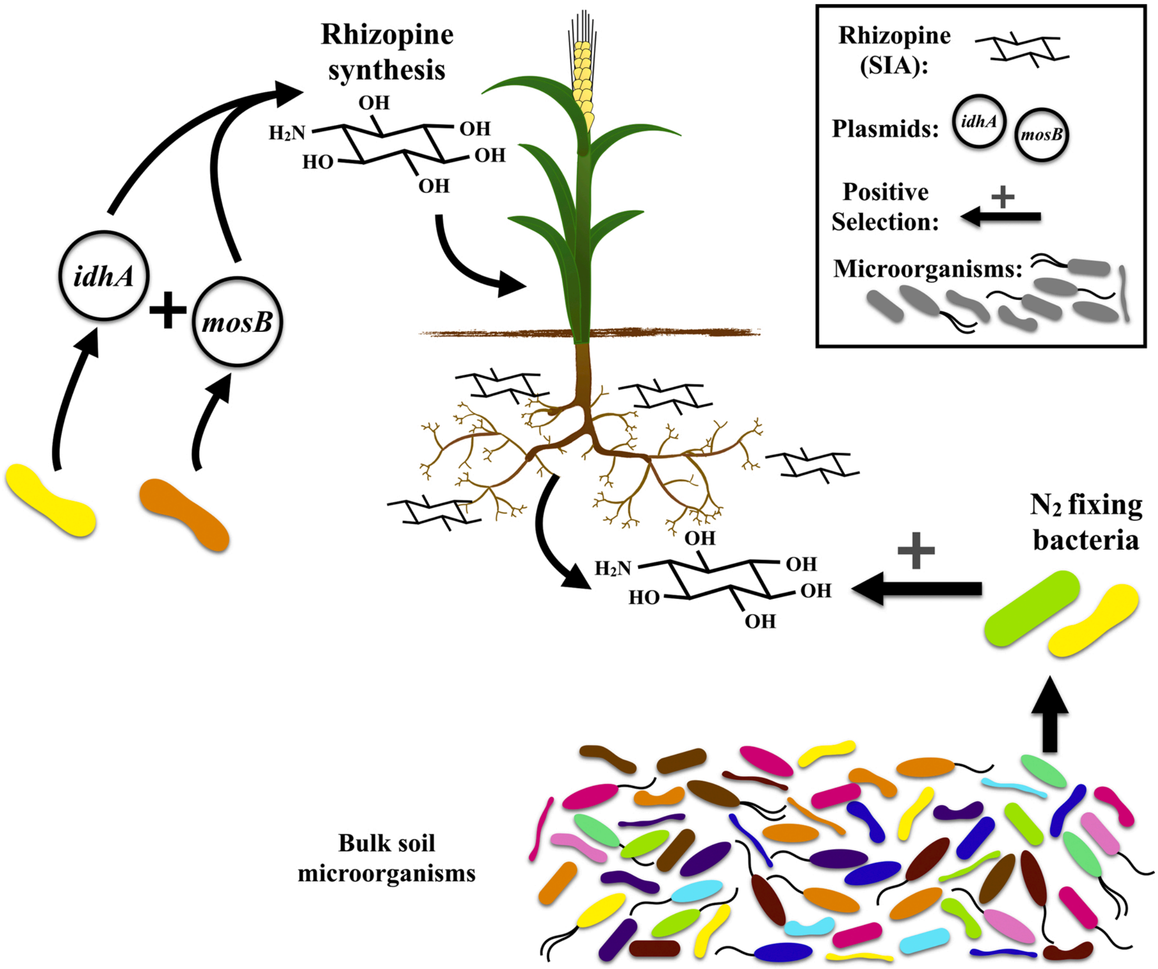

Fig. 4. Transgenic plants able to produce a bacterial-derived chemical signal, rhizopine, effectively recruited nitrogen-fixing bacteria to the rhizosphere microbiome. Geddes et al. (2019) successfully cloned two bacterial genes (inositol dehydrogenase, *idhA*, from *Rhizobium leguminosarum* and scyllo-inosose: L-glutamate aminotransferase, *mosB*, from *Sinorhizobium meliloti*) into barley and barrelclover plants. The transgenic plants produced the chemical signalling molecule scyllo-inosamine 1 (SIA) that is a type of rhizopine, which are typically rare molecules in nature, and exuded the rhizopine into its root milieu. The rhizopine around the plant roots positively selected and attracted nitrogen fixing (N_2 fixing) bacteria (i.e., *R. leguminosarum*) to the plant's rhizosphere microbiome and thus, could be used to recruit other N_2 fixing bacteria from the bulk soil to the rhizosphere to enhance plant growth and health.

we currently lack sufficient genomic information on the vast majority of fungi, viruses, and protists. The availability of microbial genomes for kingdoms of life outside of bacteria is relatively small compared to their overall diversity. For instance, of the over 80,000 fungal species that have been discovered (Tedersoo et al., 2014), fewer than 1000 of them have been sequenced. As of 2020, there were over 95,000 draft or finished genomes across bacteria, archaea, eukaryotes and viruses available in the Joint Genome Institute's Integrated Microbial Genomes database. Of all these genomes over 85 % of them were sequenced from bacteria (Chen et al., 2019), indicating a need for further genome sequencing on other taxonomic lineages.

An additional issue that is unique to metagenomic shotgun sequencing is the availability of the plant host genome. One of the first analysis steps in most metagenomic shotgun sequencing projects is the removal of reads that are from host contamination. In human microbiome studies, this step consists of mapping sequencing reads to the human genome so that they can be removed (Comeau et al., 2017). This step is especially challenging for plant soil microbiome studies as most plants lack high quality reference genomes. This lack of genomes can be partially attributed to the very large size of most plant genomes and the high quantity of repetitive elements within them. These features make sequencing and genome assembly of plant genomes difficult (Li and Harkess, 2018). Without representative host genomes, separation of reads that originate from the host and those that originate from the surrounding microbial communities is not possible, leading to mis-annotation of host derived reads.

Further limitations that are not specific to the plant microbiome include the difficulty of reproducing results in separate studies due to the use of different sequencing protocols, choice of analysis tools, and statistical methodology. Efforts made by the Earth Microbiome Project (EMP) (Caporaso et al., 2011), Microbiome Quality Control project (MBQC) (Sinha et al., 2017), and the International Microbiome Standards group (Costea et al., 2017) to produce standardized DNA sequencing protocols have helped address this issue, however, extraction and sequencing protocols are still inconsistent within the field and not all protocols can be used for every environment. Bioinformatic processing of data is still not standardized with different studies opting for different operational taxonomic unit clustering strategies and sequence denoising strategies, which can impact biological results (Caruso et al., 2019; Nearing et al., 2018). Another large concern in the field is the use of proper statistical methodology for studying the compositional framework of microbiome data (Gloor et al., 2017). There currently are many different tools for the statistical analysis of microbiome data that rely on different statistical frameworks that in some instances lead to different results (Calgaro et al., 2020).

Fortunately, efforts to solve some of the issues outlined above do currently exist. These include the expansion and creation of databases specific to microbes found within the soil (Choi et al., 2017), or large sequencing projects such as the EMP that aim to increase our knowledge on the diversity of various environmental samples including soil. Many of these issues, such as the under representation of specific domains of life in genome databases, are being addressed by this and other projects. One such project is the Integrated Microbial Genomes Virus (IMG/VR) database that is collecting viral genomes from across the world that will lead to a substantially higher number of representative genomes (Paez-Espino et al., 2019). Another similar project is the 1000 Fungal Genomes Project that aims to sequence 1000 fungal genomes, which will significantly increase our ability to map metagenomic datasets to fungi, an important group of microbes found within the soil microbiome (Grigoriev et al., 2014).

4. Safety

Understandably, live microbes applied to crops as plant growth-promoting bacteria (PGPB) may potentially pose a health threat to humans, animals, plants, and the environment. Currently, there is no internationally harmonized regulatory framework to assess the potential risks associated with PGPB application. Vílchez and co-workers had developed and proposed an Environmental and Human Safety Index (EHSI) protocol including a panel of tests and evaluation system to determine the safety of bacterial strains. The assays proposed include: *Escherichia coli* MC4100 sensitivity and microbial metabolism assays, a pathogenicity bioassay based on *Caenorhabditis elegans*, ecotoxicity tests in green lacewings (*Chrysoperla carnea*) and ladybirds (*Adalia bipunctata*), a *Daphnia magna* toxicity bioassay, and a pathogenicity test in laboratory mice (*Mus musculus* CD1). To date, this protocol has been validated using a number of well-known PGPB and pathogenic strains (Vílchez et al., 2017).

Similarly, even though bacteriophage application to crop plants has been successful, there are some concerns that should be considered prior to its more widespread implementation. There is a lack of research in the field of bacteriophage therapies on various plants other than potatoes and tomatoes. Furthermore, although studies have demonstrated success in disease mitigation, some show little effectiveness in comparison to other therapies in the market (Rombouts et al., 2016). Addy et al. demonstrated that bacteriophages can even increase the severity of plant disease, as ϕRSS1 phage use enhanced virulence factors of *R. solanacearum*, demonstrating the negative side effect of using that bacteriophage (Addy et al., 2011). It is also theorized that bacteriophages may target PGPB in the rhizosphere such as *Pseudomonas fluorescens*, which would be counter-productive in terms of plant growth. Furthermore, a study of broccoli by Nagai et al. only resulted in mitigation of disease by bacteriophage therapy in plants with injured roots, and no mitigation when roots were not injured (Nagai et al., 2017). Concerns also include persistence of bacteriophages, and the small host range of bacteriophages.

5. Concluding remarks

Here, we have stressed the importance of a healthy microbiome for plant growth and development, as well as the suppression of potential pathogens and facilitating environmental clean-up. The plant microbiome is an exciting area of research that is constantly expanding. A major question in the field is, what are the underlying mechanisms that shape the components and functionality of the plant microbiome? We have identified several contributing factors that are associated with microbiome components and functional groups; however, the causality of these associations requires further investigation. Moreover, there may not be a universal answer due to the variability of both biotic and abiotic factors present within the soil and the complex interactions. Rather, each situation has to be analyzed within a particular context, considering specific plants, microbes and various environmental conditions. Therefore, it is important to develop streamlined protocols for the characterization of a specific microbiome under various conditions, which can guide the knowledge-based precision design of plant growth promotion. Other remaining important questions are how we can harness the beneficial microbes and their plant growth-promoting traits, and what is the practical approach to recruit or apply a consortium of healthy microbiome to improve crop yield and productivity.

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