



Interference of Climate Change on Plant-Microbe Interaction: Present and Future Prospects

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Plant mutualistic association with various beneficial microbes is referred to as the plant enhancer microbiome. These microbes are found either in episphere or endosphere of the plant tissues. Several pieces of evidence have highlighted that plant microbiomes and soil play a pivotal role in making soil nutrient balance which is readily available to plants and provide strength under various stresses. Recently different technologies relevant to plant microbiome and diversity such as sequencing technologies, metagenomics, and bioinformatics have been utilized. Knowledge about factors that shape the composition of plant microbes is still less explored. Here, current insights into the issues driving the above/below plant microbial diversities are explored. Primarily, we address the distribution of microbial communities above and below ground across plant habitats that has benefitted plants. Microbial communities are efficient regulators of biogeochemical cycle which is a better approach to mitigate changing climatic patterns aids in proper utilization of greenhouse gases for their metabolic mechanisms. The present review is thereby significant for assessing microbiome mitigation toward climate change and multiple avenues of plant- microbe interaction under commuting climatic scenario. Finally, we summarize factors that promote the structure and composition of the plant microbiome.

Keywords: climate resilience, environmental factors, niche communities, plant-microbe, interactions, microbiome, sustainable

INTRODUCTION

Over the past few decades, several anthropogenic and natural activities stimulated the rise in average temperature and carbon dioxide levels which cause changes in climatic conditions globally. These changing climatic conditions involve erratic events like increase in rainfall and snowfall worldwide, excessive release of greenhouse gases, increase in air temperature which renders soil dry and decrease its moisture content forming drought lie conditions. Some other consequences consist of increase in pollution due to increased CO₂ emissions, air pollutants, ground- level ozone, aerosols, methane, and others. It induces seasonal variations by altering wind patterns. In other terms, climate change involves the transposing of climatic or weather patterns that occur by emission of greenhouse gases which are likely to be more erratic and extreme in the forthcoming years. Statistical evidence presented by International Panel of Climate Change 2019 states that within food systems, during 2007–2016, the agricultural design (including crop production

and livestock management) generated 142 ± 42 Tg CH₄ yr⁻¹, 8.0 ± 2.5 Tg N₂O yr⁻¹ and 4.9 ± 2.5 Gt CO₂ yr⁻¹ with total greenhouse gas emission 6.2 ± 1.44 t CO₂-eq yr⁻¹ to 11.1 ± 2.9 Gt CO₂-eq yr⁻¹ (Jia et al., 2019). It is likely to increase about 30–40% by 2050. These climatic conditions may affect food security through an elevation in temperature, changing rainfall patterns, extreme events, and many more. Studies conducted revealed that the climatic variations affect the crop yields in lower- and higher-latitude regions differently. For instance, the changing climatic trends impart significant drought across Ethiopia, which causes widespread crop failure and food aid to the majority of people in that region (USDA., 2016; Huntington et al., 2017). Climate alterations influence the growth behavior of different crop species. Like, it has huge impact on nutrient acquisition and mineral accumulation in the plants.

Direct effects on the plants includes morphological changes, physiological and phenotypic changes, and changes in plant productivity. Due to stress conditions, the organs and membranes of plants are impaired. The increased oxidative stress adversely influences the production of carbohydrates, proteins, secondary metabolite in the plants. It also affects soil fertility, irrigation measures, pests and diseases occurrence, and stress incidence like heat, drought. The other ill effects of climate change on production strategies includes effect on food demand, trade opportunities and unequal distribution of products (Raza et al., 2019). These alterations thus cause a negative impact on plant growth and developmental patterns and microbiomes present in the soil.

Like plants, the soil is also a home for many microorganisms like bacteria, fungi, protist, virus and many others, which may be beneficial, neutral or pathogenic. It is a well-recognized fact that these microbiomes are key indicators of plant health and play an important role in productivity and growth (Berg et al., 2016). Microbiome is a contributor of multiple aspects of plant system. They regulate plant health through their antagonist and synergistic behavior in association with the plants. They influence plant system through metabolic cooperation, inducing signaling responses and microbial dysbiosis. Studies made regarding the phenomenon by which plants acquire defense mechanism against pathogenic microorganisms and get benefitted from beneficial ones have gained much attention in recent few years. Many researchers explored basic principles of interaction with plant and microbiota, signaling process of plant defense and symbiotic responses toward microbes (Jones et al., 2016), a genetic system of microbes that transport signaling molecule to modulate host cell functions (Hwang et al., 2017) and specific binary and community level conflict in plant and microbial interactions (Hacquard et al., 2017). The study of environmental impact on plant and microbiome interaction is seldom at mechanistic and molecular levels, thus, unravels the new avenues in exploring the plant and microbial association in nature mediating ecological resilience. The present review describes large microbial population that exists in the environment, their growth patterns, along with ecological functions. Secondly, it describes the effect of changing climatic conditions on microbial diversity present in nature by a designed framework to develop a better understanding

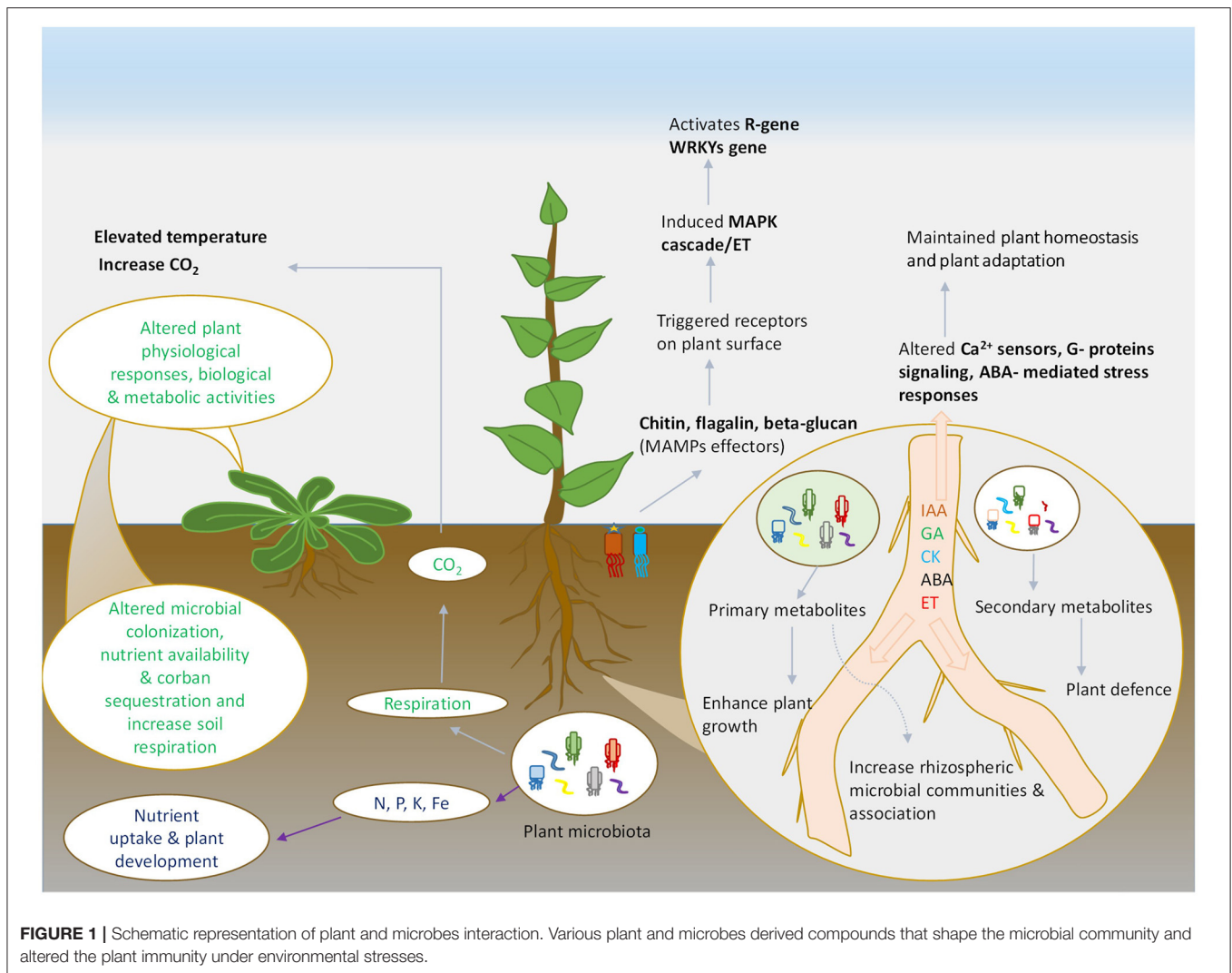
of the influence of climate on plant-microbe interaction as well.

Microbial Diversity

The interaction of plants with microbiota is unavoidable and inseparable. Plants and soil harbor a wide range of microbiome which may be present inside (endosphere) and outside (episphere) the plant tissues (Khondoker et al., 2020). Soil can be considered a repository of microbial populations, whereas plants interact with surplus microbes and other entities present in nature. The microbial communities differ significantly in rhizosphere, endosphere, and phyllosphere in the environment (Trivedi et al., 2020). Plants and microbial population encompasses to form a “holobiont.” In general terms, holobiont can be defined as the assemblage or association of a host with various species surrounding it, together forming an ecological unit. Microbiota which interacts with plants have a diverse location, ecological function in both above-ground and below-ground environment and poses a potential role in regulating resistance to climatic alterations and other stress responses.

Above-Ground Plant-Microbiome Interaction

Plants including stems, leaves and their other parts contain abundant microscopic organisms like bacteria (Proteobacteria, Bacteroidetes), actinomycetes, fungi (Ascomycota and Basidiomycota), viruses, and others (Figure 1). The region surrounding the aerial portion of the plant is termed the phyllosphere. Different plant species possess a diverse range of microbiota in their phyllosphere region (Table 1). The phyllosphere region is very dynamic and greatly influenced by several factors like temperature, precipitation, light, etc. The bacterial population present in the phyllosphere α and γ proteobacteria belong to proteobacterial (phyla- Bacteroidetes & Actinobacteria) that are mostly non-pathogenic and hyperdiverse in nature. The phyllosphere fungi associated with forest trees are saprobic and key decomposers of leaf litter along with another group which are latent pathogens (Osono, 2006). Similarly, numerous studies on several crops like apple, almond, tobacco, pumpkin and many others concluded that *Pseudomonas* are the most abundant in these crops (Alekkett et al., 2014). Phyllosphere also consists of diverse group of algal microbiome, although the study of phyllospheric microbiome is seldom. Algae are aquatic organisms having diverse groups including green microalgae, cyanobacteria along with different classes namely chlorophyceae, Dinophyceae, Eustigmatophyceae, Trebouxiophyceae, and Ulvophyceae. These species are abundant in tropical trees, mangrove forests, Taiwan rain forests, and rice crop (Lin et al., 2012; Venkatachalam et al., 2016; Zhu et al., 2018). The Atlantic forest phyllosphere has diverse and rich communities of cyanobacteria (Rigonato et al., 2016). The algal groups like Nostocales and Oscillatoriales occurs predominantly in the phyllospheric region. Thus, the above evidence is enough to conclude the fact that microbiota is not only abundant but diverse in the phyllosphere in the plants. However, the core phyllospheric regions also contain pathogenic microbiota, which is often dramatic systemic and spreads vigorously to



cause diseases in plants (Stone et al., 2018). The increased interest in phyllosphere research has disclosed the new aspects in understanding plant health, ecological principles, and atmospheric chemistry, but there are still many aspects that needed to be explored. The use of modern approaches like proteogenomics, community-based next-generation sequencing, metaproteomics, offers a great aid in understanding the role of novel proteins that stimulate phyllospheric growth. Although *in situ* interaction of microorganisms with phyllosphere using complementary approaches at microscale is needed to be attended thoroughly (Figure 1).

In contrast, fungal diversity is expected to remain lower. The endophytic fungi form a mutualistic symbiotic association with some plants, grasses, legumes, morning glory, thus producing bioactive metabolites, and perform defense mechanisms (Panaccione et al., 2014) and obligatory plant-associated. Fungal and bacterial endophytes present in plant ecosystems have a diverse role which includes stress resistance, increase biomass and decreased water consumption, altered resource allocation. They can be non-pathogenic for at least part of their life cycle (Rodriguez et al., 2009). The transmission of

bacterial endophytes can commence either by seed, pollen, soil, atmosphere, insects, wind, or water (Frank et al., 2017). The study of endospheric and phyllospheric variability of grapevine revealed the presence of diverse genera, which included *Pseudomonas*, *Sphingomonas*, *Enterobacteria*, *Bacillus*, *Erwinia*, *Methylobacteria* like organisms (Compant et al., 2019), while maize leaves predominantly contained *Sphingomonads* and *Methylobacteria* in diverse maize lines (Wallace et al., 2018). Thompson et al. (1993) studied the presence of 1,236 bacterial strains on immature, mature and senescent leaves of sugarbeet over a complete growing life cycle of a plant.

Below-Ground Plant-Microbe Interaction

Soil is a habitat of plenty of microorganisms that supports life forms and anchors the root system of the plants. Plant roots contain a diverse form of microfauna, either endophytic or rhizospheric (Table 1). The rhizosphere is the region of soil adjacent to plant roots that harbors an environment for plant roots with microorganisms. Similar to phyllospheric region, the diverse microbiota in the rhizosphere can also be dispersed through air, soil, water, insects, animals, etc. Soil

TABLE 1 | Microbial communities present in phyllospheric and rhizospheric regions of different plant species.

Microbial species	Plant species	References
Sphingomonads and Methylobacteria	Maize	Wallace et al., 2018
Pseudomonas	Apple, almond, tobacco	Aleklett et al., 2014
Pseudomonas, Erwinia herbicola	Sugarbeet	Thompson et al., 1993
Proteobacteria	Soybean, clover, rice, Arabidopsis	Vorholt, 2012
Undifilum spp., Clavicipitaceous fungi	Legumes, Morning glory	Panaccione et al., 2014
Ascochyta species, Colletotrichum gloeosporioides, Phomopsis species	Fagus species, Swida species	Osono, 2006
Pseudomonas, Sphingomonas, Frigoribacterium	Grapevine, grape clusters	Compant et al., 2019
Green microalgae, cyanobacteria	Mangrove forests, Taiwan rain forests, rice, tropical trees	Lin et al., 2012; Venkatachalam et al., 2016; Zhu et al., 2018
Pseudomonas, Agrobacterium, Cupriavidus, Rhizobium	Citrus species	Xu et al., 2018
Proteobacteria, Acidobacteria, Actinobacteria, Bacteroidetes, Plantomycetes, Choloroflexi, Gemmatimonatedes	Grapevine	Faist et al., 2016; Samad et al., 2017
Proteobacteria, Actinobacteria	Cucumber, tomato, wheat maize	Reinhold-Hurek et al., 2015
Bacteroidetes, Actinobacteria, Ascomycota, Basidiomycota, Olpidiomycota	Arabidopsis	Bergelson et al., 2019
PGPR	Jerusalem artichoke	Montalbán et al., 2017
Acidobacteria, Alphaproteobacteria, and Gammaproteobacteria	Cottonwood	Timm et al., 2018
Orchidaceous mycorrhizal fungi	Orchids	Rudgers et al., 2020
Nostoc, Anabaena	Rice	Prasanna et al., 2009
Calothrix, Scytonema	Paddy	Roger et al., 1993

harbor a wide range of bacteria, actinomycetes, fungi, and other microorganisms which interact with plant parts; some are mutualistically associated (PGPR, Rhizobia) while others perform vital ecological functions. e.g., the citrus rhizospheric microbiome contains diverse groups of microbiota that mainly includes *Pseudomonas*, *Agrobacterium*, *Cupriavidus*, *Rhizobium*, *Sphingomonas*, and many others as potential beneficial microbes (Jin et al., 2018; Xu et al., 2018). Root exudates like organic acids, amino acids, fatty acids, plant growth regulators, sugars, vitamins, and other metabolites have a pronounced effect on

the availability and composition of microorganisms around roots (Compant et al., 2019). However, the plant roots are colonized by a diverse group of bacterial and fungal endophytes that are present internally. The endophytes enter plant roots passively by penetrating the sites of cracks at root emergence region, root tips, through lateral roots and also through an active process.

Seeds, on the other hand, are important sources for microbial proliferation in the roots. In grapevine roots, the bacterial phyla that are abundant include Proteobacteria, Acidobacteria, Actinobacteria, Bacteroidetes, Plantomycetes, Choloroflexi, Gemmatimonatedes (Faist et al., 2016; Samad et al., 2017). The symbiotic association of fungi with roots in the form of endophytes and mycorrhiza are key factors in nutrient acquisition and root colonization (Kariman et al., 2018; Li et al., 2018). The roots of cucumber, tomato, wheat and maize were dominated by Proteobacteria, Actinobacteria with relative abundance in the γ -proteobacteria and α -proteobacteria (Reinhold-Hurek et al., 2015). In a similar manner, the root endosphere and rhizosphere in *A. thaliana* were colonized by abundant bacterial species that included Bacteroidetes, Actinobacteria, Proteobacteria, Chloroflexi, Firmicutes, Acidobacteria, Saccharibacteria along with fungal phylum viz., namely Ascomycota, Basidiomycota, Olpidiomycota, Chytridiomycota and many more species (Bergelson et al., 2019).

The nitrogen-fixing bacteria (*Rhizobium*, *Frankia*) form a symbiotic association with Fabaceae in specialized nodules to fix atmospheric nitrogen into nitrate, which can be utilized by plants (Menge et al., 2019). Studies conducted on PGPR revealed that they had a pronounced effect on phytoremediation strategies. In *Helianthus tuberosus*, PGPR growing endophytically in roots showed considerable resistance to elevated concentration of cadmium and zinc (Montalbán et al., 2017). The rhizosphere and endosphere of the *Populus* genus contain an abundance of Acidobacteria, Alphaproteobacteria, and Gammaproteobacteria (Actinobacteria) that play a major part in stress-specific and core stress responses (Timm et al., 2018). Plant species contains diverse range of arbuscular mycorrhizal fungi in Glomeromycotina along with a smaller part of ectomycorrhizal fungi (Ascomycota and Basidiomycota) distributed geographically (Rudgers et al., 2020). Different plant species harbor different fungal groups e.g., Ercoid fungi in Ascomycota are commonly associated with the ericaceous plant, while Basidiomycota (Orchidaceous mycorrhizal fungi) are found in orchids. Prasanna et al. (2009) identified cyanobacterial species Nostoc and Anabaena in the rhizospheric region of rice crop. Cyanobacterial species like Calothrix, Scytonema are dominant in paddy fields (Roger et al., 1993). Another algal species abundant in rhizosphere also include *Oscillatoria* and *Phormidium*. Plant roots contain pathogenic and non-pathogenic fungi. The hyaline and melanized ascomycetes fungal group are dominant in the roots of prairies (Jumpponen et al., 2017). Thus, the rhizospheric microorganisms have vast diversity among different plant species. They play a pivotal role in the physiology and development of plants. The approaches of next-generation sequencing, 16sRNA gene sequencing, ITS, CRISPR, and genome editing molecular tools have provided a better understanding of the interaction of microbiota with roots and

below-ground level. Also, incorporating traditional approaches with modern gene sequencing technique will bring new insights to explore the microbial life in the rhizosphere. Knowledge of microbial population, its functioning and activities aid in the identification of suitable microbial candidate to support plant growth and health in various environmental conditions and disease suppression (Mendes et al., 2013).

Plant-Beneficial Microbes

The role of microorganisms in understanding plant production and ecological sustainability has been deciphered since ancient times. Plants possess a huge variety of microbiomes in phyllosphere and endophytes from surrounding soil and air (Finkel et al., 2017). The beneficial microbiome present in the plants is a key indicator of plant health as they play a vital role in regulating plant immunity, production of metabolites, nutrient uptake and acquisition, disease, and insect-pest management along with several other functions. The microbial population residing in soil system includes various PGPR, fungi, actinomycetes, algae, yeasts, cyanobacteria, and many more (Manzar et al., 2021). They aid in transforming organic matter into simpler form that can be assimilated by plants. Microbiomes like filamentous fungi and several bacterial species secrete a wide range of secondary metabolites which are crucial for plant growth and phenological responses. Several studies regarding beneficial role of rhizobacteria in invigorating plant growth and developmental responses along with nutrient acquisition through production of many phytohormones like auxin, cytokinins have been made (Kudoyarova et al., 2014; Egamberdieva et al., 2017). Secondary metabolites like trichocarenes, harzianolide, harzianic acid, α -pyrone produced by various *Trichoderma* species have been reported to promote plant growth (Vinale and Sivasithamparam, 2020). Several rhizospheric and endophytic bacterial species colonizing turmeric rhizomes have been reported to induce growth promotion, disease management, secondary metabolite production and enhancing curcumin content (Kumar et al., 2017). Several bacterial species-*Arthrobacter*, *Bacillus*, *Rhizobium*, *Mycobacterium* have been found to be associated with roots of soybean (Egamberdieva et al., 2016). Similarly, orchid rhizosphere harbors *Mycobacterium* species (Tsavkelova et al., 2007) while wheat roots contains *Azotobacter*, *Azospirillum*, *Mycoplana*, and *Rahnella*. Endophytic fungi *Sinorhizobium meliloti* isolated from root nodules of *M. sativa* confer drought tolerance (Naya et al., 2007). Several bacterial species have also been reported to mediate drought tolerance in several species (Chen et al., 2017; Naseem et al., 2018; Ullah et al., 2019). In maize, *Leifsonia* sp. and *Bacillus* sp. induced cadmium tolerance thereby increasing root and shoot growth (Ahmad et al., 2016). Several mycorrhizal and endophytic organisms are known to be associated with plants viz., cereals, pulses, oilseeds which enhance their nutritional status (Bhattacharyya et al., 2016).

Anabaena species, *Calothrix* species, *Chlorella fusca* acts as biocontrol agent against plant pathogens in many plant species (Prasanna et al., 2008, 2013; Chaudhary et al., 2012; Lee et al., 2016, 2017; Kim et al., 2018). The algal species also provide protection to plants against nematode infection (Khan et al.,

2005, 2007; Hamouda and El-Ansary, 2017). Cyanobacteria increases plant growth and yield by acting as biofertilizer. Species including *A. variabilis*, *Calothrix* sp., *Hapalosiphon* sp., and *Nostoc* sp. are used as biofertilizers in many crops which increases plant growth and yield (Singh and Datta, 2007; Innok et al., 2009; Karthikeyan et al., 2009). Algal biofertilizers like *Nostoc* sp., *Anabaena* sp., fixes atmospheric nitrogen in rice. They also influences soil porosity and soil aggregation. *Anabaena azollae* is used as a green manure (Vaishampayan et al., 2001). Algal species also provide abiotic stress tolerance in the plants. *Scytonema hofmanni* provides salt tolerance in the rice (Rodríguez et al., 2006). *Chlorella fusca* and *Chlorella* strains (ABC001 & HS2) delays plant senescence in *Erinus alpinus* (Lee et al., 2020). Furthermore, several evidences of abiotic stress tolerance by algal communities in the plant species has been reported (Li et al., 2014; Arroussi et al., 2018; Lee and Ryu, 2021). Algae are efficient bioremediator of heavy metals in the plants through process of bioaccumulation and biosorption. Species like *C. vulgaris*, *Desmodesmus pleiomorphus*, *Ulva reticulata* *Cladophora fascicularis* *Spirogyra insignis* are efficiently used to remove heavy metals like Cd, Zn, Cu (Hassan et al., 2017). Algal communities are efficient drivers of CO₂ in global carbon cycle and also a better alternative to sequester greenhouse gases biologically (Tsai et al., 2017). Besides this, algal communities also produce plant growth promoting phytohormones and polysaccharides which increases plants growth (Lee and Ryu, 2021). Blue green algae and other algal species like *Anabaena*, *Chroococcus*, *Oscillatoria*, *Phormidium* are associated with rice, fix atmospheric nitrogen and accelerate nutrient acquisition in plants (Hasan, 2013; Bhattacharyya et al., 2016). Microbial consortia play major role in plant defense mechanism (Xu et al., 2011; Jain et al., 2012; Sarma et al., 2015). Microbial consortium including *Pseudomonas*, *Rhizobium*, and *Trichoderma* species studied in different species are efficient means of plant growth promotion and pathogen tolerance (Alizadeh et al., 2013; **Table 2**). Rhizobacteria and rhizofungi have an immense beneficial role against insect herbivores besides improving plant health by regulating signaling of defense hormones, secondary metabolite production and synthesis of defense related proteins and enzymes (Rashid and Chung, 2017; **Table 3**).

Factors Involved in the Availability of Diverse Microbial Populations

The plant-microbe association is influenced by several factors which directly or indirectly affects the availability of microbiota in the particular environment. They are mainly phyllospheric, rhizospheric and environmental factors that require understanding of the mechanism of the presence of microorganisms. **Table 2** determines various drivers of plant-microbe interaction that provide knowledge of their existence and diversity in the environment. Plants are living organisms that themselves harbor a wide range of microbial entities like bacteria, fungi, actinomycetes. The presence of these microbiota in the plant is mainly influenced by biotic factors including plant species, root architecture, plant genotype, plant age and developmental stages, and abiotic factors like soil pH,

TABLE 2 | Studies on plant microbe interaction and their adverse climatic conditions.

Microbes	Plant species	Abiotic stress	References
<i>S. melliloti</i>	<i>M. sativa</i>	Drought tolerance	Naya et al., 2007
<i>Glucoacetobacter diazotrophicus</i>	Sugarcane	Drought tolerance	Vargas et al., 2014
<i>Cellulosimicrobium cellulans</i>	Chili	Chromium toxicity tolerance	Chatterjee et al., 2009
<i>Pseudomonas</i> sp. and <i>Bacillus</i> sp.	Spinach	Cd, Pb, Zn toxicity tolerance	Shilev et al., 2019
<i>Pantoea alhagi</i>	Wheat	Drought tolerance	Chen et al., 2017
<i>Leifsonia</i> sp. and <i>Bacillus</i> sp.	Maize	Cd toxicity tolerance	Ahmad et al., 2016
<i>Bacillus aryabhathi</i>	Soybean	Heat stress tolerance	Park et al., 2017
<i>Pseudomonas species</i> S1	Chili	Drought tolerance	Rolli et al., 2015
<i>Trichoderma species</i>	Chickpea	As toxicity tolerance	Tripathi et al., 2017
<i>Varivorex paradoxus</i> 5C-2	Pea	Salinity tolerance	Wang et al., 2016
<i>Pseudomonas fluorescense</i>	Rice	Flooding	Etesami et al., 2014
<i>Bacillus subtilis</i> , <i>Arthrobacter species</i>	Wheat	Salinity stress tolerance	Upadhyay et al., 2012
<i>Serratia plymuthica</i> , <i>Stenotrophomonas rhizophia</i> and <i>Pseudomonas fluorescense</i>	Cucumis	Salinity stress tolerance	Egamberdieva et al., 2008
<i>Bacillus subtilis</i> and <i>Paenibacillus illinoisensis</i>	Pepper	Drought tolerance	Vigani et al., 2019
<i>Aspergillus fumigatus</i>	Soybean	Salt stress	Khan et al., 2011
<i>Pseudomonas vancouverensis</i>	Tomato	Chilling stress tolerance	Subramanian et al., 2015
<i>Rhizobium</i> sp.	Sunflower	Drought	Alami et al., 2000
<i>Pseudomonas fluorescense</i>	Groundnut	Salinity stress tolerance	Saravanakumar and Samiyappan, 2007
<i>Serratia species</i>	Chickpea	Nutrient stress tolerance	Zaheer et al., 2016
<i>Burkholderia species</i>	Tomato	Cd toxicity tolerance	Dourado et al., 2013
<i>Achromobacter xylooxidans</i>	Mustard green	Cu toxicity tolerance	Ma et al., 2008
PGPB	Sorghum	Cr stress & heat stress tolerance	Bruno et al., 2020
Cyanobacteria	Arabidopsis	Heat stress	Chua et al., 2020
<i>Pseudomonas species</i> and <i>Acinetobacter species</i>	Barley and oats	Salt stress	Chang et al., 2014

(Continued)

TABLE 2 | Continued

Microbes	Plant species	Abiotic stress	References
Microalgae-cyanobacteria	Tomato	Salt stress	Mutale-joan et al., 2021
<i>Pseudomonas frederiksbergensis</i> OS261	Red pepper	Salt stress	Chatterjee et al., 2017
Azotobacter	Maize	Drought stress	Shirinbayan et al., 2019
Salep gum and <i>Spirulina platensis</i>	Maize	Cd toxicity	Seifkhalhor et al., 2020
Seaweed extract	Cucumber	Low temperature stress	Sarhan and Ismael, 2014
<i>Oscillatoria agardhii</i>	Wheat	Drought stress	Haggag et al., 2018
<i>Scytonema hofmanni</i>	Rice	Salt stress	Rodríguez et al., 2006

soil salinity, temperature, seasonal variations, soil moisture, and organic matter (Winkel et al., 1997; Zogg et al., 2010) (Figure 2).

Plant and soil hosts multiple varieties of microbiomes. The environmental factors are key regulators in shaping structure and composition of plant microbiome. Plant associated microbiomes are greatly influenced by genotype × environment interactions (Morella et al., 2020). Particular plant species also imparts some influence on composition of microbiome in rhizosphere. Phyllospheric microbiome is affected by environmental and anthropogenic factors. Environmental factors include irradiation, ozone, animal borne sources, secretion of volatile organic compounds, and health development status of plants, plant genotype and others. Anthropogenic activities which influence microbiome abundance include urbanization, application of fertilizers, pesticides, herbicides, fungicides, biostimulants, and industrialization (Gupta and Patil, 2021). Particular plant species also imparts some influence on composition of microbiome in rhizosphere. Soil associated factors like possible available mineral content in the soil, pH, gas gradient establishes soil microbiome plays key role in shaping diversity of microbiota (Tecon and Or, 2017). Soil properties and geographical locations (altitude, latitude, and longitude), soil moisture content impact structure of microbiomes at great extent (Islam et al., 2020). The structure and composition of plant microbiome can be influenced by climatic factors like UV-radiation, temperature variations, and change in CO₂ concentration (Kemle et al., 2014; Wang et al., 2017; Hassani et al., 2018; Yu et al., 2018; Sørensen et al., 2019; Islam et al., 2020).

Effect of Resilient Climate on Microbial Diversity

Climate change and changing weather patterns is a matter of global concern among researchers and agriculturalists now-a-days. Climate change is undeniable phenomena which occurs

TABLE 3 | Role of beneficial microbe in plant defense.

Beneficial microbes	Biotic stress causing microbes	Host plants	Reference
<i>Bacillus subtilis</i> FB17	<i>P. syringae</i> pv. <i>tomato</i>	Tomato	Rudrappa et al., 2008
Rhizospheric microbes	<i>M. oryzae</i>	Rice	Spence et al., 2014
PGPR	<i>Fusarium</i> sp.	Potato	Recep et al., 2009
PGPR and <i>Trichoderma koningiopsis</i>	<i>Fusarium</i>	Cape gooseberry	Diaz et al., 2013
<i>Pseudomonas</i>	<i>Phytophthora infestans</i>	Potato	de Vrieze et al., 2018
<i>T. harzianum</i> Tr6 & <i>Pseudomonas</i> sp. Ps14	<i>Fusarium oxysporum</i> f. sp. <i>radicis cucumerinum</i>	Cucumber	Alizadeh et al., 2013
<i>Pseudomonas fluorescence</i>	Leaf folder pest	Rice	Saravanakumar et al., 2008
<i>Stenotrophomonas</i> sp., <i>Xanthomonas</i> sp., <i>Microbacterium</i> sp	<i>Hyaloperonospora arabidopsis</i>	Arabidopsis	Liu and Brettell, 2019
<i>Bacillus subtilis</i> and <i>Bacillus amyloliquefaciens</i>	<i>Botrytis cinerea</i>	Tobacco	Cawoy et al., 2014
<i>Saccharothrix yanglingensis</i>	<i>P. syringae</i> pv. <i>tomato</i> DC 3000	Arabidopsis	Zhang et al., 2018
<i>Rhizobium etli</i> strain G12	<i>Aphis gossypii</i> Glover	Squash	Martinuz et al., 2012
<i>Trichoderma virens</i> , <i>T. atroviridae</i>	<i>Alternaria solani</i> , <i>Botrytis cinerea</i> , <i>P. syringae</i>	Tomato	Salas-Marina et al., 2015
<i>Pseudomonas</i> PHU094, <i>Trichoderma</i> THU 0816, <i>Rhizobium</i> R2091	<i>Sclerotium rolfsii</i>	Chickpea	Singh et al., 2013
<i>Anabaena variabilis</i> , <i>Anabaena torulosa</i> , <i>Anabaena laxa</i> , <i>Calothrix</i> sp.	<i>Pythium debaryanum</i> , <i>Fusarium oxysporum</i> , <i>F. moniliforme</i> , <i>Rhizoctonia solani</i>	Tomato, cotton	Prasanna et al., 2008, 2013; Chaudhary et al., 2012; Lee and Ryu, 2021
<i>Pseudomonas</i> sp.	<i>Rhizoctonia solani</i>	Tomato	Pandey and Gupta, 2020
<i>Trichoderma</i> sp.	<i>Botrytis cinerea</i> and <i>Leptosphaeria maculans</i>	Tomato, canola	Vinale et al., 2008a,b
<i>Pseudomonas fluorescence</i>	<i>Desmia funeralis</i>	Rice	Karthiba et al., 2010
<i>P. fluorescence</i> Pf1, <i>B. subtilis</i> , <i>T. viridae</i>	<i>Lasiodiplodia michiganensis</i>	Tuberose	Durgadevi et al., 2018
<i>B. subtilis</i> MB1600 & <i>R. tropicum</i> R1899	<i>Fusarium solani</i> f. sp. <i>phaseoli</i>	Common bean	Estevez de Jensen et al., 2002
<i>B. amyloliquefaciens</i>	<i>Peronophthora litchii</i>	Litchi	Wu et al., 2017

(Continued)

TABLE 3 | Continued

Beneficial microbes	Biotic stress causing microbes	Host plants	Reference
<i>Ulva armoricana</i>	<i>Erysiphepolygona</i> , <i>Erysiphe necator</i> and <i>Sphaerotheca fulliginea</i>	Bean, grapevine, and cucumber	Jaulneau et al., 2011
<i>Cystoseira myriophylloides</i> and <i>Fucus spiralis</i>	<i>Agrobacterium tumefaciens</i>	Tomato	Esserti et al., 2016
<i>Trichoderma</i> species	<i>Alternaria</i> species and <i>Fusarium</i> species	Vegetables and crops	Meena et al., 2017
<i>Spatoglossum variabile</i> , <i>Stokeyia indica</i> , and <i>Melanothamnus afaqhusainii</i>	<i>Meloidogyne</i> spp.	Watermelon and egg plant	Baloch et al., 2013
<i>Oscillatoria</i> , <i>Anabaena</i> , <i>Nostoc</i> , <i>Nodularia</i> , and <i>Calothrix</i> species	<i>Alternaria alternate</i> and <i>Botrytis cinerea</i>	Pepper	Kim, 2006

mainly due to anthropogenic activities including the factors like greenhouse effect, deforestation, urbanization, global warming. Other crucial factors includes fossil fuels combustion, increase livestock farming, excessive use of fertilizers, nitrous oxide emissions, increasing incidence of different abiotic, and biotic stresses. The global warming associated with climate change along with elevated temperature, CO₂ levels, changing rainfall patterns impart a significant impact on plant developmental patterns and their physiology. However, microbial diversity and its nature activities have not been spared in the inevitable changing climatic conditions. They are microscopic, diverse, and present abundantly in marine, terrestrial and agricultural ecosystem. It is well-known fact that microbiota are efficient players in the carbon and nutrient cycling process, a key mediator to plant health, and play a crucial role in agricultural production. The study of the effect of the resilient climate in microfauna is limited and requires greater attention. Being ubiquitous, microorganisms affect climate change in marine, terrestrial and agricultural ecosystems (Bastiaansen et al., 2020). The ecosystem is influenced by changes in temperature, rainfall patterns, and stress conditions (drought, salinity, ozone stress, pathogens.). Changes in climate durability and seasonal abnormalities possess a great impact on the structural and diversity of microbial communities either directly or when they are associated with plants. The drivers of changing climatic conditions causes shifting of microbial community from particular ecosystem which further impart negative effect in its function. Global warming has direct impact on microbial respiration. Warming alters composition of microbial population (Classen et al., 2015). However, temperature, CO₂, and other environmental factors play an important part in regulating the diversity of microbial

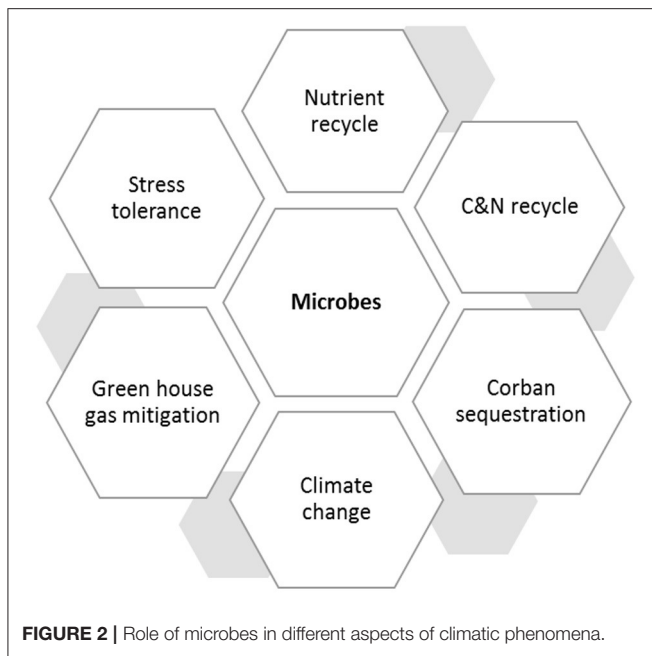


FIGURE 2 | Role of microbes in different aspects of climatic phenomena.

community both above and below ground level. The microbial populations are often associated with rhizosphere and gets influenced by soil and exudates secreted by roots.

Effect of Temperature on Plant-Microbe Interaction

Temperature is the fundamental factor that is decisive in plant growth and phenological characteristics, along with the distribution and occurrence of a particular microbial population in the community (Angilletta, 2009; Kashyap et al., 2017). The increase in human interventions and the emission of GHGs like CO₂, water vapor, methane leads to the rise in average global temperature in the past few decades. It is expected that the average temperature is going to increase by 1.8–3.6°C by the year 2100, which may lead to water deficiency and drought in many parts of the world (Compant et al., 2010). The increase in average temperature influences the activity and morphology of plants. Several studies have been made regarding the demonstration of the potential effect of elevated temperature on different crop species (Chen et al., 2021). The increased average temperature imparts a potential market effect on the composition, activities and occurrence of plant-associated microbial communities. An elevated temperature may result in faster growth of microorganisms with altered respiration. Similarly, elevated temperature and drought conditions significantly affect plant-microbe association, activity and abundance. Global warming and elevated temperature conditions have a direct influence on microbial respiration rates present in the rhizosphere (Classen et al., 2015). Studies show that soil respiration performed by microbial community increases exponentially with temperature (Karhu et al., 2014). Frey et al. (2013) found that the utilization of organic matter by soil microbes is temperature-dependent. The changing climatic conditions,

the pathogenicity of microorganisms can also be correlated with temperature alterations, CO₂ concentration and other environmental conditions (Vela'squez et al., 2018). Soil warming and drought conditions pose an indirect impact on plant nutrient uptake and carbohydrate exchange in the rhizosphere by arbuscular mycorrhizal fungi (AFM) (Newsham et al., 1995). *Glomus intraradices* and *Glomus mossae* showed increased growth and colonization with temperature (Monz et al., 1994). Elevated temperature increases the virulence of bacteria *Pectobacterium atrosepticum* causing soft rot and certain other seed born microbes that promoted degradation of cell wall enzyme and increase disease incidence in plants (Hasegawa et al., 2005). Ocean warming due to elevated temperature results in phenological shifts in sea weeds globally (de Bettignies et al., 2018). Elevated temperature adversely influences the activity of coralline algae (Page et al., 2021). Studies conducted reveals that elevated temperature has considerable effects on cyanobacterial growth and development (Deng et al., 2021). Increased temperature coupled with heat waves as consequences of global warming enhances the activity of microbial community able to mineralize microbial necromass, recycling C and N and thus, amplify warming effects in mountainous soil (Donhauser et al., 2020).

Similarly, Wang et al. (2020) also reported the increased microbial necromass nitrogen and microbial turnover in the soil with temperature. However, other environmental conditions, like moisture and UV radiation, also influence microbe survival and growth. Low moisture availability and drought conditions affect the microbial population in the soil, root endosphere and rhizospheric conditions (Cheng et al., 2019). Xu et al. (2018) studied that drought conditions reduce bacterial population in rhizosphere and root endosphere in sorghum root microbiome. Drought conditions decrease AMF colonization. AMF could not colonize plant under drought (Schellenbaum et al., 1998; Staddon et al., 2004). However, a comparative study performed by Querejeta et al. (2009) reveals that ectomycorrhiza has reduced colonization ability in oak under drought than AMF deciphering the fact that colonization by AMF under water-scarce conditions are more desirable for future climatic scenarios.

Effect of CO₂ on Plant-Microbe Interaction

The atmospheric CO₂ is very crucial in regulating carbon allocation and composition of root exudates in the soil environment, which imparts a potential effect on the rhizospheric environment with beneficial microbes (Berendsen et al., 2012; Williams et al., 2018). Microbes play a vital role in net carbon exchange through various ways, viz. respiration and decomposition of organic matter, pathogenic or symbiotic association with plants, and by altering the nutrient status of the soil. Elevated CO₂ levels alter plant physiology and metabolism and also stimulate direct and indirect effect on the microbial community in rhizospheric and phyllospheric conditions. The elevated CO₂ levels often lead to reshaping the root exudates composition along with alterations in nutrient availability (Ostle, 2008; Compant et al., 2010). Microbes like fungi consist of higher carbon assimilation efficiency than bacteria and have more significant potential to store carbon than mobilization. Thus,

an increase in the carbon emission through roots by plants stimulates the growth in the microbial population in the soil system, thereby reducing soil nitrogen i.e., available for the plant due to soil nitrogen immobilization.

The elevated CO₂ level in the atmosphere often results in increased soil respiration (Korner and Arnone, 1992; Hungate et al., 1997). The soil environment contains a higher proportion of CO₂ than the atmosphere. Microbes such as fungi, bacteria, actinomycetes show variable responses to elevated CO₂ conditions. In *Pisum sativum* cv. Solara, Gavito et al. (2000) observed no significant effect of elevated CO₂ (700 ppm) on the colonization of arbuscular mycorrhizal fungi (AMF) while in Barnyard grass, elevated CO₂ (7 ppm) showed a significant increase in mycorrhizal colonization with an increase in N and P uptake (Tang et al., 2009). A study conducted using 18S RNA sequencing-based Illumina Miseq technique indicated that long term exposure to elevated CO₂ (550 ppm) significantly reduces the presence of *Claroideoglossum* and *Glomus* species in paddy in sub-humid tropical conditions (Panneerselvam et al., 2020). Similarly, the ectomycorrhizal communities also get influenced by changing CO₂ levels in the atmosphere. Godbold and Berntson (1997) observed the increased colonization of ECM in *Boswellia papyrifera* and *Pinus strobus* under elevated CO₂ conditions (700 ppm). Similarly, Fransson et al. (2005) demonstrated a three-fold increase in biomass of ECM mycelia in *P. sylvestris* in high CO₂ conditions. Besides AMF and ECM, Plant Growth Promoting Bacteria (PGPB) have also been found to support plant growth. Several organisms that belong to this genera include *Arthrobacter*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Erwinia*, *Proteus*, *Pseudomonas*, *Rhizobium*, etc. Bacterial communities associated with the plant biome also have a significant effect on eCO₂ levels. Studies conducted in FACE conditions (Free-air CO₂ enrichment) demonstrated that elevated CO₂ (600 ppm) causes a substantial increase in the population of *R. leguminosarum* bv. trifolii in the rhizosphere of white clover (Schortemeyer et al., 1996).

Numerous studies have been made regarding the influence of eCO₂ in plant growth promoting bacteria communities in several species (Lipson et al., 2006; Haase et al., 2007; Lesaulnier et al., 2008; Xu et al., 2013). Increase in CO₂ concentration in the atmosphere also influences the microbial community in the oceanic environment. The growth and survival of seaweeds in high CO₂ environment is tempting as seaweeds are benefitted from increased organic carbon concentration (Harley et al., 2012). Recent developments in algal research determine that with increased CO₂ concentration the biomass and lipid in microalgae species also increased (Singh and Singh, 2014). Thus, elevated CO₂ conditions influence microbial communities, biological system of plants and thereby play vital role in future climatic conditions. Elevated CO₂ level may alter activities of soil microorganisms involved in nutrient acquisition (Haase et al., 2007), influences pathogenic responses of the plants (Yáñez-López et al., 2012) and help soil carbon sequestration. Moreover, the role of rhizospheric microorganisms under elevated CO₂ level is needed to be assessed for climate-resilient agriculture along with rigorous effort in scaling up to explore the long term effect of soil microbes to increased CO₂ conditions and efficient

carbon sequestration by plant-microbe interaction (Malmstrom and Field, 1997; Grover et al., 2015).

Other Factors Influencing Plant-Microbe Interaction

The inconsistent climatic conditions possess considerable impact on structure, function and diversity of plant-microbe association in the environment (Dastogeer et al., 2020). Increased climatic conditions result in the increased exposure of radiations to plants which also modify ozone dynamics in the atmosphere. It is well-known that increased UV-radiations deplete stratospheric ozone content in the atmosphere, thus alters climate. These alterations have adverse effects on the plants and associated microbiome. Increasing UV-radiations changes cell oxygen yield, photosynthetic system, and growth of cyanobacteria (Zeeshan and Prasad, 2009). However, lichens have not much considerable effects of UV-B radiations (Bjerke et al., 2005). Radiation sensitive fungi possess reduced growth as infrared radiations induces damage to cell proliferation rate. The UV radiations have adverse effect on conidial germination, hyphal growth and chemical production (Braga et al., 2015; Thind and Schilder, 2018). Similarly, it negatively affects growth and survival of bacterial communities (Vanhaelewyn et al., 2020).

The phyllospheric communities are relatively more affected to increased radiations as rhizospheric communities and are attributed to frequent and drastic changes with change in climatic conditions. The change in climatic conditions results in increased incidence of stresses in the environment. Climate change increases the activities of pathogens and heterotrophic microorganisms, shifting of beneficial microbes from one ecological niche to another. Precipitation is an important regulator of activities of plant and microbiomes. Adequate precipitation increases the activity of soil microbes' hence increasing microbial biomass carbon. The phyllospheric biomass can be positively correlated with belowground microbial biomass carbon in response to adequate precipitation (Zhang and Xi, 2021). Global warming and climatic aberrations potentially cause drought stress. The scarcity of water in the rhizospheric region reduces mycorrhizal mycelium formation in the plant roots (Singh et al., 2019). It is evident there are multiple drivers of plant microbiota association aboveground and belowground communities. They regulate the structure and activities of microbes and also have considerable influence on plant system.

Role of Microbes in Climate Resilience

Microbes are the diverse and ubiquitous organisms present on the earth's surface. Plants themselves consist of a wide range of microbial niches present in them and the soil ecosystem. Microbes are well-known to perform various ecological functions in nature. They regulate the concentration of greenhouse gases and influence radiative force. The microbiota may impact either positive or negative feedback on climate resilience. Several microbial species plays vital role in carbon sequestration, carbon mineralization and reduces the emission of greenhouse gases viz. CO₂, CH₄, N₂O (Singh et al., 2010) in the terrestrial ecosystem. Climate change has a potential effect on soil microbial biomass, organic matter decomposition, net primary production,

TABLE 4 | Role of microbes in plant physiological responses.

Microbes	Physiological trait specifications	Host plants	References
<i>Rhizobium species, Azotobacter</i>	Fixation of atmospheric nitrogen	Soybean	Naamala et al., 2016; Naamala and Smith, 2020
AM fungi & PGPR	Increased antioxidant activities, flavonoid, and phenol content	Turmeric	Dutta and Neog, 2016
Endophytic & Rhizospheric bacteria	Stimulates plant growth, secondary metabolite production, enhanced curcumin content	Turmeric	Kumar et al., 2017
Root colonizing microbes	Stimulates root development	Arabidopsis	Verbon and Liberman, 2016
<i>Bacillus anthracis</i> & <i>B. thuringensis</i>	Improved growth	Wheat	Paul et al., 2020
<i>Streptomyces</i> sp.	Plant growth promoting activities	Grapevine, wheat	Couillerot et al., 2013; Toumatia et al., 2016
<i>Bacillus cereus</i> N5	Siderophore production, phosphate solubilization	Maize	Abedinzadeh et al., 2018
<i>Burkholderia phytofirmans</i>	Promotes IAA synthesis & ACC deaminase activity	Potato, tomato, onion, maize, barley	Weilharter et al., 2011
PGPB	Growth promotion, enhanced root and shoot biomass, plant nutrient status, and nutrient use efficiency	Sugarcane	Cipriano et al., 2021
Endophytic bacteria	Promotes growth, hormone modulation, N-fixation, siderophore production	Rice	Walitang et al., 2017
<i>B. amyloliquifaciens</i>	Production of gibberellic acid	Rice	Shahzad et al., 2016
<i>Trichoderma</i> sp.	Production of secondary metabolites	Maize	Mukherjee et al., 2018

nutrient cycle, vegetation and precipitation, on local and global regimes. However, numerous significant studies have been made regarding the role of microbiota in environmental changes (Table 4).

Crop growth and productivity are directly related to changes in environmental conditions and climate vulnerability, and the role of beneficial microbes in alleviating climatic abnormalities is well-established by various studies (Carrión et al., 2019; de Souza

et al., 2020). Abiotic and biotic stresses are one of the significant consequences of climate abnormalities and are major constraints in crop production and plant growth. The presence of microbial population in or within the plants alleviates the harmful effects of stresses and possesses synergistic effects with the plant and the environment (Naylor et al., 2017; Compant et al., 2019). The phenomenon of global warming and greenhouse gases emission are parallelly correlated, which ultimately stimulates climate change. As we know, this phenomenon directly or indirectly affects the microbial population and community in the rhizospheric and phyllospheric biome. Temperature elevation due to greenhouse gases emission increases respiration, fermentation and methanogenesis of the microbial community. Microbes like bacteria, fungi, actinomycetes are efficient in decomposing organic matter, which further stimulates global warming in the environment and CO₂ flux in the atmosphere (Abatenh et al., 2018). Microbial communities influence the biogeochemical cycle, nutrient cycling, carbon, and methane cycle status in the atmosphere (Abatenh et al., 2018). Microbial respiration is a crucial pathway for carbon efflux which aids in emission of carbon dioxide naturally. Methanotrophs play an important part as a biological sink to mitigate methane emission in the atmosphere. Several species of algal communities *Oscillatoria*, *Nostoc*, *Anabaena* has potential role in combating stress conditions in different plant species. Phytomicrobiome also contributes to global food security by determining crop yield and climate resiliency. Climate change mitigation is a necessary measure that can be achieved by adopting several measures. The use of biofertilizers which are composed of microorganisms like bacteria, fungi can be an efficient alternative to chemical fertilizers, similarly, biofuels instead of fossil fuels. Soil contains plenty of microorganisms. Soil harboring microbes play an essential role in nutrient cycling, resistance to soil-borne pathogens and changing climatic conditions.

Interplay of Hormonal Crosstalk With Plant-Microbe Interactions Under Changing Climatic Conditions

Plant hormones are organic substances produced in minute quantity which stimulate plant physiological processes. They are the key regulators of plant growth and development in response to external environmental conditions. Plants synthesize various hormones which regulate their metabolism and development. They can be either growth promoters like auxins, gibberellins, cytokinins, or growth inhibitors like ABA. They are chemical messengers which are inevitable for controlling cellular activities and plant metabolic responses. Climate change causes invigoration of various stress responses in plants like drought, salinity and heavy metals toxicity, the incidence of pests and diseases and pathogen attack. These abiotic and biotic stresses are potential threats to agricultural production and food security worldwide. Besides this, these climatic calamities alter plant physiological processes and impart negative effect on plant metabolism and functioning. Although plant impose several tolerance mechanism and pathways to avoid the potential effect of stress conditions when stress conditions prevail. Phytohormones are important growth regulators which

are inevitable for plant growth and provide a defense to plant under stress conditions. Studies revealed that the application of phytohormones under stress improves plant growth and metabolism. Auxins and ABA are key regulators in abiotic stress tolerance (Hu et al., 2013). The negative effect of Pb on sunflower was mitigated by a low auxin concentration with increased root growth. Phytohormones play crucial role in alleviating stress tolerance in plants. Seed priming with auxin alleviates abiotic stress in many crop species (Rhaman et al., 2021).

Similar to auxins, the potential role of other phytohormones has also been deciphered in several studies (Singh et al., 2013; Singh and Singh, 2017; Sharma et al., 2019). The interplay of hormonal activities has also been demonstrated in biotic stresses in plants. Plant growth regulators control the defense mechanism of the plants and induce tolerance to diseases causing pathogens, insect-pest and herbivory. The key hormones regulating plant defense responses include Jasmonic acid (JA), Salicylic acid (SA), which have been widely studied in plant immunity (Aerts et al., 2020). When pathogen invasion prevails in the plant system, the latter consists certain immune response to the plants. The existing procedure of defense utilizes pattern recognition receptors (PRRs), which exists on the surface of plant cells, to detect certain patterns, possibly known as pathogen-/microbe-associated molecular patterns (PAMPs/MAMPs). PAMPs/MAMPs trigger pattern-triggered immunity (PTI) in the plants, which restricts pathogen attack.

However, another mechanism of resistance effector-triggered (ETI) immunity functions in response to pathogen attack (Figure 1). Additionally, the plant has also developed intracellular resistance to counteract pathogen attack via the establishment of R-proteins, which stimulates ETI to develop defense responses in plants. Defense mechanism (PTI & ETI) induces certain responses against pathogen infection in plant parts, including necrotic lesions at the infected site to cease pathogen movement, increase in Ca^{2+} concentration inside the cell, stimulation of MAPKs, defense-related proteins (e.g., PR-1, β 1,3- glucanase, chitinases, ribonuclease like defensin etc.), production of phytoalexins and antimicrobial components (Checker et al., 2018). Furthermore, the activation of certain phytohormones like SA, JA, ethylene, gibberellins, brassinosteroids, auxins etc. have also been implicated in conferring defense mechanism against biotic stresses. The signaling crosstalk of these hormones, either synergistically or antagonistically, plays a fundamental role in the defense mechanism in plants. The signaling of the SA is crucial for defense against biotrophic pathogens, whereas the JA signaling is essential for controlling necrotrophic pathogens (Shigenaga et al., 2017). Activation of jasmonate and ethylene together stimulates the induction of plant defense in *Arabidopsis* against *Alternaria brassicola*; however antagonism of hormone ABA-CK that modulates resistance in tobacco against *Pseudomonas syringae* (Penninckx et al., 1998). Similar studies of hormone crosstalk have been conducted in different plant species against various pathogenic responses (Naseem et al., 2012; Piisila et al., 2015).

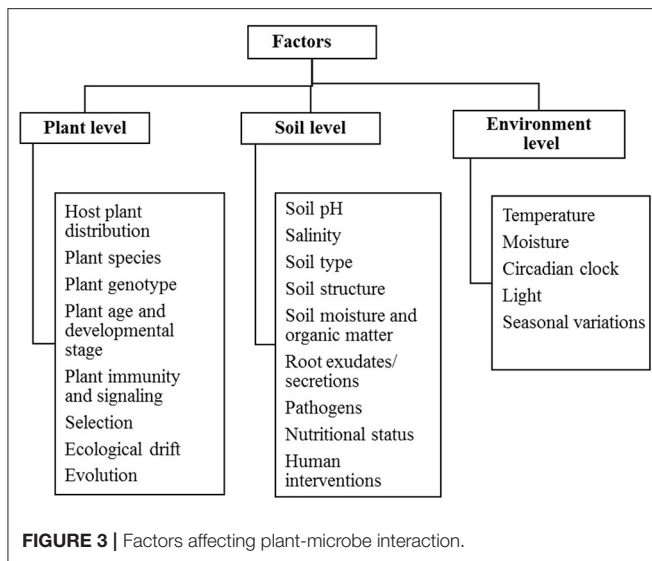
Plant hormones thus play a significant role in stimulating stress tolerance by modulation of genes, downstream signaling by Ca^{2+} sensors, involving G-proteins signaling, ABA-mediated

stress responses; thereby maintaining homeostasis and plant adaptation to environmental challenges and climatic abnormalities (Ku et al., 2018). Microbial communities are key regulators of stress tolerance under changing climatic perturbations. Studies conducted regarding the potential role of microbial populations in ameliorating stress conditions are evident for few decades. Plant beneficial microbes play a significant role in mitigating stress conditions in plants by implicating several mechanisms (Forni et al., 2017; Figure 1). Plant hormones widely influence the microbial colony associated with the plants (Foo et al., 2019). The rhizospheric region of plant system harbors a wide variety of microbial population that participates in plant growth and development by secretion of various polysaccharides, metabolites, and hormones. Root associated microbes stimulate mitigation of salt stress and osmotic stress by the production of phytohormones (Yandigeri et al., 2012).

PGPR provides considerable protection to plants under abiotic and biotic stress responses by inducing phytohormone signaling and activating defense responses (Shilev et al., 2019; Khan et al., 2020; Kashyap et al., 2021). Thus, it is now evident that phytohormones have a positive role in increasing plant stress tolerance in changing climatic scenario. Microbial mediated phytohormones production and stimulation influences not only rhizospheric growth but also alleviates abiotic and biotic stress tolerance concurring plant life cycle. Further studies are required to identify the phytohormone modulation in plant tissues by the microbial population under stress response. Also, the identification of receptors and transcription factors are needed to identify the gene expression after microbial phytohormone application. Hormonal crosstalk and signaling mechanism of microbial communities like PGPR and plant growth promoting fungus in nutrient acquisition in the plant requires more attention. The role of biotechnological approaches in plant-microbe hormonal crosstalk under stress conditions warrants a thorough investigation.

Approaches

Now-a-days, climate change is globally increasing. It is a prevalent phenomenon that affects the demand for food supply to a growing population, thereby affecting global food security. The major consequence of climate change includes the increased concentration of CO_2 in the atmosphere, elevated temperature changing rainfall patterns in various parts of the world (Figure 3). As climatic aberrations are progressing, it may lead to several abiotic stresses and pathogen attack, which is detrimental for crops. Besides, the changing climatic patterns disturb the hydrological cycle and water availability which may also impart a negative impact on agricultural production (Kashyap et al., 2018). Temperature and light alterations decrease the photosynthetic rate, translocation of photosynthates, and increase transpiration. Elevated CO_2 concentration also possesses variable effects on different plant species. Also, reduced or excess rainfall altered cell growth, protein synthesis, decreased plant metabolism, and favored pathogens. These climatic conditions have a real effect on plants in the long term. However, the potential effect of altered climatic conditions has been incessantly studied in many



crops (De Oliveira et al., 2013; Raza et al., 2019). Climate change has a pronounced effect on soil microbe, plant microbes and their interaction. Microbes regulate a wide range of ecological functions in the plant and soil ecosystem. The potential impacts of changing climatic conditions have been reviewed extensively in many studies in different species (Classen et al., 2015; Verheijen et al., 2015). Thus, climate change mitigation approaches are a crucial step for environment sustainability, production and provide protection to plant from climatic aberrations. A proper mitigation approach is required to be taken to tackle changing climatic conditions.

Some of the traditional agricultural practices that involve building resilient climate include agroforestry, intercropping, crop rotation, cover cropping, traditional organic composting, which are gaining rounds for mitigation approaches and can be adopted as an alternative method for sustainable agriculture in changing climatic conditions, but modern agricultural practices along with traditional strategies are needed to be addressed (Singh and Singh, 2017). Modern approaches and biotechnological tools for climate change mitigation are acquiring more importance now-a-days. As discussed, greenhouse gases are the main cause of global warming. Biotechnological methods are effective in reducing the emission of greenhouse gases e.g., use of biotechnological methods increases fertilizer efficiency by many folds (Ferrante et al., 2017), enhanced CO₂ absorption, thereby increasing photosynthetic efficiency (Yang et al., 2017), utilization of biofuels instead of fossil fuels (Delangiz et al., 2019). Climatic mitigating strategies include diverse methods such as conventional technologies that include decarbonization and CO₂ emission technologies, negative emission technology, including capturing and sequestering CO₂ from the atmosphere, potentially removing CO₂ and radiative forcing geoengineering technology, including alteration of the earth's radiation balanced by managing solar and terrestrial radiation (Fawzy et al., 2020).

Furthermore, the development of climate-resilient crops is required by integrating modern technological methods. The use of next-generation breeding approaches (Genomic selection and genomic editing), high throughput phenotyping are desirable to develop climate resilient crops (Varshney et al., 2018). Recent progress in genomics and genome editing technologies has been coming across various approaches of genetic study to make climate-resilient crops (Scheben et al., 2016). Several other strategies are incorporated to develop climate resilient/smart crop including SNP genotype, trait mapping and plant breeding methods. Besides this, the role of bioinformatics tools has also been enunciated to tackle stress responses in changing climatic conditions (Laha et al., 2020). The CRISPR/Cas technology has been efficiently used in enhancing productivity in rice crop in fluctuating climatic conditions (Biswal et al., 2019). Similarly, the potential effect of genome editing CRISPR/Cas technology has been depicted to mediate abiotic stress tolerance in different plant species (Zafar et al., 2019). Genetic engineering—the use of genetically modified organisms, is getting much attention in developing climate-resilient crops to changing climatic conditions. The genetic engineering approach helps manipulate photosynthetic apparatus in climatic alterations (Ortiz et al., 2014). Transgenic technologies have been employed in several crop species in order to confer mitigation to altered climatic conditions (Rubin et al., 2014). Microbial mediated green nanotechnology has emerged as a modern technology to mediate climate resilience. Microbes used in such a process include *Bacillus*, *Fusarium* species, *Pseudomonas*, *Aspergillus*, *Candida albicans*, *Caulerparacemosa*, Tobacco mosaic virus with several other microorganisms. Fabrication of nanoparticles with microbes is a potential method for crop improvement and stress tolerance (Kashyap et al., 2018).

The rhizospheric region possess a vast network of microbial activities that play vital role in several ecological processes like crop production and productivity, nutrient recycling, organic matter decomposition, uptake and recycling of carbon along with storage. In recent years the climatic disruptions have potential effect on rhizospheric ecology and its functioning (Ahkami et al., 2017). Climatic changes including abiotic stresses have additional effect on plant growth and production and they also influence disease development (Glick et al., 2007). Microbes inhabiting the rhizospheric region play an important role in mitigating detrimental effects of climate change which fundamentally causes abiotic stress and pathogen attack. Plants also stimulate secretion of plant growth promoting substances like secondary metabolites, hormones, organic acids which get accumulated in the rhizosphere (rhizodeposition) favoring microbial growth adjacent to or within the plant roots. The root zone also harbors beneficial microorganisms which enhance plant immunity and production (Rodriguez and Durán, 2020). The changing climatic conditions possess adverse effect on rhizospheric and phyllospheric biology. Studies commenced on plant- microbe interactions have unraveled different aspects of symbiotic association of plant with microbes and their beneficial roles in plant health. However, it also demands exploiting the biotechnological strategies by engineering microbial community to enhance plant growth

under changing climatic conditions. Affirmatively, the microbial engineering can be practiced traditionally, and in recent terms, for understanding different aspects of plant interaction with microbes. Engineered microbes can be used in soil amendments, microbial consortium, microbial breeding, and transplantation techniques, host mediated microbial engineering to develop climate resilient crops (Arif et al., 2020). Rhizosphere supports wide variety of microbial activities. Engineering of rhizosphere influences overall growth, nutrient cycling, carbon allocation, and production of crops which can be achieved by engineering the microbiome. The engineering of rhizosphere with PGPR has fundamental role in nutrient availability, crop sustainability and phytohormone production (Hakim et al., 2021). Plant consists of numerous endophytic microorganisms that reside inside the plant. They perform several physiological functions like resistance to plant pathogen and abiotic stress, plant growth promotion like activities either by synergistic or symbiotic association with the plants. Microbiome engineering also stimulates transfer of several genes, thereby activating multiple functions of the plant at one time (del Carmen Orozco-Mosqueda et al., 2018). Thus, the microbial engineering may have significant effect on agricultural productivity and sustainability along with tolerance to several existing climatic calamities. Studies related to phyllospheric engineering are limited and need greater attention (Wu et al., 2017). The rhizo-engineering and synthetic biology approaches open up the new avenues of interaction of plant with soil microorganisms to provide better adaptation to plants against changing futuristic climatic scenario.

CONCLUSIONS AND FUTURE PERSPECTIVES

The key issues that influence the plant microbial communities and their dynamics in the plant and the soil are now

well-known, and research in this aspect is still progress. Our knowledge on understanding the behavior and assemblages of plant microbes above and below the ground, and several factors that influence the plants is still lacking. Microbial association with plants followed two steps: first, recruitment of host-specific plant microbes just close to the root, referred to as rhizosphere, and after that, enter inside the root. Subsequently, various signal molecules coordinate the gathering of the plant microbiomes of rhizosphere and phyllosphere. Signal mechanisms linked to microbiome composition and diversity in their function provide vast scope for future research. Climate change is concurrent phenomenon of global concern and increase in climatic adversity, the food security has been emerged worldwide as alteration in existing climatic patterns adversely affects plant and microbial growth. The adverse effect of climate change is also a matter of discussion for microbe structure & functioning in ecological niches. To what extent we can manipulate the plant microbiome to increase sustainable agricultural yield, maintaining an eco-friendly environment, needs to be investigated. Recently host genetic factor could facilitate study of microbiome diversity and structure which may help in selection of traits based microbiomes. To explore broader knowledge of the host-specific plant microbe interaction, there is a need of advance integrated novel molecular approaches such as ecological models, meta-omics and bioinformatics that could interlink the correlation between microbial community and environmental function.

AUTHOR CONTRIBUTIONS

BSH and PD conceptualized and designed the review. BNS and BSH did the writing of the review. PD reviewed and edited the entire manuscript. All authors contributed to the article and approved the submitted version.

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