Chapter 12
Climate Changing Impact on Microbes and Their Interactions with Plants: An Overview

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Abstract Global warming and climate change are the burning issues that affect all domains of life on earth directly or indirectly. In the context of microorganisms, it is now well known that diverse communities of microbes are associated with plants and play a crucial role in plant health by stimulating plant growth, enhancing resistance to diseases, biotic and abiotic stresses. Climate change is an emerging threat to disrupt plant–microbe interactions network at local to global scales. Interactions between plants and their associated microbes have critical influences on population dynamics, community composition, plant ecosystem, and on evolutionary processes. In the recent past, several researchers have highlighted that the plant microbiome has an important role in maintaining soil nutrient balance which is easily available for plants and it also provides strength to plants under stress conditions. In this review, we have highlighted recent research works related to climate influence on plant–microbe interactions and the mechanisms by which environmental factors create an impact on diverse plant-associated microbes, symbiotic associations, and plant-microbiota interactions. This review has indicated that presently, there is a great need for in-depth research in this area to increase an accurate understanding of climate change's impact on plant–microbe interactions in nature.

Introduction

Climate is defined as the long-term weather conditions of a place that includes humidity, temperature, atmospheric pressure, wind, precipitation, etc. A climate is a complex system that has developed due to the interactions of multiple factors, such as water bodies, oceans, ponds, the earth's environment, atmosphere, glaciers

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as well as different forms of life or organisms. Climate change has been considered a major emerging threat to all domains of life on this planet. As the most diverse and abundant organisms, microorganisms and their associated activities are greatly affected by a changing climate. Microorganisms have a diverse community, colonizing soil, plants, and animals in aquatic and terrestrial conditions [5, 29, 33]. In the global warming era, the study to understand the impact of the resilient climate on microfauna and microflora is very limited and it requires more attention on it. Being ubiquitous, microorganisms are affected in all different environments such as marine, terrestrial, and agricultural ecosystems by climate change [7]. Due to variations in temperature, rainfall patterns, and biotic and abiotic stress conditions such as drought, salinity, ozone stress, pathogens, climate durability, and seasonal abnormalities have created a great impact on the structural and bio-diversity of microbial communities associated with plants. Plants harbor diverse types of microbiomes, such as endosphere-if the microbes are present inside termed and episphere-if present outside of the tissue and/or plant [39]. Soil is also considered as one of the best repositories of microbial population, whereas plants interact with this diverse microbial community and other entities present in nature. The microbial communities are classified as a rhizosphere, endosphere, and phyllosphere in the environment [78]. Plants and microbial populations encompass to form a "halobiont". Generally, halobionts are defined as the association of a host with various microbial species around them and together they form an ecological unit. Microbes interact with plants at diverse locations and do ecological functions in the both above-ground and below-ground environments. Microbes also act as major drivers of the different element cycles, such are nitrogen, carbon, and phosphorus. Over and above, microbes also play a potential role in maintaining resistance to the climatic change impact and against other types of stress responses. Earlier in the case of microbes, most of the studies were focused on their role as pathogens while at present, advances in the high-throughput sequencing and molecular techniques have helped us to improve our understanding of the beneficial roles of microbial communities for hosts and ecosystems [5, 29, 33]. Network of plant–microbe interactions involve a diverse variety of microbial populations from a number of different kingdoms [64, 85]. Plant-associated microbes are further defined by species of host plants and parts of plants, such as leaf, stem, root, and tissue location [3, 41]. Beneficial impacts of plant–microbe interactions like plant health have been demonstrated in number of research findings, such as root-associated microbiota play an important role in plant growth promotion and also enhance resistance against biotic and abiotic stresses [50, 85]. The leaf-associated microbial community has also been shown to be involved in fitness and growth promotion of the host [18, 66], resilience to abiotic stresses [41], and plant protection against pathogens and disease [31]. Further, positive correlations have been found between the plant-associated diverse microbial community and ecosystem's productivity [42], and it also has been observed that the decrease in microbial diversity was correlated with pathogen infection and disease propagation [40]. These observations and experimental data of plant-associated microbes have been strongly indicating the importance of an accurate understanding of the molecular mechanisms of host-microbe interactions to drive the better adaptation of plants to climate change and the global warming effect. While climate change is emerging as a big threat but conversations on its crucial link with plant-associated microbes are still rare outside of the microbiologist and allied science community. It has already been well reported that climate change severely affects the crop yield of many agriculturally important crops around worldwide [40, 76, 92] and it is expected to intensify the negative impact of climate variability on crop yield in the coming decades. Therefore, some innovative approaches are urgently required to minimize the influence of climate change on plants. In order to tackle climate change and plant health issues, it is very much important to learn how a changing climate will affect the microbes and their relationships with plants and their environment.

Impact of Global Warming and Drought

Due to climate change, different forms of life across the earth are currently experiencing the rising temperatures [46]. O'Brien and Lindow have reported that due to rising temperature, bacterial colonizing pathways are affected in plant leaf surfaces [56]. A few recently published articles also have shown the influence of rising temperatures on plant–microbe interactions, [15, 82], immune system of host plants, [12] and soil microbes [26]. Numbers of studies have shown that temperature plays as one of the main drivers to develop and maintain the community composition of soil microbes [23], phyllosphere fungal [16], and ectomycorrhizal fungi [74]. The impact of intra-annual changing of temperature also have been studied via seasonality, which is observed to be a key determinant to maintain the composition of the microbial community in soil, such as in the rhizosphere [24] and the phyllosphere [25, 34, 58, 63]. Apart from temperature, abiotic factors also vary with seasonality and these variations also have a crucial role in the shaping of microbial communities. For example, in case of phyllosphere fungal assemblage, the number of days of frost in spring was found to be one of the key factors for dissimilarities in assemblage of phyllosphere fungal [16]. Peñuelas et al. have found that the bacterial and fungal phyllosphere communities were higher under spring and winter in comparison to Mediterranean summer [58]. Other studies also have reported that the root associated microbial communities are extremely variable during the growing season but clear predictable patterns in community composition still to be detected [21, 61]. Furthermore, Grady et al. observed variation of core leaf bacterial and archaeal communities in the early, mid, and late phases of switch grass growing season [25]. These observations have indicated that seasonality also influence the assembly of microbial community. Soil community composition of bacterial and archaeal has been found to vary significantly between semi-arid, arid and Mediterranean climates, which is indicating the availability of water acting as a key component in shaping communities composition in ecosystems [4]. Further, dry climatic condition influences the fungal community of soil, such as it increases the fungal diversity and total abundance in soil [28, 35]. While it reduces bacterial diversity, the soil with a history of water stress have shown lower bacterial diversity and abundance [44]. Generally, warm climate condition increases bacterial diversity and bacterial abundance used to enhanced under normal precipitation patterns, while drought along with warming condition significantly decreases the bacterial abundance [68]. However, the combined impact of drought and warming on microbial growth and diversity determination still have to be investigated for proper understanding. It is also reported that drought-adapted microbiota are observed for plants subjected to subsequent water stress [35, 44]. It is also now well known that some endophytes can improve host drought resilience, such as *Lolium* sp. and its endophyte *Epichloe* [47]. It was also found that functionality of leaf and root microbiota is affected by drought condition [30]. As global change in climates accelerating, these research findings and observation have highlighted the need to enhance our understanding about the impact of climate variation on microbial community diversity/abundance and its role for the maintenance of ecosystem productivity to tackle the prolonged warming and drought.

Climate Variation Impact on Plant Microbiomes Assemblage

Plant microbiome assembly is a complex ecological process of continuous coevolution over millions of years that is governed by a number of factors. Plants system attracts the desired soil microbe's community to colonize and develop the plant microbiomes. The seed-associated microbiome facilitates the germination of seed and plant growth. Last few decades, host microbiome is gaining more attention from concerned researchers. Host microbiome is defined as the microbial community present in a particular species, irrespective of environmental conditions, seasons, and management, and plays a crucial role in the host's functions [72, 77]. Microbes are very sensitive to temperature and moisture to perform their physiological and metabolic function and therefore, climate variability act as an important factor that affect the assembly of the plant microbiome directly or indirectly.

Due to rapid fluctuation in the environmental conditions, the direct influence of climate change is likely to be more pronounced on the microbial communities covering the outer surface (phyllosphere) in comparison to those microbes in the internal plant tissue environments *i.e.,* the endosphere community [77]. The soil microbiome is directly influenced by climate, while the rhizosphere microbiome is not only impacted by the external climate but also indirectly influenced by the plant host responses such as root exudation, plant physiology variation, morphology, and immune response. In the recent past, many researchers suggested that plant-associated microbiome always give a consistent response to climate change [55, 83, 88]. Under reduced moisture conditions and drought, it was observed that a number of plant species selectively recruit gram-positive bacteria (due to thicker cell walls) to enhance tolerant against desiccation, while it reduces the gram-negative bacterial population in the root region and rhizosphere [55, 89]. The exact understanding of impacts of climate change on plant–microbiome assembly is a big challenge due to the interconnection of multiple factors and complex interaction processes.

Under climatic stress, plant–microbiome interactions are modulated by chemical communications. For example, plants have developed an exudation-mediated 'cry for help' mechanism for the recruitment of a stress-relieving microbiome when plant is exposed to stressful environmental conditions [49]. In the current scenario, there is a very limited knowledge available regarding the indirect influence of climate change on microbiome assembly in the host plants. Over and above, plants also have developed a mechanism to incorporate desired microbes and it acts as a multi-layered microbial management system for the most favourable microbes for incorporation into the plant tissues and to distinguish friend from foe [27, 75]. In the plant's first immune layer, where pattern recognition receptors recognize the microbe-associated molecular patterns, such as bacterial flagellin or fungal chitin, it induces microbe-associated molecular patterns' triggered immunity (MTI) while in the case of the second immune layer, pathogen effectors are recognized by nucleotide-binding leucine-rich repeat (NLR) resulting to the plants' effector-triggered immunity (ETI). Changing climate, warming, and drought have altered the plant immunity and the shape of the plant–microbiome. It is reported that warming can affect both an increase [11] and decrease [32] in MTI and to suppress ETI in plants [12, 19]. Suppression of ETI disrupts the host-mediated microbial colonization network which may cause dysbiosis in endosphere microbial communities living inside the plant tissues. Further, under the suitable environmental condition of mechanism of effector-triggered immunity suppression, plants reduce their immune response to the colonization of beneficial microbes and these microbes coordinate with the host to provide stress relief. During rapidly fluctuating surrounding environments, plants also modulate immunity through dynamic changes in hormonal pathways, such as salicylic acid (SA), abscisic acid (ABA), jasmonic acid (JA), and ethylene [48]. During warm and drought climates, salicylic acid production decreases and it is involved, via interaction with some other plant hormones such as jasmonic acid, in the assembly of both epiphytic and endophytic microbial communities [45]. Drought-induced production of abscisic acid, antagonistically it acts to salicylic-mediated immune signalling, changes in the different classes of defense metabolites and it allocation or distribution, plant hormones, and signalling molecules under climate change play a role in plant microbiome assembly.

Climate Changing Impact on Plant–Microbe Interactions

At present, climate changing is increasing globally and it is a prevalent phenomenon affecting our food security worldwide. Climate change has resulted in the increased concentrations of CO_2 in the atmosphere, temperature elevation, and has changed the patterns of rainfall across the various parts of the globe (Fig. 12.1). The progression of climatic aberration may lead to several abiotic stresses and pathogen attack, which is detrimental to plants and crops. Besides, the changing climatic patterns disturb the hydrological cycle and availability of water which may also influence on agricultural

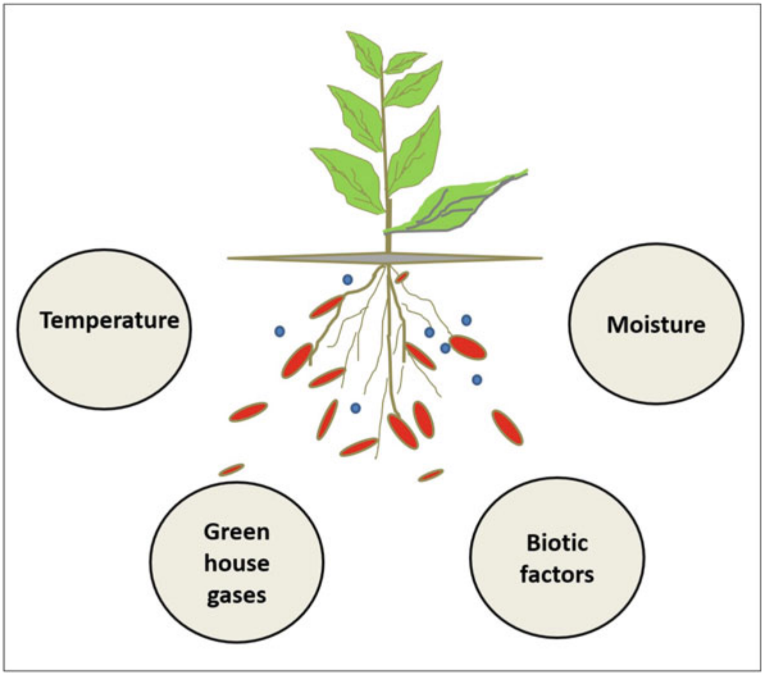

Fig. 12.1 Climate change and plant-microbe interactions

production [36]. The variable climatic conditions also have affected the structure, function, assemblage, and interactions of microbes with host and non-host plants [17].

Plant–Microbiome Communication

A system of communication exists between the host plant and microbiomes. Under stress environment, generally, plants exude some metabolites to recruit selective microorganisms to enhance plant resilience [44]. For example, in the drought-affected area, plants induce the secretion of glycerol-3-phosphate (G3P) in the roots enriching actinobacteria with the genetic potential to transport and utilize G3P for growth [89]. Drought induces a reduction in the iron and phytosiderophore availability in the rhizosphere and facilitates the actinobacteria population, which can adapt under low iron conditions and increase both the fitness and plant growth promotion ability [89]. The microbiome, associated with plants, also influences the host's phenotypic plasticity, which can impact plant phenology in a changing climate [17]. It is reported that microorganisms present in the rhizosphere may modulate the timing of flowering through the nitrogen (N) cycle and by the conversion of tryptophan in root exudates to the phytohormones-indoleacetic acid [49]. Moreover, plants also use volatile organic compounds to attract microbes, insects, and nematodes [87]. Rising of climate temperature increases the volatile compound emissions and it is also hypothesized that root exudate-mediated variation in microbial community composition may influence the changes in the immune responses of host plants, or signalling within the host. Deciphering the molecular mechanism of abiotic stresses influence the reshaping the microbes' composition and function of the plant microbiome is very much required to understand for developing strategies to enhance plant resilience under climate stresses.

Beneficial Plant–Microbe Interactions

Climate change also has the diverse type of effects on beneficial plant–microbe interactions [12]. A warming climate decreases the photosynthate allocation in the underground part of the plants which affects the development of roots in diameter as well as in length [60]. Consequently, root colonization of arbuscular mycorrhizal fungi (AMF) is reduced or AMF species with lower carbon (C) requirements get more favoured [8, 51]. Few members of the plant-associate microbial community have traits that alleviate the impact of abiotic stresses on host plants [77, 79] (Table 12.1). For example, 1-aminocyclopropane-1-carboxylate (ACC) deaminase increases the stress tolerance by regulating the level of plant ethylene, and extracellular polymeric substances (EPS) developed the hydrophobic biofilms that help plants from desiccation. Plant hormone enhances level to stimulate the plant growth and induces accumulation of osmolytes and/or detoxifies reactive oxygen species. It also influence nutrient and water uptake by increasing root surface area and modulating the plant's epigenetic regulation that help in the adaptation to new environmental conditions. For example, Enterobacter sp. SA-87 induces thermotolerance by developing a novel mechanism in which heat shock factor A2 (HSFA2) constitutively expressed via ethylene signalling pathway and transcription factor EIN3 and these processes enhance the thermotolerance in plants [69]. In some plants, it also reported that growth-promoting bacteria help the plants to cope with multiple stresses [9, 43]. Researchers have validated that under stress conditions, improved plant performance is the result of the number of interactions in the plant microbiome that provide support against abiotic and biotic stresses. The scientific community still has a very limited understanding of the intertwined molecular mechanisms and the interactions between host plants and their microbiota under today's climate change. Identifying and understanding these mechanisms and the factors that influence them will help in the development of some noval approaches to neutralize the impacts of climate change on plant health.

Table 12.1 Plant–microbe interaction under adverse climatic conditions

Sl No	Microbes	Plant species	Abiotic stress	References
1	*S. meliloti*	*M. sativa*	Drought tolerance	[54]
2	Azotobacter	Maize	Drought stress	[71]
3	Salep gum and *Spirulina platensis*	Maize	Cd toxicity	[67]
4	*Achromobacter xylosoxidans*	Mustard green	Cu toxicity	[59]
5	*Glucoacenatobacter diazotrophicus*	Sugarcane	Drought	[81]
6	*Pseudomonas* sp. and *Bacillus* sp.	Spinach	Cd, Pb, Zn toxicity tolerance	[70]
7	*Bacillus aryabhatti*	Soybean	Heat stress tolerance	[57]
8	PGPB	Sorghum	Cr stress & heat stress tolerance	[52]
9	*Rhizobium* sp.	Sunflower	Drought	[2]
10	Microalgae-cyanobacteria	Tomato	Salt stress	[53]
11	*Burkholderia* sp.	Tomato	Cd toxicity tolerance	[20]
12	Cyanobacteria	Arabidopsis	Heat stress	[13]
13	*Serratia* sp.	Chickpea	Nutrient stress tolerance	[91]
14	*Bacillus subtilis* and *Paenibacillus illinoinensis*	Pepper	Drought tolerance	[84]
15	*Pseudomonas frederiksbergensis* OS261	Red pepper	Salt stress	[10]
16	*Varivorax paradoxus* 5C-2	Pea	Salinity tolerance	[86]
17	*Pseudomonas vancouverensis*	Tomato	Chilling stress tolerance	[73]
18	*Bacillus subtilis*, *Arthrobacter* species	Wheat	Salinity stress	[80]
19	*Cellulosimicrobium cellulans*	Chili	Chromium toxicity tolerance	[80]

Pathogen–Plant Interactions

A tripartite environment–host–pathogen interaction regulates the plant's health and productivity from resistance to different diseases. Climate change and associated factors alter the pathogen behaviour by changing the host–pathogen interactions and they also enhance the emergence of new pathogens and disease conditions [14].

Simultaneously, pathogens also can adopt different strategies of infection by modifying their virulence system that potentially leading to the breakdown of R gene-mediated plant resistance. It is already reported that warming and drought conditions can break down effector-triggered immunity (ETI) and promote disease in plant system [12]. Climate change studies on host–pathogen interactions have generally used a simplified model system which composed of a single pathogen interaction with a single host plant. However, in nature, plants interact with a large number of pathogenic microbes (pathobiota) [6] wherein the pathogen establishment and disease state depend on the competition between the pathogens and members of the plant-associated microbiome. Currently, there is lack of proper understanding of the interaction between pathogenic microbes and plant microbiota under exposure to long-term abiotic stresses.

Hormonal Crosstalk with Plant–Microbe Interactions Under Changing Climatic Conditions

Plant hormones are organic substances that stimulate plant physiological processes. Phytohormones act as key regulators of plant growth and development and plant response to the surrounding environmental conditions. Climate change causes various stresses in plants, such as drought, salinity, heavy metals toxicity, incidence of pathogen attacks, and different diseases. Phytohormones are important regulators which provide a defence system to plants under abiotic and biotic stress conditions. Studies have shown that phytohormones improve plant growth and metabolic process under stress. ABA and auxin play key regulators role in abiotic stress tolerance [1]. The adverse impact of Pb on sunflower plant was mitigated by using the low auxin concentration with increased root growth. It is reported that seeds priming with auxin alleviate in many plant species that helps under abiotic stress [62]. Microbial communities associated with plants play key role for stress tolerance under changing climatic perturbations. Besides, the microbial colony associated with the plants influenced the plant hormone [22]. Microbes, associated in root, stimulate mitigation of osmotic stress and salt stress by the production of phytohormones [90]. PGPR also provides protection to the plant under stress by inducing phytohormone signalling as well as activating the defence responses [37, 38, 70]. Thus, it is now well established that hormones have a positive role against stress in changing climatic scenarios. However, to identify the phytohormone modulation in plant system by the microbial population, under stress response, require further in-depth study. Over and above, identification of transcription factors and receptors are needed to understand gene expression levels after the application of microbial phytohormone. Hormonal signalling and crosstalk mechanism of plant associated microbe like PGPR and plant growth promoting fungus in nutrient acquisition requires deeper attention. The role of biotechnological approaches in plant–microbe hormonal crosstalk, under stress conditions, warrants a thorough investigation.

Conclusion and Future Prospects

Plant-associated microbial communities and their dynamics are well-known and concerned researchers in this aspect is still working toward a better understanding of the interaction networks of the microbe and its assemblages in plant systems. Above and below the ground, detail understanding on the several factors, that influence the plants-associated microbes, is still lacking. Recruitment number of desired microbes by plants near their root is called the rhizosphere that later enters inside the root system. Subsequently, various signal molecules coordinate the gathering of the plant microbiomes of the rhizosphere and phyllosphere. Molecular mechanisms linked with microbiome assembly, composition, and diversity in their function will provide tremendous scope for future research. Climate change is a global concern and it is enhancing climatic adversity as well as adversely affecting plant and microbial growth. The negative impact of climate change on microbial structure and their functioning in ecological niches is also a matter of concern. It is very much necessary to understand to what extent manipulation of plant-associated microbial composition could be done to enhance crop yield through sustainable agriculture that could maintain the environment in an eco-friendly manner. To explore in-depth knowledge about the plant–microbe interaction and host specificity, there is an urgent need for an advanced level of integrated innovative molecular approaches, such as metaomics, ecological models, and bioinformatics, which may confirm the interlink of the correlation between plant-associated microbial community and environmental factors under climate changes.

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