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Shifting Environmental Conditions, Plant Microbes Stability, and Chemical Defense Responses: Emerging Trends

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ABSTRACT
The increasing speed of global environmental change, e.g. climate warming, precipitation regimes, severe droughts and flooding, and increasing anthropogenic disturbances have a far-reaching impact on plant-microbe interactions and plant defense chemistry. Ecosystems rely on these interactions to be functioning effectively, to be productive in crop production and to be resilient. Plants respond directly to environmental stressors, and the ecology and stability of the microbial community (microbiomes) inhabiting the rhizosphere, phyllosphere, and endosphere is also transformed by environmental stressors. Microbial symbionts like mycorrhizal fungi, fixation of nitrogen-containing bacteria and growth-promoting endophytes are major controlling factors in plant nutrition, stress resistance, and immunological competence. Environmental changes tend to alter the organization and activity of these microbiomes, which may undermine mutualistic advantages and change host defensesignaling pathways. Abiotic stress and microbial cues contribute to modulation of plants reacting with both constitutive and induced chemical defenses such as phytoalexins, volatile organic compounds, and reactive oxygen species. The knowledge of the impacts of stressors on microbial stability and the management of plant chemical defense is of a vital concern to sustainable agriculture and ecosystem stability. This review summarizes the current research on these interdependent dynamics, identifies existing knowledge gaps, methodological developments and future directions of research.
Keywords: Plant-microbe interactions, Environmental stress, Microbiome stability, Chemical defense, Climate change

INTRODUCTION

The interaction between plants and microbes is one of the primary factors of productivity and wellbeing of terrestrial ecosystems. Over millions of years, plants have also co-evolved together with a broad range of microorganisms that are colonizing external (rhizosphere, phyllosphere) and internal (endosphere) tissues, such as bacteria, fungi, archaea, and protists. Such microbial communities assist in nutrient uptake, hormonal balance, reduction of stress and activation of defense (Berendsen, Pieterse, and Bakker, 2012). Microbes, in turn, supply plants with carbon and provide niche conditions and develop dynamic and often mutualistic interactions.

The environmental conditions however are changing and are increasingly challenging the stability of these plant-microbe associations. Ecosystem homeostasis is destroyed by global climate change, which presents in the form of rising temperatures, changes in precipitation, high occurrence of extreme weather events, high atmospheric CO_2, and pollution (IPCC, 2014). These changes do not only impact on plant physiology, but on microbial abundance, diversity, and community makeup as well. The microbial communities in the soil which are critical in nutrient cycling and plant development are especially vulnerable to changes in soil moisture and temperature (Fierer et al., 2009). In like manner, microorganisms inhabiting the phytotrans have changing humidity and radiation levels which control colonization and activity. Microbiomes stability is essential in the persistence of useful plant activities. Microbial partners can also increase tolerance of the host to stress through various mechanisms in stable associations including induction of systemic resistance, hormonal regulation, and improved nutrient uptake (including but not limited to nitrogen and phosphorus) (Compant, Clement, and Sessitsch, 2010). As an illustration, the arbuscularmycorrhizal fungi (AMF) enhance drought tolerance through the improvement of water uptake, whereas endophytic bacteria promote antioxidant defense to hosts in response to salinity or heavy metals. Disturbances at such communities, either with environmental stress or land use alteration, have the potential to reduce the resilience of plants and cause greater susceptibility to disease and poor productivity.

To add to this complication, there are the chemical defense mechanisms of plants. Plants have a rich chemical defense against pathogen and herbivore invasion using secondary metabolites like phenolics, terpenoids, alkaloids, and small signaling molecules such as jasmonic and salicylic acid. Such compounds are defense as well as communication signals that influence the colonization and interaction of microbes (Schafer et al., 2009). Indicatively, some roots exudates may attract useful rhizobacteriawhich may cause resistance, whereas other metabolites may suppress the growth of pathogen.

Notably, the environmental stressors affect the synthesis of the chemical defenses by the plant, as well as the structure of the microbial assemblages. Drought stress tends to enhance the level of phenolics and reactive oxygen species, whereas heat stress can interfere with the signaling pathways and metabolic fluxes. Plant immunity can therefore be directly and indirectly modulated by abiotic stress as it changes the microbial surroundings in which the defense signal works. Through the elevation of CO_2, carbon distribution to the root exudates has been established to escalate carbon distribution to taxa of microbes, which may be either harmful or beneficial to the host (Drigo et al., 2008).

These dynamics directly pose food security and health of crops in agricultural systems. Already, intensive agricultural methods, such as fertilizer and pesticides, monocultures, and soil ploughing, pose a threat to soil microbial diversity. These factors together with climate stressors could lead to destabilized microbiomes, reduced plant resistance and a more significant dependence on chemical inputs to sustain yields. Increasing excitement, consequently, lies in the utilization of useful microbes and the microbiome stability as resilient cropping system strategies (Busby et al., 2017).

Although this has improved, there still exist massive gaps in our comprehension on how environmental variability can regulate the stability of plants and microbes and also how this responds to the chemical defense. Experimental manipulations usually tend to deal with single stressors under controlled conditions but natural environments deal with multifaceted stressors. Also, most of the information is obtained in model species, including Arabidopsis thaliana or important crop plants, and responses of many wild plants remain under-characterized. With the introduction of high-throughput sequencing, metabolomics, and network analysis software, there are new possibilities of systemic studies, but the issue of why something causes something is a methodological challenge.

The review examines the trends that are emerging in the interface of changing environmental status, stability between plants and microbes and chemical defence mechanisms. We look at the interaction between climatic and anthropogenic stress on microbiomes, and how plants adjust their own defense chemistry to stress, and how these interactions play off against each other. We emphasize both natural and controlled ecosystem case studies and comment on the consequences of sustainable agriculture and ecological stability.

2. Review in detail

2.1 Stress and Stability of the Microbiome Environment

Host factors and environmental conditions influence the composition of microbial communities that are related to plants. Examples of soil moisture and temperature gradient include soil moisture, soil temperature, and patterns of movements and distribution of microbes (Fierer et al., 2009). During drought, the bacterial diversity is likely to decrease, as the tolerance to drought is features of taxa. Extreme arid environments also eventually eliminate functional diversity because of the resilience of the spores in fungal communities, especially AMF. Switches between dry and wet in the phyllosphere are rapid, and therefore, affect colonization success and survival.

An increase in temperature changes the rate of metabolism and community structures, maybe to the advantage of opportunistic or stress-resistant microorganisms and disadvantage of sensitive mutualists. The cool-warm transitions may influence the nutrient cycling indirectly by changing the proportion between the microbial decomposers and the nutrient assimilators. In the case of nitrogen fixing bacteria, heat stress can impair the symbiosis effect leading to a decreased level of nitrogen uptake into the plant. Microbiomes are further disturbed by anthropogenic pollutants which include heavy metals and agrochemicals. Metals, such as cadmium and lead, interfere with membrane system and enzyme systems of the microbes, decreasing the total microbial biomass and diversity. The antimicrobial impacts of pesticides may be nonspecific leading to the reduction of useful taxa along with pests. Excessive use of fertilizers changes the nutrient dynamics of soil, discriminating in favor of copiotrophic but suppressing oligotrophic and symbiotic organisms.

Plants have constitutive and inducible defense. Structural barriers such as cuticles and basal defense of defensive metabolites are constitutive defenses and they are always present. Activation of inducible defences in response to stress or attack may be mediated through hormonal signal pathways.

Some of the important signaling molecules of a chemical defense are:

- Salicylic acid (SA): This is linked to resistance to biotrophic pathogens.
- Jasmonic acid (JA): It is mostly implicated in antagonism of necrotrophs and herbivores.
- Ethylene (ET): Is an interactor with SA and JA, and regulates various stress responses.

Under abiotic stress, those are produced as secondary metabolites that can keep off herbivores, prevent microbial pathogens, and serve as antioxidants (in the case of flavonoid, terpene, and alkaloid). As an illustration, phenolics tend to grow in stress in UV radiation, which provides photoprotection, in addition to affecting the colonization of the microorganism at the phyllosphere.

Drought and salinity stress often increase the production of antioxidants and the flux of the phenylpropanoid pathway that can reinforce the abiotic stress tolerance and pathogen resistance. Chronic or severe stress, however, may inhibit the process of defense activation through allocation tradeoffs with primary metabolism.

2.2 Interaction between Microbiomes and Plant Defenses

Microbial symbionts have the ability to regulate plant defense. Positively advantageous rhizobacteria like Pseudomonas fluorescens are able to prime systemic acquired resistance (SAR), which make plants more sensitive to the attack by the pathogen. AMF tend to cause global alterations in the levels of host hormones, making them more tolerant to root pathogens and enhancing their ability to gain nutrients.

On the other hand, pathogenic microbes are able to repress host defense mechanisms with effecter proteins that regulate signaling pathways. Mutualists are however likely to buffer the plants as they are likely to compete against the pathogens in terms of space or they may activate the host immune systems.The stress on the environment is complicated by the fact that it alters not only ecological communities but also plant defense reactions. High CO2 can also tend to allocate more carbohydrates, which can lead to root exudation and microbial activity, although it can also decrease nitrogen levels in leaves, changing the feeding habits of herbivores and the interactions between plants and insects. SAR and JA pathways may be disrupted in case of climate extremes and may result in the impaired immunity.

2.3 Case Studies

Drought Stress:

Drought tends to lower the diversity of microbes in soil and Actinobacteria drought-tolerant is predominant. Drought in legumes decreases nodulation efficiency affecting the fixation of nitrogen. At the same time, abscisic acid (ABA) buildupas a result of drought overlaps with the pathways of defense, in some cases repressing the defense of pathogens by SA.

Heat Stress:

Heat waves interfere with the microbial colonization of roots and leaves, preferring thermophilic microbes. An increase of temperature can also hasten the plant respiration and result in oxidative stress. The rate of AMF colonization has been observed to be decreased by heat stress which can decrease mutualistic benefit.

Pollution Impact:

Heavy metal contamination decreases the biomass and functional potential of microbes. However, there are metal-tolerant microbes which confer tolerance to plants either by sequestering metals or triggering detoxification pathways. Plant secondary metabolites also have the ability to chelate metals hence reducing their toxicity but in some cases at the cost of growth.

2.4 Advances in Methodology

Metagenomics, metatranscriptomics and metabolomics techniques have enabled a more comprehensive study of plant-microbe-environment interactions. These methods uncover the functional potential, alterations in gene expression, and fluxes of metabolites that form the basis of stress reactions. Network analysis packages assist in the determination of keystone taxa and metabolite hubs that are of critical stability. Nevertheless, there are still some issues: the need to connect correlation with causation in complex microbial networks; the need to distinguish between the response to stress and the response of a microbial community; and the need to extrapolate the results of the laboratory studies to the field.

3. Conclusions

The multifaceted pressure that the environment change is placing on plant systems and on the associated microbes and chemical processes underlying defense and adaptation has been observed. Plant-microbe interactions are fundamentally important in determining the health of the ecosystem, agricultural productivity, and the ability of vegetation to respond to an increasingly changing climate.

Flora communities of plants are homeostatic yet exposed to external pressures. These communities are greatly restructured by soil moisture change, thermal extremes, pollutants and altered nutrient cycles. Although a few of the microbes display survival or even flourishing in stressful conditions, numerous mutualistic taxa at the core of plant health including nitrogen-fixing bacteria and AMF are upset by changes in the environment. The effect of destabilizing the microbiomes is not only on individual plants but also on the nutrient cycling, soil structure and the plant community dynamics.

External stressors also regulate plant chemical defensesystems which are evolved in coordination with microbial partners and antagonists. Alterations in signal transduction and at least one metabolite production by stress can reinforce some yet weaken others. Indicatively, drought can increase antioxidant defenses and inhibit SAR, thus changing the pathogen susceptibility. The cross-talking between the signaling pathways by means of such molecules as SA, JA, ET and ABA is complex and environment-dependent. Consequently, the defense responses of plants are not fixed responses but they are dynamically tuned to integrated biotic and abiotic interactions.

Finally, the phenomenon of environmental change creates new invisible yet so essential relations between plants and their microbial partners and changes the chemical defenses which developed to survive. These developments also question the historic paradigms of plant health and require multi-disciplinary research that cuts across the fields of molecular biology, ecology and environmental sciences. Since the planet is still warming and the ecosystems are faced with unprecedented perturbations, the study of these complex, interlinked systems is necessary to maintain biodiversity, secure agriculture, and prevent ecosystem dysfunction.

4. Future Direction

4.1 Integrated Multi-Stressor Research

The systematic study of combined stressors is one of the significant directions of research in the future. The majority of the present research is focused on individual stress factors e.g. drought or heat, but in a natural ecosystem, plants and microbes are under simultaneous stresses e.g. drought and heat and pressure of pathogens. Future studies must be factorial and long-term field manipulations to study the interactions between stressor combinations as either synergistic or antagonistic.

Ecological relevance will be enhanced by integrated environmental chambers, sophisticated phenotyping platforms, and field experiments with the addition of soil moisture and temperature control. These are to be complemented with high temporal resolution of microbiomes and plant metabolomes to record both dynamic changes in communities and chemicals.

4.2 Mechanistic Understandings of Microbiome-DefenseSignaling

It is important to decipher mechanistic interplay of microbiome composition and plant defensesignaling. The existing knowledge is often based on the correlations. The work of the future must use gene editing (e.g., CRISPR-Cas9) and synthetic microbial communities to establish causal relationships. As an example, a specific removal or addition of selected microbial taxa can be used to understand the effects of those microbes on the JA, SA, and ET pathways during stress.

The single-cell transcriptomics will reveal the cell-type specific reactions of the plant, and the combination of metagenomics and proteomics and metabolomics (multi-omics) will de-goolaginize the complicated regulatory networks. These integrative analyses will require advanced bioinformatics modeling of cross-kingdom interactions.

4.3 Evolutionary Views about Adaptation

The other frontier is to understand the evolution of plant-microbe systems in a changing environment in rapid time. Adaptive responses can be demonstrated in generations when stress gradients are present in evolutionary ecology experiments in which selection lines of plants and microbes are used. The relevant questions that should be studied include whether microbiomes are co-adaptive to environmental pressure on host plants and whether a rapid evolution of microbiomes helps to buffer host responses to environmental challenge.

Comparative analyses of plants with and without phylogenetic diversity and their microbiomes will provide general patterns and exceptions. This can recognize robust plant- microbe assemblies that can be used to enhance crops.

4.4 Applications and Agronomic Strategies in the Field Scale

Applicability of laboratory findings to the field is crucial to agriculture. Future studies are needed to evaluate microbiome based interventions in different environmental conditions and in different soil types and crop varieties. These involve the assessment of microbial inoculants (biostimulants and biofertilizers) which improve stress tolerance and how the native microbiomes can affect inoculant success. Agronomic practices like cover cropping, minimal tilling, organic supplements and selective irrigation ought to be considered regarding their ability to stabilize microbiomes and decrease the use of chemical pesticides in addition to strengthening the chemical barriers of plants.

Historically, breeders focused on the yield and disease resistance but did not pay much attention to the interactions of microbiomes in plants. As the genomic tools emerge, there is the possibility of intentional breeding programs to choose traits which are conducive to the recruitment of specific microbes and resistance to stress. Candidate loci to be used in breeding will be identified by genomewide association studies (GWAS) that associate genetic variation in plants with microbiome composition and defense response phenotypes. Future perspectives involve the creation of cultivars with desirable exudate profiles and strong signaling pathways in response to environmental gradients, thus aiding microbial stability as well as natural defense chemistry.

4.5 Predictive Modelling and Big Data Integration

As multi-omics data is accruing, predictive models that predict plant-microbe-environment interactions are required. It is possible to combine soil physicochemical data, climate parameters, microbial community structure, and plant transcriptome to forecast disease outbreak risk or stress tolerance efficiency in the approach of machine learning and systems biology.

The dynamic models will facilitate the decision support of agriculture and ecosystem management. Structures that involve remote sensing and ground-level biological data can extrapolate small-scale (plot) to large-scale (landscape) knowledge. The policy should be informed by scientific findings to reduce the effects on the environment. Further directions involve working with policymakers and land managers to help them become acquainted with knowledge about the stability of the microbiome and the defenses of plants and apply them in practice to make the ecosystem resilient. This can involve incentives on practices to conserve soil biodiversity, pollution control mechanisms, and agroecosystem micromanagement frameworks of monitoring microbial health of agroecosystems.

4.6 Moral and Social Aspect

Lastly, we should focus on ethical aspects like fairness in accessing technology in microbiomes, privacy of information in genetic research as well as preserving knowledge by indigenous agriculture. Joint studies with the local communities, farmers, and other stakeholders will make sure that innovations are acceptable by the society, economically viable, and environmentally sustainable

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