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Plant–microbiome interactions under a changing world: responses, consequences and perspectives

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Summary

Climate change is increasing global temperatures and the frequency and severity of droughts in many regions. These anthropogenic stresses pose a significant threat to plant performance and crop production. The plant-associated microbiome modulates the impacts of biotic and abiotic stresses on plant fitness. However, climate change-induced alteration in composition and activities of plant microbiomes can affect host functions. Here, we highlight recent advancements in our understanding of the impact of climate change (warming and drought) on plant–microbiome interactions and on their ecological functions from genome to ecosystem scales. We identify knowledge gaps, propose new concepts and make recommendations for future research directions. It is proposed that in the short term (years to decades), the adaptation of plants to climate change is mainly driven by the plant microbiome, whereas in the long term (century to millennia), the adaptation of plants will be driven equally by eco-evolutionary interactions between the plant microbiome and its host. A better understanding of the response of the plant and its microbiome interactions to climate change and the ways in which microbiomes can mitigate the negative impacts will better inform predictions of climate change impacts on primary productivity and aid in developing management and policy tools to improve the resilience of plant systems.

I. Introduction

The global mean surface temperature is predicted to increase by 2.6–4.8°C by the year 2100 if no mitigation efforts are made (IPCC, 2014). Elevated temperatures will reduce soil water content

and increase the frequency, severity and duration of drought in many regions (Samaniego *et al.*, 2018). Heat and drought affect plant communities, influencing all aspects of plant biology including growth, reproduction, migration and resilience. The exact impacts of climate change on natural vegetation and

agriculture are difficult to predict but could have devastating consequences for humankind. Climate variability has already reduced the production of major crops world-wide (Zhao *et al.*, 2017; Tito *et al.*, 2018), and its negative impacts are expected to intensify in coming decades. Therefore, new approaches to mitigate the negative effects of climate change on plants are urgently required.

Plants are intimately associated with diverse, taxonomically structured communities of microorganisms. The plant microbiota includes bacteria, fungi, protists, nematodes and viruses that colonize all accessible plant tissues (Trivedi *et al.*, 2020). The microbiome (microbiota and their genomes) inhabiting the soil, rhizosphere, roots and other plant tissues establishes complex and dynamic interactions with the host plant. These interactions are highly influenced by the environment and can improve plant resilience to environmental stresses (Naylor & Coleman-Derr, 2018; Singh *et al.*, 2020a; Trivedi *et al.*, 2020, 2021). Despite growing recognition of the microbiome's importance to plant growth and health, harnessing the microbial interactions and traits to improve plant resilience to climate variability remains a significant challenge. A better mechanistic understanding of the plant–microbiome relationship is needed to develop future tools to predict and mitigate the impacts of climate change on primary productivity and plant diversity.

This article examines many aspects of the impact of climate change on the interaction between nonwoody crop plants and the microbiomes that are tightly and directly associated with hosts. We discuss how climate change will impact the community composition of the plant microbiome and highlight the response of functional properties, including metabolic and signalling interactions, and the genes driving plant–microbiome interactions. Possible mechanisms of eco-evolutionary processes on climate adaptation are described that can be harnessed for the development of microbial tools for climate-proof primary production. A number of climate change factors such as drought, elevated temperature, increasing CO_2 and changes in the freeze/thaw cycles affect plant–microbiome interactions impacting plant performance. In this article, we focus on warming and drought, two abiotic stresses that are postulated to increase in occurrence and severity across the globe and have direct significant impacts on plant productivity and ecosystem sustainability. In proposing new concepts, we have been deliberately provocative, but our arguments are embedded in strong scientific frameworks. Our aim is to initiate new discussions on the topic and shape future research in this discipline.

II. Impact of climate change on the assembly of the plant microbiome

Plant microbiome assembly is a complex ecological process driven by coevolution over millennia (Dini-Andreote & Raaijmakers, 2018; Trivedi *et al.*, 2020). The seed microbiome (heritable) helps the plant germinate and, along with the seed exudates, shapes the host microbiome. Exudate signals attract desired soil microbes to colonize plants and modulate their immune systems, forming the plant core microbiome. Some 'social cheaters' and pathogenic microbes also use this pathway. The concepts of core-and-hub

microbiota are gaining increasing evidence in host–microbiome research (Singh *et al.*, 2020b). They include the microbiota present in a particular species, irrespective of growing seasons, environmental conditions and management practices, and provide key host functions (Singh *et al.*, 2020b; Trivedi *et al.*, 2020). Given their importance, it is critical to decipher the impact of climate change on the 'core-and-hub' microbiota that potentially organize community-scale processes in plant–microbiome relations. Increased knowledge of the ecological principles that govern the response of microbiome structure and function to climate change will advance our understanding of microbiome properties (e.g. resistance and resilience) that improve plant fitness under novel environmental conditions.

Microbes differ in their physiology, metabolism and sensitivity to temperature and moisture. Therefore, climate change can have direct impacts on the assembly of the plant microbiome. The direct impact of climate change is likely to be more pronounced on communities that occupy the plant surface (e.g. the phyllosphere), where environmental conditions fluctuate more rapidly as compared to the relatively stable internal plant tissue environments (i.e. the endosphere) (Trivedi *et al.*, 2020). The majority of the bulk soil microbiome (a reservoir of available microbes that can colonize the plant) are directly impacted, while rhizosphere microbiomes are influenced not only by external climatic factors but also indirectly by host responses, which include changes in plant physiology, morphology, immune response and root exudation (Fig. 1). Some reports suggest a consistent response of the plant-associated microbiome to climate change (Naylor *et al.*, 2017; Xu *et al.*, 2018; Vescio *et al.*, 2021; Wipf *et al.*, 2021). Under drought conditions, many plant species selectively recruit and enrich monoderm (or Gram-positive bacteria that are tolerant to desiccation due to thicker cell walls) and deplete diderm (or Gram-negative) bacteria in the rhizosphere and roots (Naylor *et al.*, 2017; Naylor & Coleman-Derr, 2018; Xu *et al.*, 2018). Elucidating how climate change impacts plant–microbiome assembly is a challenge due to the complexity and interconnectedness of the factors that govern this process. Plant–microbiome interactions under climatic stress appear to be largely modulated by chemical communications (Fig. 1). For example, plants have evolved an exudation-mediated 'cry for help' response when exposed to stressful environmental conditions, leading to the recruitment of a stress-relieving microbiome (Liu *et al.*, 2020). We have limited knowledge about the indirect influence of climate change on plant–microbiome assembly via changes in root exudation patterns.

Plants have also developed a multilayered microbial management system to incorporate the most favourable microbes into plant tissues and to distinguish friend from foe (Hacquard *et al.*, 2017; Teixeira *et al.*, 2019). These protective barriers include: (1) first immune layer, where pattern recognition receptors (PRRs) recognize microbe-associated molecular patterns (MAMPs), such as bacterial flagellin or fungal chitin, resulting in the plant MAMP-triggered immunity (MTI); and (2) second immune layer, where nucleotide-binding leucine-rich repeat (NLR) proteins recognize pathogen effectors, leading to the plant effector-triggered immunity (ETI). Both warming and drought-induced changes in plant immunity may shape the plant–microbiome, particularly inside
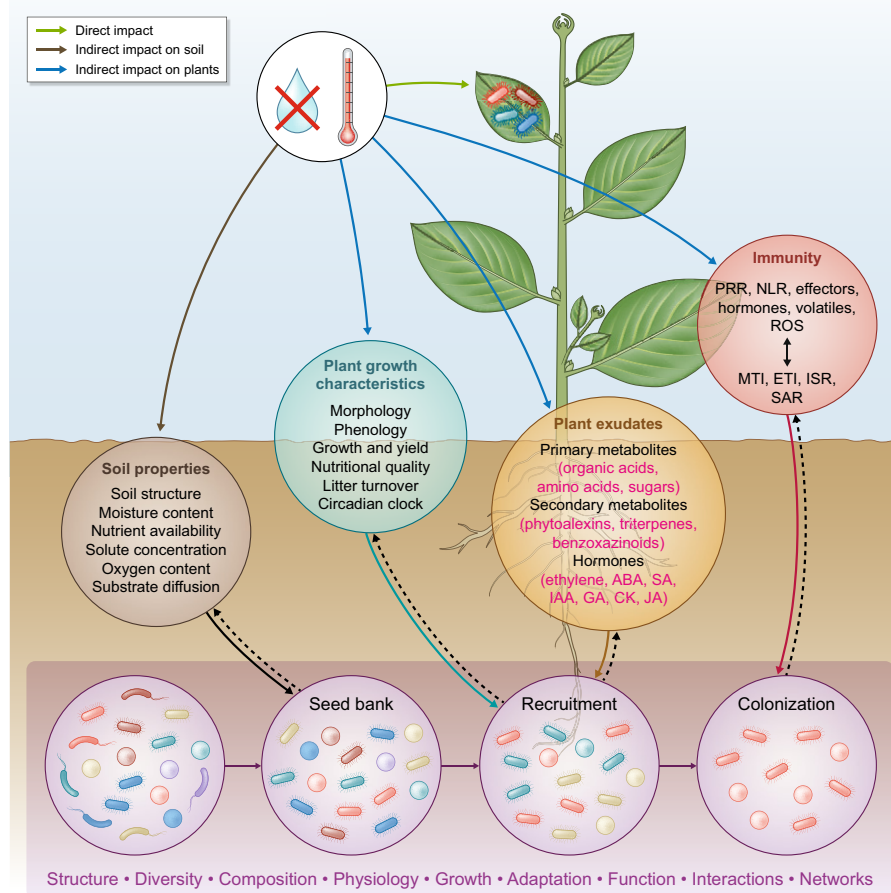
Fig. 1 Impact of climate change on the plant-associated microbiome. Climate change can have a direct (light green arrow) and indirect impact (brown and blue arrows representing the impacts on soils and plants, respectively) on the plant–microbiome. Different climate change drivers will have a variable impact on the microbiome. For example, the direct impact of warming is likely to be stronger on the aboveground epiphytic microbiome than drought. In comparison, drought will have a stronger indirect impact on the soil microbiome than warming. The indirect impact of climate change on the microbiome can be mediated by changes in soil properties (brown circle), plant growth characteristics (green circle), exudation (yellow circle) and immunity (pink circle). Climate change can impact the bulk soil 'seed' microbiome directly or indirectly via affecting soil properties (black arrow). These impacts will select tolerant (circular) and opportunistic (oblong) groups while reducing sensitive (curved) groups. As the initial soil microbiome is the source for the plant microbiome assembly, a variation in the composition and functioning of the soil microbiome can determine the outcomes of plant–microbiome interactions under climate change. Plants undergo a set of physiological responses that allow them to adapt to short- and long-term environmental fluctuations (green and yellow circles). Recent reports suggest that plant exudates (yellow circle) are critical to the ecosystem responses to climate change (William & de Vries, 2020). It is likely and equally important that the quantity and quality of root exudate directly affects climate resilience via its impact on the plant-associated microbiome. Growing evidence for the 'cry for help' hypothesis posits that plants recruit specific microbes that can alleviate plant stress in a given situation by regulating root exudation patterns. Changes in plant growth characteristics and exudation patterns will impact the microbial recruitment process (green and light brown arrows), selecting the microbial groups (green-, red- and yellow-coloured ovals and circles) that can adjust to the new conditions and metabolize stress-induced communication signals. Plant colonization of microbes (red-coloured circles and ovals) will be determined by changes in the plant immune responses (pink arrow) that are postulated to be significantly impacted by climate change drivers. Plant immune-mediated impact on microbial colonization will be stronger for endophytes than for epiphytes. Direct and indirect impacts mediated by climate change can alter many plant-associated microbiome features (purple text in shaded box). Climate change-induced alteration in plant-associated microbiome assembly will have a strong impact on many aspects of plant–microbiome interactions. These interactions will further influence plant growth characteristics, exudation patterns and immune response (dashed black lines). Successive changes in the microbial community composition are shown by purple arrows. ABA, abscisic acid; CK, cytokinin; ETI, effector-triggered immunity; GA, gibberellic acid; IAA, indoleacetic acid; ISR, induced systemic resistance; JA, jasmonic acid; MTI, microbe-associated molecular pattern-triggered immunity; NLR, nucleotide-binding domain leucine-rich repeat receptors; PRR, pattern recognition receptor; ROS, reactive oxygen species; SA, salicylic acid; SAR, systemic induced resistance.

plant tissues. Warming is reported to cause both an increase (Cheng *et al.*, 2013) and a decrease (Janda *et al.*, 2019) in MTI and to suppress ETI in plants (Cheng *et al.*, 2019; Desaint *et al.*, 2021). Suppression of ETI can disrupt host-mediated control of microbial colonization and can cause dysbiosis in microbial communities

living inside plant tissues. Effector-triggered immunity suppression may also act as a novel mechanism by which plants reduce their immune response to allow colonization by beneficial microbes, which can then tune their genetic machinery to provide stress relief. Overall, strong evidence is emerging that the reciprocal interplay

between the microbiota and the plant immune response shapes plant–microbiome assembly.

In rapidly changing environments, plants modulate immunity through dynamic but finely orchestrated changes in many hormone pathways, including abscisic acid (ABA), salicylic acid (SA), jasmonic acid (JA) and ethylene (Li *et al.*, 2021). Both drought and warming decrease SA production, which is involved in both epiphytic and endophytic microbiome assembly (Lebeis *et al.*, 2015). Salicylic acid may act via canonical signalling pathways, via interaction with other hormones such as JA, or directly on microbial community members, promoting or inhibiting their growth. Drought-induced ABA production acts antagonistically to SA-mediated immune signalling. It should be noted that climate-induced changes in plant hormones can vary with plant developmental stage and tissue type. For example, under drought conditions, maize stimulates benzoxazinoid defences in aboveground tissues, while terpenoid phytoalexins are stimulated belowground (Vaughan *et al.*, 2018). Changes in the allocation or distribution of different classes of defence metabolites or signalling molecules under climate change have the potential to further impact microbiome assembly.

III. Plant–microbiome interactions under a changing climate

Pathogen–plant interactions

Plant health and productivity are impacted by tripartite environment–host–pathogen interactions that operate on a continuum from resistance to disease. Climate change can alter pathogen abundance and behaviour, change the host–pathogen interactions and facilitate the emergence of new pathogens (Cohen & Leach, 2020). A proportion of many plant pathogens are predicted to increase as global temperatures rise (Delgado-Baquerizo *et al.*, 2020), and to compound the problem, many widely used approaches fail to control diseases at high temperatures (Burdon & Zhan, 2020). Simultaneously, pathogens can adopt new invasion strategies by modifying their virulence system potentially leading to the breakdown of *R* gene-mediated plant resistance. Both elevated temperatures and drought can break down ETI and promote disease in many plant pathosystems (Cheng *et al.*, 2019). Most studies on the effect of climate change on host–pathogen interactions have used simplified models composed of a single host plant interacting with a single pathogen. However, in their natural environment, plants interact with a wide variety of potentially pathogenic microbes (pathobiota) (Bartoli *et al.*, 2018) wherein the pathogen establishment depends on cooperation or competition between the pathobiota and members of the plant microbiome. We currently have no understanding of how the interaction between pathobiota and plant microbiome will respond under exposure to long-term abiotic stresses.

Beneficial plant–microbe interactions

Climate change will have variable effects on beneficial plant–microbe interactions (Cheng *et al.*, 2019). Warming can decrease

belowground photosynthate allocation, leading to limited root development in both length and diameter (Qiu *et al.*, 2021). Consequently, root colonization by arbuscular mycorrhizal fungi (AMF) is reduced and/or AMF species with lower carbon (C) requirements are favoured (Ma *et al.*, 2018; Bergmann *et al.*, 2020). Certain members of the plant microbiome have traits that alleviate the effects of abiotic stresses on plants (Trivedi *et al.*, 2020, 2021). These include the following: (1) the production of 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which increases stress tolerance by regulating plant ethylene levels; (2) the production of extracellular polymeric substances (EPS) resulting in hydrophobic biofilms that can protect plants from desiccation; (3) the production of phytohormones that can stimulate plant growth, induce accumulation of osmolytes and/or detoxify reactive oxygen species; (4) directly influencing nutrient and water uptake by increasing root surface area; and (5) modulating the plant's epigenetic regulation leading to acclimation and adaptation to new environmental conditions. For example, root endophytic bacterium *Enterobacter* sp. SA-87-induced thermotolerance is shaped by a novel mechanism in which constitutive expression of heat shock factor A2 (*HSFA2*) via the ethylene signalling pathway and the transcription factor *EIN3* results in methylation of heat stress memory genes that enhance thermotolerance in plants (Shekhawat *et al.*, 2021). Some plant growth-promoting bacteria can even help plants to cope with multiple stresses (Lata *et al.*, 2018; Bokhari *et al.*, 2019). It is validly postulated that improved plant performance under stress is the net result of multiple microbiome mechanisms that may be activated simultaneously. However, we have a limited understanding of the intertwined molecular mechanisms that open the cascade of interactions between plants and their associated microbiome under climate change. Identifying these mechanisms and the factors that influence them will allow for the development of new tools to predict (Box 1) and mitigate the impacts of climate change on primary productivity.

Plant–microbiome communication

A communication system exists between the microbiome and the host plant. When stressed, plants exude metabolites to selectively recruit microorganisms able to enhance plant resilience (Liu *et al.*, 2020). For example, drought-induced secretion of glycerol-3-phosphate (G3P) in the roots enriches Actinobacteria with the genetic potential to transport and utilize G3P for growth (Xu *et al.*, 2018). Drought causes a reduction in iron and phytosiderophore availability in the rhizosphere, facilitating the enrichment of Actinobacteria, which can thrive in low iron conditions increasing both the fitness advantage and plant growth promotion ability of Actinobacteria (Xu *et al.*, 2021). The plant microbiome also contributes to host phenotypic plasticity, which can impact plant phenology in a changing climate (Dastogeer *et al.*, 2020). For example, rhizosphere microorganisms can modulate flowering time by impacting the nitrogen (N) cycle and converting tryptophan in root exudates to the phytohormone indoleacetic acid (Lu *et al.*, 2018). Furthermore, plants use volatile organic compounds (VOCs) to communicate with insects, nematodes and

microbes (Weisskopf *et al.*, 2021). Climate warming is increasing VOC emissions, and we postulate that root exudate-mediated shifts in microbiome composition under drought and warming may be tied to changes in plant immune responses, or to a stress signalling network within the host. Deciphering the molecular dialogues through which abiotic stresses influence metabolites to reshape the composition and function of the plant microbiome is essential for developing strategies to increase plant resilience to climate stresses.

IV. Evolutionary and eco-evolutionary responses of plant–microbiome interactions under climate change

Climate change may influence the eco-evolutionary interaction between the host and its microbiome. A recent study demonstrated that drought induced the reorganization of hormonal signalling pathways and altered gene expression, resulting in the evolution of virus–plant interactions from pathogenic to mutualistic (González *et al.*, 2021). Further, evolution makes microbes more cooperative with their local host genotype, and cheaters cannot outcompete cooperative microbes (Batstone *et al.*, 2020). It is proposed that the eco-evolutionary interactions between hosts and their associated microbiomes will play a key role in plant resilience to climate change (Fig. 2). Furthermore, studies have provided evidence that while plant habitats strongly shape the microbiome, ecological and evolutionary processes also play a role. For example, drought reduces the host impact on the assembly of the plant fungal community and increases the impact of stochastic forces (e.g. drift or stochastic dispersal) (Gao *et al.*, 2020). The evolutionary interactions between microbial species depend on stress levels. Under moderate stress, microbes display more competitive interactions, whereas under adverse conditions, they display more cooperative or neutral behaviour. Deciphering the principles that underlie the ecological and evolutionary properties of microbial communities can allow for the construction of models that predict the eco-evolutionary dynamics of microbial communities.

Eco-evolutionary responses suggest that in short to medium time frames, plant resilience and productivity under global warming are likely driven by host-associated microbiomes (Fig. 2a). Our argument is based on the divergence of timescales for physiological, ecological and evolutionary responses of plants and microbes, the extremely short replication and evolutionary time frame of microbes, and the emerging concept of the 'holobiont', that is an assemblage of a host and the many other species living in or around it, which together form a discrete ecological unit (Zilber-Rosenberg & Rosenberg, 2008; Lyu *et al.*, 2021). In addition, recent findings show that the same plant phenotype can be achieved either by altering the plant genome or by manipulating its microbiome (Ravanbakhsh *et al.*, 2021). Further, soil and plant microbiota have been shown to provide relief to plants from recurrent biotic stress events (e.g. pathogen attacks) by inducing plant resistance against invading pathogens. Extreme weather events (e.g. drought, heatwaves) are projected to increase in frequency and intensity. As microbiomes undergo more rapid eco-evolutionary adaptation to
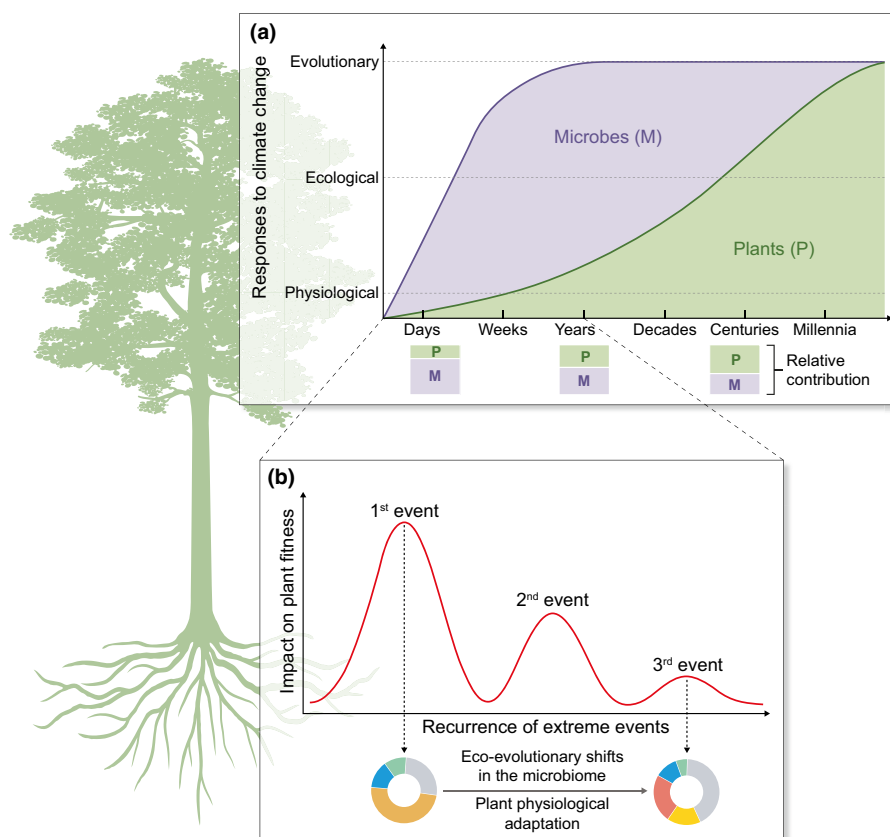
Fig. 2 Eco-evolutionary response and climate change adaptation. (a) Perennial plants live for centuries to millennia, and significant changes in temperature and water availability may require a compensatory physiological response (e.g. decreased respiration rate; production of stress alleviating hormones and metabolites). The large genome size (up to several thousand times larger than many bacterial genomes) with multiple copies of genes that provide similar phenotypes in plants provides flexibility for physiological adjustment under different environmental conditions (Hartley & Singh, 2018). Microbiomes can also contribute substantially to enzymes, hormones and metabolites for plants to cope with altered environmental conditions. On the contrary, the enormous diversity in the microbiome and the short replication times (minutes to days) mean that microbiomes have an enormous advantage in terms of ecological and evolutionary adjustments. There is evidence that not all microbes are active at the same time, and active and dominant populations vary within a microbial community in different seasons and climatic conditions. There is also evidence that associated microbes are able to sense their host's stress and respond quickly via changes in population dominance, provision of metabolites and priming the host physiological and immune responses (Liu *et al.*, 2020). Rapid replication rates in microbes mean that ecological responses in terms of a shift in the community can happen within hours to days with dominance of stress-tolerant microbial populations that can help plants to cope with climate changes. Fast replication rates also mean microbial components of the holobiont are more able to acquire new genes (horizontally and vertically) and mutate genomic traits to cope with climate change. Intimate association means some of these microbial phenotypic traits can directly benefit the host. Plant hosts do not have the advantages of such rapid ecological and evolutionary responses in the short and medium terms. However, in the long term, the plant community will also adopt eco-evolutionary mechanisms to adapt to climate change, but this will require centuries to millennia because of the slow rate of community shifts and the development of heritable traits. (b) Previous works have shown that plant and soil microbiome can develop, adapt and contribute towards plant resistance against the re-occurring pathogen attacks (Raaijmakers & Mazzola, 2016). Similarly, it is likely that in future with increasing frequency of drought and heatwaves, as projected under climate change, plant microbiomes can adapt (via eco-evolutionary mechanisms) and confer some resistance to drought/heatwaves to its plant host.

these recurrent events than plants, they may provide some immediate resistance and resilience to host plants (Fig. 2b). In the long term, a plant community is likely to achieve a similar level of eco-evolutionary adaptation to climate change (Fig. 2a). It should be emphasized that there are multiple potential pathways for plant microbial adaptation to climate change including those that are summarized in Box 2.

V. Conclusion and future perspective

Manipulating the plant–soil microbiome to increase plant productivity in the face of climate change has been recognized as a priority by many national and international policy agencies (Singh *et al.*, 2020b; Trivedi *et al.*, 2021). These interventions can range from direct manipulation of the plant microbiome, functional manipulation via land management practices and/or the use of probiotics. Through breeding, advanced genome-editing tools (e.g. CRISPR) and synthetic biology approaches (Geddes *et al.*, 2019), it will be possible to engineer microbe-friendly plants that release exudates, which promote specific beneficial plant–microbe interactions. The wild relatives of domesticated crops contain a reservoir of genetic diversity (Pourkheirandish *et al.*, 2020) including those traits that promote the assembly of distinct microbiomes that may support the plant adaptation to climate change (Pérez-Jaramillo

Box 2 Other possible mechanisms of plant microbial adaptation to climate change.

This article addresses a specific concept of climate adaptation, but there are other concepts that may also play important roles – some are briefly mentioned below:

(**1**) Response of biodiversity and its impacts on immunity and productivity. Climate change is expected to have a strong negative impact on plant and soil biodiversity (Maestre *et al.*, 2015). This can have a significant impact on primary productivity as increasing evidence suggests that increasing plant diversity is linked to increased primary productivity. Similarly, given the crucial role of the soil–rhizosphere microbiome and plant diversity on plant immunity and adaptation to abiotic stresses, a climate-linked decline in biodiversity can potentially impact both biotic and abiotic resilience of plant communities with significant consequences for adaptation. We postulate that increased plant diversity provides diverse pattern recognition receptor (PRR) repertoires that can recognize a range of microbe-associated molecular patterns (MAMPs), thus increasing the immune potential within an ecosystem. Systemic signals can then be passed from one plant species to others through volatiles (produced by both plants and microbes) or root exudates that influence plant adaptation and primary productivity (Weisskopf *et al.*, 2021). Legacy impact of management practices influences plant physiology by soil microbiome wherein monocrop and rotational plants showed significant differences in the expression of genes involved in plant hormone and immune response (Li *et al.*, 2019). We postulate that manipulating aboveground biodiversity will impact plant-associated microbiome diversity and create greater immunity and productivity (via enhanced nutrient cycling), thus leading to significant ecological gains. However, we have a limited understanding of the impact of climate change on the molecular interactions that drive the relationship between aboveground and belowground diversity.

(**2**) Response of ecosystem properties emerging from aboveground and belowground connectivity: both biotic and abiotic properties of the ecosystem are likely to respond simultaneously. How these changes will interact can have a substantial impact on plant adaptation abilities. For example, prolonged drought and warming can encourage plants to invest in root biomass or new and more robust association with mycorrhizal fungi to secure available water from a distance. Such phenotypic and biotic changes can have a significant impact on soil physical properties (e.g. porosity). Understanding how these biotic and physical changes can impact plant adaptability can better predict productivity and resilience. However, this will require integrating understanding at different temporal and spatial scales and across different dimensions of the systems, particularly the physical properties of the ecosystems.

(**3**) Plant cognitive abilities and gnosophysiology. It is proposed that plants possess cognitive abilities and can acquire, process and memorize information that can modify their response to future natural stimuli (Michmizos & Hilioti, 2019). Plants can extend their cognitive abilities to the environment via root influence and association with mycorrhizal fungi and other microbes that associate with them (Parise *et al.*, 2020). However, in the absence of brain and nervous system the way in which a plant cognitive system operates remains largely unknown. Well-established mechanisms of cellular and molecular learning and memory can provide a potential path for adaptation based on previous events (e.g. prolonged drought, heatwaves). However, a role and relative contribution of plant gnosophysiology in climate adaption needs the development of strong theoretical and experimental evidence.

Box 3 Key future research directions.

(**1**) Better understand the direct impact of climate change on the assembly and functions of the plant microbiome over space and time under multiple climatic scenarios (e.g. warming and drought individual and combined effects).
(**2**) Decipher the impact of climate change on plant physiology and the immune system: what are key changes in root exudates, photosynthates and immune systems? Obtain experimental evidence on how these changes may affect the plant microbiome assembly, activities, traits and ultimately the host functions.
(**3**) Identify changes in the composition of key signal and communication molecules and their interaction (*in vitro* and *in vivo* tests) and the response of microbes and, ultimately, the consequences for host functions and fitness.
(**4**) Improve understanding of the underlying genetics, biosynthetic pathways, regulation and precise biological roles of phytohormones modulated by arrays of climatic conditions and how these changes impact the assembly, functions, and plant–microbiome and microbe–microbe interactions.
(**5**) Define the timescale and frequency of events (e.g. heatwave, drought) required for eco-evolutionary adaptation in plant microbiomes and the degree to which these can provide climate resistance and resilience to the host.
(**6**) Obtain advanced fundamental knowledge about the molecular interplay driving plant–pathogen or plant–beneficial microbe interactions in a range of climate change scenarios, taking into account the community context.
(**7**) Develop approaches to manipulate the plant microbiome *in situ* to reduce the impact of climate change on primary productivity.

et al., 2018; Chen *et al.*, 2021). While the effectiveness of transplanting faecal microbiota in humans has been broadly demonstrated, research on the re-colonization of native soil bacteria of domesticated crops and their role in improving plant resilience to climate stress has not been fully explored.

Overall, our knowledge of the intimate and multifaceted plant–microbiome interaction and the consequences of plant fitness and productivity has started to emerge. However, how these interactions will respond to climate change at ecological, evolutionary, biochemical and molecular levels remains poorly understood and, in some cases, completely unknown. Future research should examine how these interactions change over time and space under multiple climate change scenarios (Box 3). A system-based, reductionist approach where both plant and microbial eco-physiological responses are measured with explicit consideration of time, multiple stresses and environmental conditions can unravel these interactions. Further efforts to obtain detailed and potentially predictive insights into plant–microbiome interactions are needed to develop new computational and modelling tools to predict the response of beneficial plant interactions to environmental stresses. This knowledge will facilitate predictions of the impacts of climate change on the plant-associated microbiome and will open new avenues for applied research to harness plant–microbiome interactions to improve the climate resiliency of plant communities.

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