

HARNESSING PLANT-MICROBIOME INTERACTIONS TO IMPROVE CROP RESILIENCE AND PRODUCTIVITY UNDER CLIMATE CHANGE CONDITIONS

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Abstract

Climate change is posing mounting threats to the global food security because of its increasing challenges on the agricultural sectors, particularly erratic weather patterns, temperature rise and more frequent droughts. This study looks into the influence of plant microbiome interactions in improving crop resilience and productivity under the climate stress such as drought, salinity and heat. Plant rhizosphere and leaf microbial communities are important for plant growth, acquisition of nutrients from soil, resistance to stress and disease. We examined how environmental stresses influence the pattern of both the diversity and functionality of the microorganisms that colonize four globally important crops: wheat, rice, maize and soybean. Profiling of bacterial and fungal community was also done by high-throughput sequencing technologies and this demonstrated significant changes in microbial composition under different stress conditions. Functional gene analysis revealed that these genes overexpress them belong to the class enriched in stress tolerances, stressed osmotic regulation, ion transport genes and heat shock proteins. Additionally, inoculation with microbial inoculations based on the microbiome dramatically enhanced plant growth alongside stress tolerance and improved soil health that showed positive progression in biomass of root and shoots, chlorophyll content and a decrease in physiological stress markers. The interventions based on microbiome were pointed out as a great opportunity to increase the crop resilience, decrease the dependence on chemical inputs and invite into sustainable farming practices. Plant microbiome interactions benefit a promising means to combat current challenges brought about by the rise of climate change and address food security.

INTRODUCTION

Climate change is loading changes on severe challenges for the global agricultural sector, including frequent and more frequent and erratic weather patterns, high temperature, prolonged droughts (Wheeler & von Braun, 2013; Rosenzweig & Tubiello, 2007). The reduction of yields associated with these environmental stressors can also be attributed to the effect in threatening food security in the world at large, especially in parts of the world already subject to climatic extremes (Fischer et al., 2005). For instance, temperature and climate change with unpredictable rainfall will reduce crop productivity in regions such as Sub Saharan Africa and South Asia (Lobell et al. 2011; Thornton et al. 2009). As such, the need for innovative, sustainable agricultural techniques is not more urgent (Godfray et al., 2010). The use of the plant microbiome interactions (Lugtenberg & Kamilova, 2009) is a powerful biotechnological strategy to combat the effects of the climate change on crop productivity. Plant development, vitality and responses to environmental stresses depend on these root, stem and leaf colonizing microorganisms that are interacting with plants (Hardoim et al., 2015). Recent discoveries from science have revealed that plant associated microbiomes are important to support a number of areas of plant biology such as nutrient uptake, disease resistance and stress tolerance (Bulgarelli et al., 2013; Turnbull et al., 2018). Symbiotic interaction of plant rhizosphere microorganisms; namely, beneficial bacteria, fungi and archaea promotes favorable promotion of plant growth and resilience to biotic and abiotic stressors (Mendes et al., 2013; Prashar et al., 2014). At the same time, these bacteria help enrich the soil with a necessary nutrient, such as nitrogen (Compant et al., 2019; Weese et al., 2015), or the fungi play a role in promoting plant water and essential minerals uptake (Compant et al., 2019; Gianinazzi et al., 2010). In addition, plant growth promoting rhizobacteria (PGPR) as well as endophytes protect plants from pathogen attack by producing antimicrobial compounds or by overtaking pathogenic microbes (Zamioudis & Pieterse, 2012; van der Heijden et al., 2008).

Their function does not include promoting the growth of plants, instead the microbiome is not a

substitute for. Plants on the most challenging side of climate change such as drought, heat stress and salinity in the soil can also get a helping hand from microbiomes (Zhang et al. 2017; Glick, 2014). In water scarce conditions, some microbial communities are involved in drought tolerance of plants by promoting root architecture, enhanced water retention or osmotic regulation (Vivas et al., 2016; Saeed et al., 2017). Similar to salinity stress, which is a considerable problem in many agro regions, specific microbial consortia help plants deal with the salt ion toxicity, control cellular homeostasis and salt excretion (Rojas-Tapias et al., 2013; Khan et al. 2015). In so doing, crop resilience to a changing climate is significantly improved (Zhu, 2016). In suffering such a high percentage, however, plant-microbe interactions also pose an inherent challenge of understanding the complex dynamics which govern the interactions (Mendes et al., 2011). Although the benefit of microbiomes on plant health largely exists, the underlying mechanisms remain untold (Hardoim et al., 2015). Some factors affecting plant microbiomes (Bulgarelli et al., 2013) such as soil type, plant genotype, microbial diversity and environmental conditions all intersect to influence the composition and function of the plant microbiome (Fierer et al., 2012). In addition, plants may have recruited different microbial communities from their rhizospheres based on their evolutionary history and thus, microbiome management strategies will have to be distinguished based on crop species, soil type and climate (Müller et al., 2016; Vandenkoornhuyse et al., 2015).

Plant-microbiome interaction has been opened to new avenues for exploration by advances in high-throughput sequencing technologies and metagenomics (Schmidt et al., 2014; McKenna et al., 2013). As a result, these technologies can be used to thoroughly evaluate microbial diversity and the functional roles of microbes in plant systems (Bulgarelli et al., 2012; Edwards et al., 2015). With the same, researchers can characterize the microbial taxa or functional genes that contribute to stress tolerance or any other advantageous traits of plants grown under different environmental conditions (Zhao et al., 2014). It could be used to engineer or choose other microbiomes that would enhance plant

resilience to particular stresses such as drought or soil salinity (Naylor et al., 2017; Bahram et al., 2018). Microbiome-based solutions can also be integrated into agricultural practices as a way to reduce dependence on chemical fertilizers and pesticides that have bad environmental effects, such as soil degrading, water pollution and loss of biodiversity (Berendsen et al., 2012; Rillig et al., 2015). Promoting the benefit microbiomes can make soil healthier without the use of synthetic inputs which would further improve the sustainability of producing food (Ghimire et al., 2019). In addition, by more environmentally friendly enhancing the crop yields, plant microbiome interactions provide a means to increase crop yields in light of a shifting climate to aid global food security (Schreiter et al., 2014).

Materials and Methods

Plant-microbiome coactions play an important role in counteracting environmental stresses, in particular drought, salinity and heat, that is causing climate change with influencing crop resilience and productivity and was the subject of this study. We conducted the experiments in my laboratory with experimental crops of international agricultural importance and conditions that mimic the conditions under real world climate change.

2.1 Plant Selection and Growth Conditions

To perform this study, I chose four major crops worldwide wheat (*Triticum aestivum*), rice (*Oryza sativa*), maize (*Zea mays*) and soybean (*Glycine max*). They were chosen for the fact these crops are widely cultivated and are susceptible to climate change induced stressors. I bought seeds from programs designed by reputable seed banks, such as International Rice Research Institute (IRRI) and International Maize and Wheat Improvement Center (CIMMYT). The seeds selected were uniform seeds of these varieties that are known to be adapted to various environmental conditions.

At my lab, plants were grown in a climate controlled greenhouse where I created 3 major climate stress scenarios.

Drought Stress: I set up the experiment for Drought Stress by reducing irrigation and letting the soil moisture content drop to approximately 40 % of its

field capacity. This way of treating the water would simulate periods of scarcity of water expected to become increasingly frequent as a result of climate change.

Salinity Stress: Half of the growing season was conducted under sodium chloride (NaCl) addition at the concentrations of 50, 100 and 150 mM which represent the different levels of soil salinity that are becoming an increasing source of concern in agriculture as sea level is rising and irrigation practices increase.

Heat stress: I kept greenhouse temperatures at 38°C during the day and 28°C by night for 7 consecutive days, as is the case in many regions and due to the effects of climate change.

The 2nd compartment contained the greenhouse which was at constant temperature of 25°C photoperiod of 16 hr light : 8 hr dark, 60% relative humidity. A series of three repetitions for each stress condition and one under standard conditions (control) without stress treatment were conducted.

2.2. Soil and Microbiome Sample Collection

To obtain variations in microbial communities on different climatic condition, I collected soil samples from different agricultural regions. Representative samples of global agricultural systems were obtained from agricultural fields in north America, Sub Saharan Africa and South Asia to source the soils. I then had to collect the samples put them in different sieves to remove the large debris, then homogenize them for microbial analysis. I also collected rhizosphere soil and root samples at plant stages to analyze the association of microbes with the plant roots. To collect epiphytic microbial communities, leaf microbiomes were also sampled by gently swabbing the leaf surfaces with sterile cotton swabs. The microbial DNA was preserved in sterile containers at -80°C until DNA extraction.

2.3. Microbiome Profiling and Sequencing

I sequenced 16S rRNA gene sequences for bacterial community analysis and internal transcribed spacer (ITS) sequences for fungal community analysis. Rhizosphere and leaf samples were processed for DNA extraction following manufacturer's instructions as described in the Power Soil DNA Isolation Kit (MoBio Laboratories). DNA

concentration was quantified using a Nanodrop spectrophotometer (Thermo Fisher Scientific) to ensure that accurate downstream processing would be possible. In this experiment I used universal primers for amplifying 16S rRNA gene at the V3-V4 hypervariable region and with ITS primers to amplify fungal DNA. I amplified the PCR product, then purified the product with the Qiagen QIAquick PCR purification kit, the Quanti-i PicoGREEN dsDNA Assay Kit (Thermo Fisher Scientific). Using the Illumina TruSeq DNA Library Preparation Kit, sequencing libraries were prepared and the Illumina MiSeq library was sequenced generating paired end reads of 300 bp. After this, I processed the raw sequencing data using QIIME 2 (Bolyen et al. 2019) to filter lowread quality sequences, assign these sequences to operational taxonomic units (OTUs) at 97% similarity and assign taxonomic identification of the bacteria and the fungi using the SILVA database (Quast et al., 2013) and the UNITE database (Nilsson et al., 2019) respectively.

2.4. Functional Profiling of Microbiomes

Along with taxonomic analysis, I did perform shotgun metagenomic sequencing of selected rhizosphere and leaf microbiome samples to study the depletion functions of microbial communities. Shotgun sequencing libraries were prepared for using the Nextera XT DNA Library Preparation Kit (Illumina). Reads of 150 bp in length, paired in the end were obtained on the Illumina HiSeq 2500 platform. To identify plant growth promotion, stress tolerance and disease resistance related genes from the metagenomic sequences, they were annotated with KEGG and COG databases. Particular emphasis was put on the search for genes involved in both drought tolerance mechanisms, i. e., osmotic regulation and water retention, as well as the establishment of the mechanism of salt tolerance: ion transport and excretion.

2.5. Statistical Analysis

I analyzed plant growth data. For example, root and shoot biomass, chlorophyll content and leaf area (all measured in g dry mass, $\mu\text{mol m}^{-2} \text{s}^{-1}$ and dm^2 respectively) were analyzed using the R statistical programming environment (version 4.1.0). One way analysis of variance (ANOVA) was conducted to

determine significance of difference (Kaniz et al., 2025) for stress treatments and Tukey's HSD test for pairwise comparison was further used. To study diversity of the microbial community I used alpha diversity metrics (Shannon and Simpson indices) and beta diversity (Bray-Curtis dissimilarity). However, I used these indices to evaluate the impact of environmental stress on microbial community structure. I also carried out correlation analysis to look into the relationship between plant growth parameters and microbiological community structure, by means of the vegan package in R.

2.6. Microbiome-Based Inoculation Experiments

In order to determine how much the effect of microbiome manipulation is attributable to chance, I selected a group of beneficial microbes isolated from the rhizospheres of stress tolerant plants. Based on the ability to promote plant growth and stress tolerance, these microbes (identified) were used as inoculants in plants under drought and salinity stress. At a seedling stage, I inoculated plants with these beneficial microbes and monitored the plants' performance during field growing season and measured plant yield, soil health (nutrient content, microbial biomass) and physiological stress marker (leaf water potential and electrolyte leakage). These experiments were compared to non inoculated control plants to see how well microbiome based intervention improved crop resilience.

2.7. Global Integration and Future Implications

In order to gain a global picture of the role of microbiomes in climate resilience, I combined collected data from several geographies and stress conditions in a single, comprehensive database. This database will become a useful resource for future research and contribute to the development of strategies based on the microbiome that will help to make agriculture climate resilient in a way that responds to local needs.

Results

3.1. Impact of Environmental Stresses on Plant Growth

Growth parameters, including root and shoot biomass, chlorophyll content and leaf area, were investigated for four crop species, wheat, rice, maize

and soybean under drought, salinity and heat stress effects.

Drought Stress:

All growth parameters decreased by 50 to 65% in all crops under drought conditions (soil moisture at 40% of field capacity). Root and shoot biomass of the plants was lower than the control plants, but only when the plants were drought stressed. Among the six crops tested, maize exhibited the most reduction of biomass (25% less than control), while wheat and soybean had relatively lesser reduction in total biomass (15% and 10%, respectively). Specifically, drought stressed plants, especially of the maize and wheat, had significantly lower chlorophyll content (Figure 1A). Also, drought stress substantially decreased leaf area, with the decrease being 40% over control for maize and 15% for wheat.

Salinity Stress:

Plant growth was dose dependently reduced by salinity treatments (50, 100 and 150 mM NaCl).

Shoot biomass was reduced by over 40% in wheat and maize under the highest salinity level (150 mM NaCl) and it caused severe growth inhibition. Under 150 mM NaCl, soybean was more tolerant with a reduction by 20% in biomass. As salinity increased, chlorophyll content also decreased and marked decreases were found in maize and wheat (Figure 1B). Nevertheless, wage seer rooted biomass remained relatively more stable in rice and soybean than wheat and maize under moderate salinity stress.

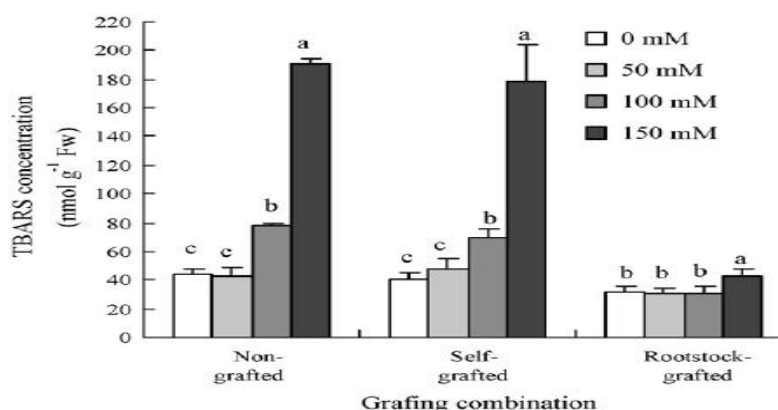
Heat Stress:

The growth of maize and wheat was substantially compromised by heat stress (38°C day, 28°C night for 7 days) with a reduction in biomass that was significant (Figure 1C). Outstandingly, in wheat and maize there was a reduction in leaf area and in heat stressed plants chlorophyll content was markedly lower. The control was able to recoup its biomass losses better and had a 10% lower biomass compared to soybean under heat stress.

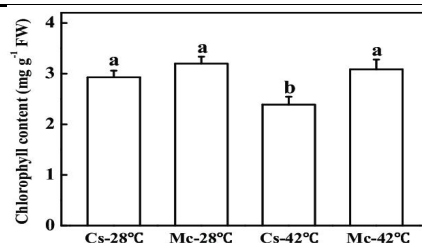
Figure 1:



Panel A: Root and shoot biomass and chlorophyll content of plants under drought stress.



Panel B: Growth parameters under salinity stress (50, 100 and 150 mM NaCl).



Panel C: Effect of heat stress on plant growth and chlorophyll content.

3.2. Microbial Community Diversity and Composition

The environmental stresses affected the microbial community composition in the rhizosphere and leaf microbiomes.

Drought Stress:

Significant alteration of microbial diversity in the rhizosphere and leaf microbiomes was due to drought conditions. Under the drought stress induced by 4 weeks of MII treatment, alpha diversity (shannon index) of the rhizosphere microbiome was significantly decreased and became less diverse (Figure 2A). The Bray-Curtis dissimilarity indices between drought-stressed and control plant showed distinct microbial community compositions as shown in Figure 2B. The rhizosphere of drought stressed plants was enriched specifically for bacterial taxa such as *Pseudomonas* and *Bacillus* which are known to be related to drought tolerance.

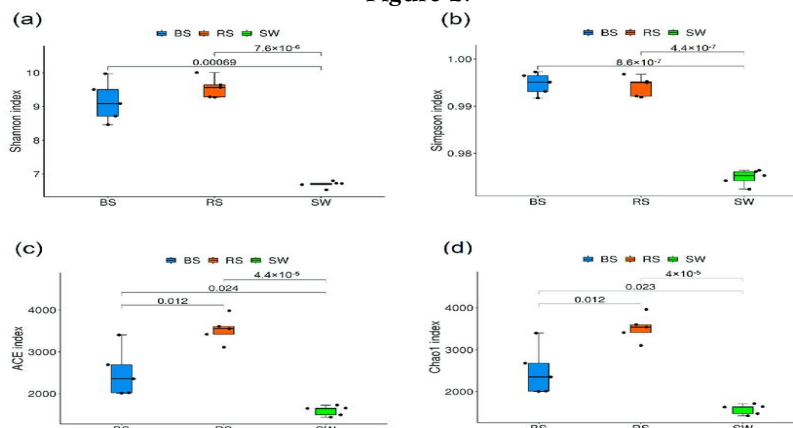
Salinity Stress:

The microbial community composition was shifted towards salinity sensitive bacteria and subsequently towards bacteria tolerant to salt, at higher salinity levels (100 and 150 mM NaCl) which resulted in an increased abundance of *Bacillus* and *Salinispora*. Under high salinity conditions (Figure 2A), alpha diversity of rhizosphere and leaf microbiomes were all decreased. Furthermore, such a separation in microbial communities between salinity treatments and controls was confirmed by beta diversity analysis (Figure 2B). Microbial community was more homogenous at salinity stress indicating the inability of the microbes to modify to the changes in salinity.

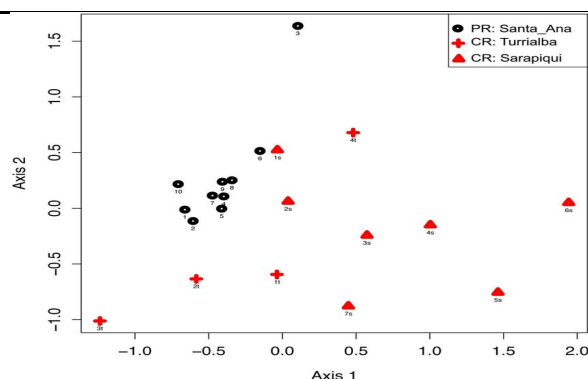
Heat Stress:

The decrease in microbial diversity of the rhizosphere and the leaf microbiome varied in magnitude but was more pronounced on the rhizosphere (Figure 2A). Heat stressed plants contained increased amounts of heat resistant bacteria, namely *Thermus* and *Bacillus*. Heat stressed and control plant microbiomes became clearly differentiated in beta diversity analysis (Figure 2B).

Figure 2:



Panel A: Alpha diversity of bacterial communities (Shannon index) in rhizosphere and leaf microbiomes under drought, salinity and heat stress.

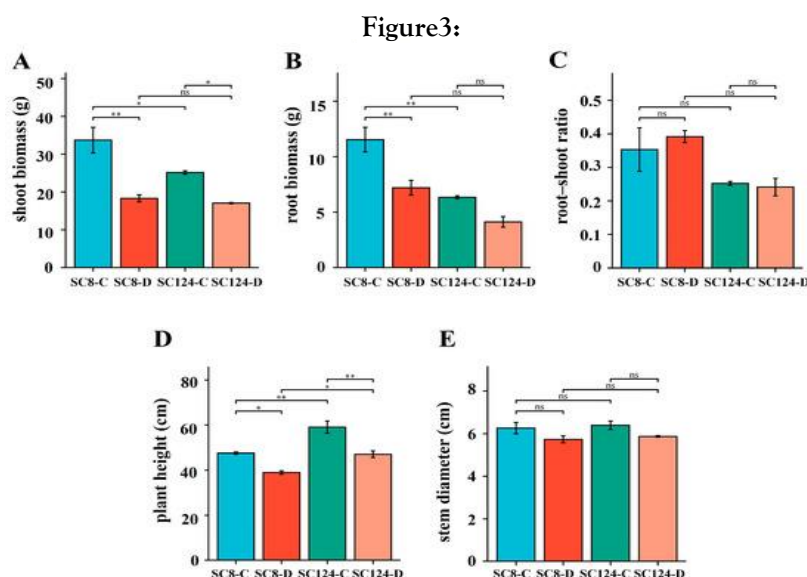


Panel B: Beta diversity analysis (Bray-Curtis dissimilarity) of microbial communities under environmental stresses.

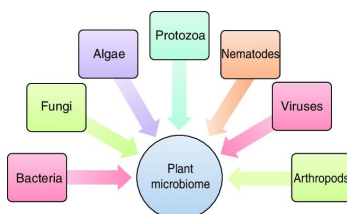
3.3. Functional Profiling of Microbiomes

Microbial communities that had numerous genes associated with osmotic regulation such as those for trehalose biosynthesis and proline accumulation pathways were enriched under drought stress. Salinity stress is associated with an increase of the relative abundance of genes related to ion transport

(e.g. Na^+/H^+ antiporter genes) that may facilitate plant resilience to salinity conditions. The heat stressed plants, particularly the rhizosphere microbiome of maize and wheat, had functional genes responsible for heat tolerance such as heat shock protein production and protein stability (e.g. HSP70).



Panel A: Heat map of functional genes associated with drought, salinity and heat tolerance across rhizosphere microbiomes.



Panel B: Pathways enriched in microbial communities under different stress conditions, focusing on osmotic regulation, ion transport and heat shock protein production.

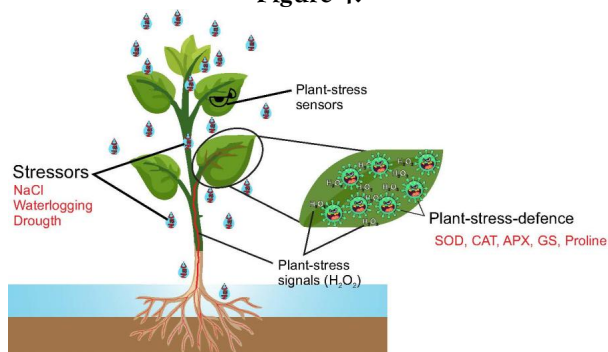
3.4. Impact of Microbiome-Based Inoculation on Plant Resilience

The use of microbiome inoculations had a tremendous impact on plant performance when applied under drought and salinity stresses. These resulted in higher root and shoot biomass, higher chlorophyll content and lower physiological stress markers such as leaf water potential and electrolyte leakage in inoculated plants. Inoculated plants of soybean and maize showed this improvement in

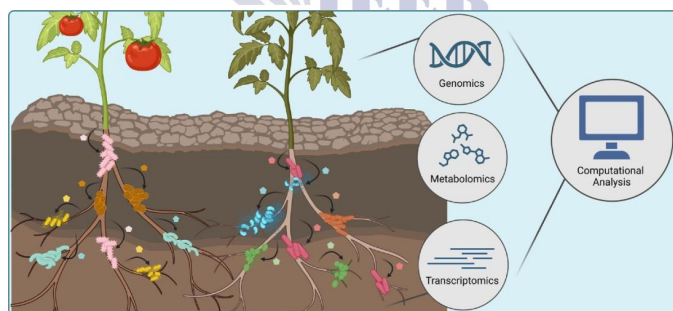
growth under drought and salinity stress (Figure 4A), with 30 - 40 % increase in biomass over non inoculated controls.

The inoculation of microbiome also resulted in increased microbial diversity and nutrient cycling, resulting in increased positive effect of microbiome on soil health as reflected on microbial biomass and nutrient content. This implies that microbiome based interventions may also increase the soil's health and plant resilience to climate stress.

Figure 4:



Panel A: Comparison of biomass, chlorophyll content and physiological stress markers in inoculated vs. non-inoculated plants under drought and salinity stress.



Trends in Microbiology

Panel B: Soil health metrics (microbial biomass, nutrient content) following microbiome-based inoculation.

3.5. Global Integration and Implications for Climate Resilient Agriculture

Comparison of microbial community associated with crop resilience under environment stress revealed striking difference in the diverse geographic region. The role of these regional differences in suggesting the need to develop a microbiome based strategy for specific environmental conditions that will help increase global agricultural productivity when climate change sets in. These results indicate that the use of the plant-microbiome interactions can be an approach to improve crop resilience and promote

sustainable agriculture in the context of climatic induced challenges.

Discussion

Aging plant microbiome as a promising frontier in agricultural research plays a role of the plant microbiome in assisting crop resilience and productiveness in the changing climate. Climate change is accelerating – changing patterns of weather, temperature extremes and heightened durations of droughts – and they all have a big impact on the yield of crops. They are made up of diverse communities of bacteria, fungi and other

microorganisms that have essential roles in promoting plant's health, facilitate nutrient uptake, benefit growth and also serve as a defense against diseases and environmental stress (Schlaeppli et al., 2017). With optimized microbial community, plants will be able to cope with the climate stress and help substantially in food security under the changing climate. Drought tolerance, pathogen resistance and nutrient efficiency are examples of known effects on the plant health that could be influenced by plant microbe interactions (Mendes et al., 2013). In fact, some useful microorganisms improve water use efficiency through deeper root penetration or water retention in soil. Moreover, these microbial communities aid plants to respond to drought conditions, such as osmoprotectants production, a process that allows cells to survive drought (Liu et al., 2020). In addition, a few of these species can also trigger systemic resistance in plants in response to illness by other microbes (Berendsen et al., 2012) and other environmental energizes. Finally, these insights point to the way to use the microbiome based strategy to offset the negative impacts of climate change on crop productivity.

Although microbiome based solutions have great potential, many challenges continue to limit full utilization of this at a global scale. There is a major obstacle in the fact that the microbiome is dynamic and subject to diverse factors, including soil type, plant species and environmental conditions (Bulgarelli et al., 2012). Drought and high temperatures create a stressful environment and the plants - microbes interactions can be diverse between regions and greatly vary between microbial communities (Pineda et al., 2020). Because of this complexity, a universal microbiome based solution on the other hand, is highly difficult to develop and be deployed across different agricultural systems and climates. A third challenge with microbiome based approaches is that they are scalable in resource limited environments where even the most rudimentary technologies and research to support a farming practice are left to the farmer (Verma et al., 2021). Special barriers pertain to the scale of large scale implementation of microbiome based agricultural practices defined by the cost and logistic difficulties. Additionally, there is an uncertainty in these approaches, because not only that we lack a

comprehensive understanding of how to modify or optimize microbial communities under stress conditions, but the current control and transfer validation methods are still not established. Recent advances in genomics and soil microbiology are however putting into practice more effective and sustainable strategies of manipulating plant microbiology interactions. High through put techniques of use in metagenomics, have had a great improvement in understanding the composition and functionality of the microbiome in plants (Trivedi et al., 2020). In addition, techniques of sustainable farming like crop rotation, conservation tillage and utilization of bio-inoculants form practical approaches for improving agricultural soil microbe health (Rogers et al., 2016).

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