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Advances in understanding plant–microbe symbiosis in stressful environments

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Abstract In recent years, the interplay between plants and microbes has gained significant attention in understanding resilience mechanisms under stressful environmental conditions. Plant-microbe symbioses, including mycorrhizal associations and beneficial bacteria interactions, play crucial roles in enhancing plant tolerance to abiotic stresses such as drought, salinity, and nutrient deficiency. Advances in molecular and genomic technologies have facilitated the exploration of these complex interactions, revealing the underlying genetic and biochemical pathways that mediate plant responses to stress. Studies have demonstrated that beneficial microbes can modulate plant hormone levels, activate stress-responsive genes, and enhance nutrient uptake, thereby improving growth and productivity in adverse conditions. Furthermore, the concept of the phytomicrobiome emphasizes the collective influence of microbial communities associated with plants, highlighting their dynamic and interactive nature. This review synthesizes recent findings on the mechanisms of plant-microbe interactions and their implications for agricultural sustainability in the face of climate change. By leveraging these insights, researchers aim to develop innovative strategies for enhancing crop resilience and productivity, ultimately contributing to food security. The integration of microbiome management in agricultural practices holds promise for improving crop performance under varying environmental stressors, paving the way for a new paradigm in sustainable agriculture.

Keywords: Plant-microbe interactions, Abiotic stress, Symbiosis, Phytomicrobiome, Stress tolerance

Introduction to plant–microbe symbioses

Plant–microbe symbiosis refers to the mutual exchange of beneficial substances between plants and microbes. These interactions occur ubiquitously and shape ecosystems worldwide (Lino-Neto and Baptista, 2022). Although important for carbon and nutrient cycling (Imam *et al.,* 2016), symbiotic interactions are historically underrepresented in ecosystem flux models. Indirect carbon losses from sustaining microbial partnerships may equal one- to sixfold the amount allocated directly to mycorrhizal fungi. Understanding

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symbiotic relationships is critical to both ecosystem function and the global carbon cycle.

The rhizosphere: A dynamic interface

The rhizosphere, the narrow region of soil influenced by root exudates and inhabited by a variety of microorganisms, is one of the most dynamic interfaces on Earth. Many studies have demonstrated the importance of beneficial microbes for plant growth and health assumptions in relation with nutritional regimes (El Amrani, 2022). The rhizosphere is a dynamic interface where living biotic and physicochemical abiotic zones interact to form a holistic environment (York *et al.,* 2016). Plant communities can yet experience changes on time scales ranging from annual and seasonal to daily and even hourly. Measurable parameters of the rhizosphere that change with time include root elongation rates, exudate diffusivity, soil water content, and microbial cell division, growth, and dispersal rates. Circadian regulation of a broad set of plant processes, including defense signaling and glycogen metabolism has been confirmed at the gene expression level (Raaijmakers *et al.,* 2009). A knock-on effect on gene expression and activity by a set of root water channels (aquaporins), which influence water flow in the rhizosphere and root osmotic uptake capacity, has direct consequences on both the availability and solubility of nutrients mediating water percolation through the soil. Both the disassembly and reassembly of plasmodesmatal membranes, and the amount of root sugars exuded in a diurnal pattern also vary with environmental conditions. Diurnal fluctuations in nutrient availability and consequently uptake are mediated by differential root, rhizosphere, and bulk soil processes that have received little attention. Nutrient uptake rates often exceed those predicted by mass flow at night, and can account for 10–30% of total assimilation for cations and anions following the early daylight maximum. Although there is a lower transpiration demand at night, rhizosphere bacteria that mineralize soil available nutrients and the microbial grazers that regulate their activity are generally more active at this time. Circadian regulation of nitrate assimilation occurs in a complex interplay between transcriptional and translational levels, and also varies with the physiological status of the plant. The dynamic nature of the rhizosphere makes it an external manifestation of plant status, an extension of the plant’s genetics, and relevant to the long-standing definition of the rhizosphere as the zone of soil influenced by the root.

Microbial diversity in the rhizosphere

The rhizosphere constitutes the narrow zone of soil surrounding plant roots where interactions between plants and soils occur (Hartman and Tringe, 2019). This narrow zone acts as a primary interface of interaction between plants and their surrounding environment, playing a critical role in shaping the plant microbiome (El Amrani, 2022). The rhizosphere constitutes a hotspot for microbial diversity and activity, sustaining some of the highest microbial densities in soils. Members of nearly all microbial taxa (bacteria, fungi, and protists), as well as diverse animals (e.g., micro-arthropods, nematodes), inhabit this narrow interface.

Root exudates and microbial interactions

Root exudates constitute a primary conduit through which plants recruit microorganisms to the rhizosphere and establish symbiotic associations. The capacity of host plants to actively colonize the rhizosphere or rhizoplane by their root microbiome is governed by the physico-chemical characteristics of root exudates, which differ among cultivars and depend on plant developmental stage and the abiotic environment. Aerial and subterranean microbiomes are highly differentiated microbial ecosystems. The root microbiota shares greater similarity with communities of the surrounding soil than does the phyllosphere; thus, the rhizosphere is an exclusive site for recruitment of soil microbes. The microbial grassroots strategies employed to colonize plants and establish rhizosphere competence are oligotrophic and competitive, involving secretion of antibiotic compounds, biofilm production, and activation of type III secretion systems and phosphonate metabolism in response to plant signals (Hartman and Tringe, 2019). Bulk soil is the main reservoir of rhizospheric and root-colonizing microorganisms. Rhizoplane and root-acquired microbes originate predominantly from soil and differ from the surrounding non-rhizospheric soil, with enrichment of bacteria belonging to proteobacteria, actinobacteria, and some bacteroidetes and crenarchaeota. Rhizosphere and root microbiota, particularly bacterial clades, are shaped by stimulus-response mechanisms leading to microbial succession. The host plant plays a key role in modulating temporal patterns of microbial colonization, particularly during early stages of root development. Plant-mediated microbial selection is achieved through variations in root exudate patterns (Pan *et al.,* 2022).

Mechanisms of symbiosis

Although the mechanisms involved in symbiosis remain largely unknown, the formation of symbioses between plant roots and beneficial microbes' phyla requires molecular recognition between the roots and the microbe. Structural and functional adaptations lead to the establishment and maintenance of symbiotic associations (Wang and Song, 2022). Several microorganisms interact with the roots, and different molecular mechanisms regulate these interactions. Roots first recognize microbes to establish symbiosis and maintain this through continuous cross-talk and exchange of molecules. Examples include the legume–*Rhizobium* symbiosis, where legumes establish symbiosis with nitrogen-fixing bacteria; the mycorrhizal association between roots and fungi; and the epiphytic and endophytic interactions of sugarcane with diazotrophic bacteria. Root colonization is a key early step in all interactions, enabling microorganisms to penetrate plant tissue and promote the establishment of those associations that provide a direct advantage to the plant (Meena *et al.,* 2017).

Molecular signaling pathways

Symbiotic relationships between plants and microbes form the basis for living organisms to thrive on earth under diverse ecosystems. The most ubiquitous, economically advantageous, and ecologically pivotal are those nitrogen-fixing, mycorrhizal, and other rhizosphere plant–microbe interactions. These non-obligate symbioses promote plant growth and survival; simultaneously, they uphold ecosystem function and agricultural sustainability (Smith *et al.,* 2015). The rhizosphere comprises the soil zone under direct influence of the plant root and surrounding microorganisms; it is the crucial interface, from the molecular to the ecosystem level, at which these symbioses form and operate. The propagation of symbiotic associations in the rhizosphere depends on a series of cascaded molecular signaling events. The initiation of symbiotic relationships relies on the emergence of specific signal molecules upon surface-recognition events, followed by the delivery of key symbiotic effectors to the partner cell. Flavonoids secreted by legumes regulate nod gene expression by *Rhizobium* bacteria during symbiosis development. Rhizobial lipochitooligosaccharides (Nod factors) are perceived by plant receptors which trigger nodule development and enhance growth, particularly under stressful environmental conditions. Chitooligosaccharides derived from rhizobial exopolysaccharides activate the plant immune system and confer disease resistance; these compounds play a major role in balancing defense responses during the establishment of symbiotic interactions.

Nutrient exchange mechanisms

A pivotal aspect enabling plant–microbe symbiosis is nutrient exchange between partners, sustaining the mutualistic relationship and facilitating co-evolution as a united entity. The meristematic structures of symbiosis function as transport modules, with nutrient exchange and support for meristem activity as principal drivers. Consequently, the molecular underpinnings of both nutrient transfer and control of meristematic processes are receiving increasing attention. The mechanisms involved are diverse because the specific requirements of each partner depend on factors such as the type of association, the identity of the partners, their nutritional status, and the conditions associated with the host environment and behavior. In the context of root nodule symbiosis (RNS), ammonium is transferred from bacteroids to the plant, while dicarboxylic acids — malate, fumarate, or succinate — are supplied to the bacteroids. In arbuscular mycorrhizal (AM) symbiosis, fungi exclusively deliver phosphorus, nitrogen, and sulphur to the plant but also acquire water and micronutrients from the soil in exchange for carbon. These reciprocal exchanges underpin mutualistic stability, with partner sanctions limiting fungal colonization in response to imposed nutrient flux adjustments. The operation of such sanctions resembles a biological market and plays a crucial role in sustaining stable mutualism. Furthermore, AM fungi enhance drought resistance by aiding in the maintenance of root water uptake and improving water use efficiency (Bapaume and Reinhardt, 2012). Plants have evolved numerous strategies to overco me nutrient deficiency, of which AM symbiosis represents a prominent example. Specific transporters from either the plant or the AM fungus mediate transmembrane uptake of soil nutrients into the symbiotic interface. The nutrient status of the symbiotic partners can influence colonization levels, indicating a regulatory link between nutrient availability and symbiotic establishment. In mycorrhizal plants, specialized transporters dedicated to symbiotic nutrient acquisition have frequently been identified. The formation of AM symbiosis typically correlates with enhanced expression of $NO3^-$ transporter genes, reflecting an increased nitrogen requirement in symbiosis. Despite progress in characterizing phosphorus transporters in AM fungi, further investigation is necessary for nitrogen transporters and for elucidating the pathways of nitrogen uptake and transfer within the symbiosis. A better understanding of phosphorus and nitrogen coordination is essential to optimize plant growth and to harness full mycorrhizal benefits. Most prior research has focused on model species such as *Medicago truncatula, Lotus japonicus,* and *Oryza sativa*; consequently, studying the symbiotic nutrient transport system in cultivated crops remains a priority. Advances in 'omics' technologies now open promising avenues for dissecting the regulatory networks underpinning nutrient signaling associated with AM symbiosis (Rui *et al.,* 2022).

Impact of environmental stress on symbiosis

Environmental stressors such as drought and salinity influence plant–microbe symbioses through multifaceted effects on microbial activities, symbiotic efficiency, and host physiology (Khan, 2023). A broad number of microbes also modulate the impact of abiotic stress on their host plants via diverse mechanisms, underscoring the potential of these interactions for sustainable agriculture under severe environmental conditions. Soil moisture affects not only the composition of the rhizosphere bacterial community but also functional parameters such as indoleacetic acid (IAA) production and motility (Shree *et al.,* 2022).

Drought stress and microbial adaptation

Drought stress presents a significant challenge to agricultural production worldwide, affecting the productivity of major crops such as maize, wheat, rice, and soybean. Developing drought-tolerant crop varieties is complicated by the multifaceted impact of water stress on plant growth, the regulatory sequences involved in drought responses, and the specific genes mediating tolerance. Advances have enabled genome-wide screening for drought-related markers, facilitating marker-assisted selection and genome-wide association studies to identify and introgress alleles that confer tolerance into elite cultivars. High-throughput sequencing techniques contribute to identifying candidate genes responsive to drought, while strategies such as the exogenous application of melatonin have proven effective in improving seed germination and seedling growth under water-deficit conditions in plants like soybean and wheat, by enhancing photosynthesis and antioxidant enzyme activities (Petrushin *et al.,* 2023). Microorganisms inhabiting the rhizosphere, the soil environment influenced by plant roots, are pivotal in facilitating the growth of terrestrial plants and enabling them to withstand diverse abiotic stresses. The rhizosphere is regarded as a vital microhabitat where complex microbial communities develop, engage in intense interactions, and significantly impact ecosystem processes at various trophic levels. These microorganisms have been demonstrated to alleviate abiotic stresses, promote nutrient acquisition, and contribute to sustainable crop production. Harnessing plant–microbial interactions under changing climatic scenarios offers promising opportunities for achieving environmental sustainability and securing food provision (Poudel *et al.,* 2021). Plants modulate belowground microbial communities during drought, with soil bacterial communities responding to both plant presence and drought, while soil fungal communities are primarily influenced by plant presence. Root fungal communities experience pronounced changes under drought, whereas root bacterial communities are less affected. The proportion of water-stress opportunistic bacterial taxa increases following drying phases but declines in soils with established vegetation, indicating that plants influence soil and root-associated microbial drought responses through tight linkages. These interactions have substantial consequences for ecosystem functioning, nutrient cycling, and plant health, with post-drought trajectories varying according to plant habitat and microbial group (Veach *et al.,* 2020).

Salinity effects on plant–microbe interactions

Sea level rise due to climate warming will increase plant exposure to soil and water salinity (Otlewska *et al.,* 2020). Saline soils cover more than 800 million hectares worldwide, and their spread is increasing rapidly (Meinzer *et al.,* 2023). Microbial symbiosis has been shown to improve plant tolerance to salinity stress (Acuña-Rodríguez *et al.,* 2019). A portrait of the molecular dialogue within *Pseudomonas mandelii* IB-Ki14, which protects wheat plants against the toxicity of chloride and maintains osmotic balance under salinity, was derived from large-scale transcriptome studies. To determine the roles of microbial symbionts in plant salt tolerance, lettuce plants (*Lactuca sativa*) subjected to saline stress were inoculated with a consortium of halotolerant rhizobacteria and root-fungal endophytes from Antarctic vascular plants. Physiological and biochemical mechanisms involving proline accumulation and expression of the NHX1 gene controlling sodium transport were characterized, and the overall effect on plant biomass was evaluated, providing insight into microbial contributions to crop productivity in saline soils.

Temperature extremes and symbiotic relationships

Symbiotic interactions between plants and microbes encompass a broad spectrum of relationships classified as mutualism, commensalism, and parasitism. Mutualistic associations provide supply or access to life-supporting resources and provisioning for defense or other benefits (Dastogeer *et al.,* 2022). Such interactions are critical drivers of ecosystem functioning, maintenance, and development and therefore are vital to the health of the biosphere as a whole. As agriculture faces severe challenges to continuing productivity and stability brought about through environmental change and escalating levels of stress, a particular focus has been brought to understanding symbiotic systems and associated dynamics. Amongst the numerous microbial symbionts of plants, the most common are arbuscular mycorrhizal fungi (AMF), encircling approximately 80% of terrestrial plants. Symbiotic associations of microbes directly with plants are generally established in the zone surrounding the root where the most intimate interactions occur, namely the rhizosphere and root endosphere. Through complex signaling, recruitment, crosstalk and exchange of metabolites and nutrients, a sustainable biological platform and environment is established whereby the plant and microbial symbionts are able to foster and support one another within the soil environment. Within this symbiotic system, cooperation between plants and microbes enhances the collective fitness of such partnerships in their respective ecosystems (Shree *et al.,* 2022). Such interactions play a critical role in driving the success and stability of contemporary natural ecosystems and of the vast majority of commercial agricultural systems worldwide.

Genomic insights into plant–microbe interactions

High-throughput sequencing technologies have revolutionized the investigation of plant–microbe interactions, enabling detailed investigation of the underlying genetic bases (Imam *et al.,* 2016). As sessile organisms, plants have evolved complex strategies to cope with environmental challenges by shaping rhizosphere microbiota. Such assemblages can greatly enhance plant salt tolerance through symbiotic interactions; although the genetic factors controlling recruitment and regulation of beneficial microbiota remain poorly explored. The recent development of high-throughput sequencing techniques facilitates identification of stress-resilient beneficial strains and dissecting underlying genetic bases (Wang and Song, 2022). Both roots and the surrounding soil comprise a crucial habitat for microbes that can create dynamic associations with their hosts. Microbiotas, which are recognized as an extended plant phenotype, have therefore attracted considerable interest in efforts to develop solutions for sustainable agriculture and food security. Plant-mediated recruitment of specific microbes under salt stress is considered to constitute an adaptation of ecological importance. Studying the genes involved in this process will provide fundamental insights into plant interactions with their microbiota and facilitate development of novel and cost-effective microbial approaches to combat salt stress. Various omics techniques offer a useful approach to dissecting the complexity of plant-mediated regulation at the molecular level. Genomics provides a robust framework, enabling evolutionary patterns and genetic variation to be analysed in order to identify genomic regions and candidate genes relevant to particular interactions. Appropriate identification and investigation of comparative genomic resources (such as loci under selection and segmental duplication events) also provide insight into multidisciplinary gene functions, which underpins genetic improvement of plant–microbiota interactions.

Genomic approaches to study symbiosis

The advances in genomic technologies have paved the way to dissect the components of plant and microbial genomes that govern the interaction mechanisms that underpin plant–microbe symbiosis. Plants host a genetic repertoire of plant growth promoting (PGP) traits, which mediate direct and indirect interaction with the symbiotic microbiota (Wang and Song, 2022). Concurrently, the microbial partners encode physiological and biochemical properties ranging from nitrogen fixation to modulation of plant hormonal homeostasis and mineral solubilisation. The interaction mechanisms largely revolve around biotic communication signals, which trigger cascades of events that culminate into symbiotic association (Imam *et al.,* 2016). The symbiosis involves complex and multifarious cascade of regulatory signalling pathways. Both symbiotic partners are genetically equipped with determinants that encode the functional components that coordinate the functional synergy of the symbiotic interaction.

Functional genomics of symbiotic partners

Functional genomics provides a powerful platform for characterizing gene functions and regulatory mechanisms underlying the establishment of plant–microbe symbiosis. Comparative genomics and transcriptomics reveal a core regulatory network underpinning rhizobial symbiosis. In this interaction, rhizobia colonize host legume roots and establish intracellular infection threads, prompting nodule organogenesis for nitrogen fixation. Microarray and RNA-sequencing analyses of model legumes (*Lotus japonicus* and *Medicago truncatula*) and alfalfa identify common symbiotic genes and candidate regulatory elements (Wang and Song, 2022). Free-living rhizobial cells become motile in response to plant-secreted flavonoids and undergo chemotaxis to the root surface, initiating nodulation (Hacquard *et al.,* 2016). Microarrays of Bradyrhizobium japonicum under chemotaxis-inducing conditions reveal a distinct set of chemotaxis-related genes. Nod factors trigger early signaling changes in roots, leading to transcriptional reprogramming and nodule development. The Nod factor receptor induces macroevolutionary shifts from immunity to symbiosis responses, facilitating infection and nitrogen fixation.

Metabolomics in plant–microbe symbiosis

Abiotic stress phenomena such as drought and flooding present a growing challenge to both natural and managed plant communities. Microbial partnerships have long aided plants in overcoming these challenges, and emerging "omics" methods offer an increasingly sophisticated window into these relationships. Recent meta-analyses have delineated broad patterns in microbial response to drought, salinity, and high and low temperature extremes. Abiotic stress tends to induce significant shifts in the composition, structure, and activity of the plant microbiome, and many specific microbial traits or genes that are important in stress adaptation have been identified. Host plant phylogeny, functional traits, and compartmentalization may mediate the strength of this stress response, while enhanced sampling of both commonly studied and understudied ecosystems promises to both broaden and clarify the conceptual framework for plant–microbe–environment interactions. The rhizosphere is the narrow zone of soil surrounding plant roots and a key zone for plant–microbe interactions to occur. The rhizosphere microbial community acts as an extension of the plant genome and is continually shaped by plant development and environmental stimuli. Direct exchange of resources occurs between the plant root and the rhizosphere microbiota, and many microbes enhance host plant stress tolerance and overall plant performance. The plant's extended genomic capacity also affects broad levels of ecological function (Carper *et al.,* 2022). Clearly, the centrality of the rhizosphere for plant–microbe symbiosis can be viewed across diverse spatial, taxonomic, functional, and temporal scales.

Metabolite profiling techniques

The main metabolomic analytical interfacing platforms used in plant–microbe symbiosis studies are nuclear magnetic resonance (NMR), direct mass spectrometry (MS), as well as hyphenated techniques such as liquid chromatography-mass spectrometry (LC–MS) and gas chromatography-mass spectrometry (GC–MS). Each platform offers specific advantages and limitations; the selection depends mainly on the sample matrix and study aims. For instance, the high sensitivity (low detection limits) of MS-based methods often makes them the best choice when analyzing samples characterized by a single compound at a low concentration. Both GC–MS and LC–MS are therefore preferred because the hyphenated technique provides enhanced chromatographic separation of isomers or isobaric compounds before MS detection. On the other hand, pre-separation in GC entails derivatization to ensure that the compounds of interest are volatile and thermally stable at the injector temperatures. LC–MS has a simpler sample preparation step, typically only filtration and/or dilution, whereas GC–MS requires many more pre-analytical steps (Piasecka *et al.,* 2019).

Role of secondary metabolites in symbiosis

Sessile plants have evolved multiple mechanisms to guarantee adaptation to environmental changes. Among these, biosynthesis of secondary metabolites enables local and long-distance chemical communication (Rizaludin *et al.,* 2021). Chemical environment is a major determinant in recruitment of symbiotic partners and defines identity and specificity of the symbiotic system. Secondary metabolites contribute in plant-microbes interactions under adverse conditions (Santisree *et al.,* 2019). Specialized plant metabolites correspond to compounds that plants produce to achieve flexibility and fine-tuning of plant chemical and physiological environments to face diverse environmental conditions. They mediate communication between partners of the symbiotic system, allowing recognition of potential partners, development of the symbiotic program, and accommodation of microbes within host cells. Secondary metabolites protect partners from detrimental effects of various stresses by scavenging free radicals and reactive oxygen species, chelating toxic metals and ions, and preserving cell integrity. These specialized molecules modify surrounding environment and regulate responses to stresses, including bio-elicitor signaling, allelopathic effects against pathogens, protection against biotic and abiotic cues, and assembly of symbiotic microbial community.

Microbial community dynamics

The concept of microbial communities has attracted significant attention. Community succession and assembly rules are frequently examined in relation to N das, “keystone species,” or the stochasticity of community dynamics. Despite progress, critical questions remain concerning community assembly and succession. What determines when communities stabilize or continue to change? Are there fundamental assembly rules or driving forces? Why does community succession sometimes appear cyclic? Addressing these questions is particularly important. In the rhizosphere, microbial succession may follow a cyclic pattern arising from the system's intrinsic dynamics, with stochastic niche breadths playing a key role. The community becomes increasingly consistent over time in response to plant species. The concept of a "core microbiome" is increasingly accepted, replacing the "everything is everywhere" hypothesis (Khan, 2023). Microbial communities depend strongly on the host, even if many microbes are common generalists (Lareen *et al.,* 2016).

Community assembly in the rhizosphere

Microbial community assembly is a key challenge for linking biodiversity with ecosystem functioning, and the rhizosphere is an ideal system in which to address such predictors, given its high microbial diversity and evidence for distinct co-existing ecological strategies. Studies in soils have documented a succession pattern, whereby communities change continuously with time. This temporal signature is described by a negative exponential model, indicating that change is highest during the early stages of succession and slows towards a predictable stable state. Changes in the similarity of two communities over time, however, have received little attention. This study tests the hypothesis that the rate of change in similarities between microbial communities behaves similarly to taxonomic succession. Root exudates support a rhizosphere effect for a broad diversity of bacteria and fungi that clearly differ from communities found in neighbouring bulk soils. The rate of root colonization and extent of bacteria increases with root developmental stage (Rüger *et al.,* 2021). Few fungal root colonizers are exclusive to a rhizosphere stage, but transition the soil-torhizosphere at an early seedling stage where they exploit the developing rhizosphere and further proliferate inside the root. Bacteria and fungi increased in abundance during transition from soil to rhizosphere and the main driver for microbial assembly is the plant root system (Matthews *et al.,* 2019).

Influence of plant type on microbial communities

A significant number of studies indicate that more affinity exists between the plant type and the microbial community than the location region—i.e., the plant species plays a major role in structuring the microbial community (Jones *et al.,* 2019). More than 6000 cultured bacteria, mainly bacteria of the genera *Pseudomonas, Streptomyces,* and *Agrobacterium*, colonize the rhizosphere. Numerous microbial communities exhibit mutualistic and synergistic interactions with their plant host. An example of a mutualistic interaction is the mycorrhizal association; an example of a synergistic interaction is the production of extracellular enzymes such as acid phosphatase, urease, glucosidase, protease, and deaminase, which facilitate the solubilization of insoluble nutrients and their supply to plants.

Biotechnological applications of plant–microbe symbiosis

Agricultural productivity is increasingly hindered by abiotic stresses such as high salinity, drought, high temperature, heavy metals, and ultraviolet-B radiation. Microbe-plant partnership helps to sustain the growth and development of plants under such stresses. Alteration in the plant ecosystem under these stresses strongly affects plant-microbe interaction. A detailed understanding of phytohormones and other secondary signaling metabolites facilitates targeted manipulation to optimize their concentrations for increased crop productivity under field conditions.

Various bioinoculants such as *Piriformospora indica, Penicillium* spp., *Bacillus* spp., *Pseudomonas* spp., *Rhizobium* spp., cyanobacteria, and other endophytes are used for the production of different growth hormones (e.g., auxin), exopolysaccharides, and for the activation of various stress-responsive genes. These microorganisms actively participate in the enhanced uptake of various nutrients such as K^+, Zn^{2+}, $PO4^{3-}$ under different abiotic stresses when inoculated to the host plants. Together, these activities increase the plant growth and productivity. Bioagents are also used for enzyme-mediated phytoremediation of toxic compounds such as nitrogen oxides, volatile organic compounds, and organophosphates from the environment (Imam *et al.,* 2016). Rhizospheric microorganisms and endophytes substantially help the plants to cope with abiotic stresses (Meena *et al.,* 2017). The plants offered with a combination of abiotic stress and microbial symbioses are also studied. Studies on microbial community dynamics associated with the plants under abiotic stress provide an insight into the ecological behavior of a particular microbial group in its natural ecosystem under the influence of a specific stress, which can be exploited to develop microbial inoculants for alleviation of that stress. A detailed understanding of stress-responsive genes and associated regulatory networks may help in the overproduction of such metabolites using bioresources by optimizing metabolic flux. The development of microbial sustainability or engineering of metabolite secretion is also helpful in the long-term mitigation of abiotic stress through microbial symbiosis.

Enhancing crop resilience through symbiosis

Plant productivity is significantly affected by abiotic stresses such as high salinity, drought, and extreme temperatures, all of which have intensified in recent years (Ramoneda *et al.,* 2019). Root-associated microorganisms play important roles in supporting nutrient uptake and enhancing tolerance to various abiotic and biotic stresses. These symbiotic relationships offer cost-effective and eco-friendly alternatives to agrochemicals, contributing to more sustainable agricultural practices. When the symbiosis is not balanced, the relationships can be antagonistic. Even plant pathogens produce molecules that interfere with the establishment of symbiosis and other plant processes. Plant growth-promoting rhizobacteria (PGPR) are important in alleviating some of the damaging effects of abiotic stresses, such as drought, salinity, and flooding. Modern OMICS techniques, including metabolomics and genomics, are critical tools to understand the precise role of these beneficial microorganisms in stress remediation. Studies of microbial community dynamics can reveal transformations in soil ecosystems and colored bacteria in response to climate change.

Biofertilizers and sustainable agriculture

Various beneficial microorganisms commonly inhabit the rhizosphere, including the genera *Agrobacterium, Arthrobacter, Azospirillum, Bacillus, Burkholderia, Enterobacter, Erwinia, Flavobacterium, Pasteuria, Pseudomonas, Rhizobium, Serratia, Streptomyces* and *Xenorhabdus*. These microorganisms have been recently developed as biofertilizers that can improve the phosphorus (P) and nitrogen (N) use efficiency in plants and sustain crop yield at an optimum level over long-term periods. For example, inoculation with soil beneficial fungi (e.g., *Trichoderma afroharzianum* and *Penicillium* sp.) improved the nitrogen and phosphorus uptake and the salinity tolerance of maize plants through the modulation of phytohormones, antioxidants and ion homeostasis. Plant-growth promoting bacteria (PGPB), such as the genera *Bacillus* and *Pseudomonas*, can also act as biofertilizers, phytostimulators and antagonists to plant pathogens, both under normal and stress conditions. Accordingly, inoculation with these bacterial genera was considered a crucial step for the sustainable development of agriculture worldwide. Seaweed-based products are recognized as an environmentally sustainable strategy for crop and soil management. Seaweed-derived biofertilizers have been shown to improve the physiological status of plants subjected to heat and salinity. Such products can be used safely on various crop species to promote sustainable agriculture worldwide (Bargaz *et al.,* 2018; Mukhopadhyay *et al.,* 2023).

Future directions in research

Research on the phytomicrobiome is advancing rapidly and is expected to inform the development of tailored microbial communities capable of mitigating a wide range of environmental stresses in agriculture. Elucidation of microbes that comprise the core microbiome and characterization of their interactions with hosts, other microbial species, and abiotic environments are needed to inform such efforts. To this end, models of plant microbiomes can be used to probe host–microbiome interactions under combined abiotic stresses. Core microbiomes may be selected through multi-omics data analysis, phenotype-based computation, community network interrogation, and artificial intelligence-guided synthesis. The quality and stability of microbiome-enhanced stress resistance depends on host genotype, root exudate chemistry, and microbial assembly dynamics; therefore, monitoring of transcriptional, metabolic, post-translational, and phenotypic outputs of plants exposed to various core-microbiome combinations is useful in the selection of optimal strains. Microbiome engineering strategies include host-dependent alteration through selective breeding and genetic modification as well as direct manipulation through construction of microbial synthetic communities. Co-engineering of plants and microbes to incorporate desirable traits represents a valuable addition to these approaches. Availability of generalized platforms combining molecular and systems-biology insights with high-throughput plant phenotyping can accelerate elucidation of microbiome complexity and enable predictive-design protocols for construction of strain assemblages tailored to specific crops and environmental conditions. While many advances have been made in high-throughput characterization of microbially driven plant phenotype and in laboratory assessment of candidate microbial assemblages, field validation remains a relatively rare and critical step towards realising the full potential of the core microbiome. Such investigations yield novel constructs that not only support agricultural sustainability but also deepen ecological understanding of plant-microbiome interactions in the context of a truly complex environment (Ali *et al.,* 2023; Khan, 2023).

Integrating multi-omics approaches

Given the extensively studied role of the rhizosphere in plant–microbe symbiosis, future research directions should focus on the development of multi-omics approaches to improve our understanding of molecular mechanisms as well as to facilitate the emergence of efficient microbial solutions that can be applied to the agro-ecosystem (Meena *et al.,* 2017). A better understanding of the role of these symbiotic interactions in altering the adaptive response through the modulation of the transcriptome, metabolome, proteome and epigenome will be essential. Because the phytomicrobiome substantially influences plant growth and stress tolerance, in-depth knowledge of the microbial community and bacterial functions that aid in these processes will therefore provide critical insights into the development of effective and sustainable plant–microbe interactions (Khan, 2023). Multi-omics strategies can be considered as promising research tools for breaking new ground in the manipulation of the phytomicrobiome. Furthermore, the transition from synthetic to natural community studies will provide a better understanding of the ecology of the rhizosphere microbial community, while the exploration of the microbiome and mining of the large datasets generated by next-generation sequencing will allow for the recovery of many novel genes, pathways and genomes relevant to symbiotic interactions. Combining multi-omics approaches (genomics, metabolomics and microbial community analyses) with field studies is essential to identify beneficial microbial interactions, and therefore to enhance plant performance by facilitating the development of sustainable agriculture and boosting global food security.

Field studies and ecological implications

Field experiments and physiological indices are critical to understanding how plant–microbe symbioses function under realistic environmental conditions (Khan, 2023). Laboratory investigations permit controlled assessments of mechanisms at multiple scales, but ongoing research aims to test hypotheses generated in vitro in field situations. Empirical information amassed over decades illustrates how symbioses mediate key processes in biogeochemical cycling, ecosystem succession, and biodiversity enhancement. Measuring symbiotic outcomes and processes in the field therefore contributes to an improved understanding of the functioning of ecosystems and global biogeochemical cycles.

Case studies of successful symbiotic relationships

In salt-stress areas, a dominant and naturally isolated strain of Pseudomonas helped the halophyte Sueda procumbens withstand high salinity. This bacterial strain, a species of *Pseudomonas* closely related to *P. putida*, contained genes for the synthesis of siderophores such as pyoverdines as well as genes for PO_4^{3-} solubilizing enzymes. At salinity levels above 75 mM NaCl, the bacterium enhanced the germination of Arabidopsis thaliana, probably by secreting these pyoverdines and phosphatases (Wang and Song, 2022). Field experiments on rice plants involved a mixture of five well-known symbiotic species, three from the genera *Bradyrhizobium* and *Sinorhizobium* and two from the arbuscular mycorrhizal (AM) genera *Glomus* and *Gigaspora*. In addition to a positive influence on growth and biomass production, plants inoculated with this microbial consortium acquired a remarkable degree of tolerance to drought, salinity, temperature extremes and pathogens. In situ bacterial diversity in the nodules of these plants was also enhanced, but the diversity of AM fungi was either unaffected or diminished. Introductions of specific combinations of microbes therefore not only led to synergy within the inoculum but also improved the functioning of natural symbionts. A strain of the species *Rhizobium miluonense* emerged as a model case of drought tolerance in the rhizosphere of the leguminous plant *Lespedeza davurica*. The physiological basis of drought resistance was the capacity of the bacterium to accumulate trehalose, a nonreducing sugar that plays a well-known protective role against dehydration. *Muciniphila*, a member of the phylum Verrucomicrobia, is a key strain for the salt-tolerance of *Suaeda salsa* at the germination stage. The relative abundance of the genus *Muciniphila* in the rhizosphere community can be regulated by the plant itself through fucose secretion in the root exudates. Such a system closely matches the original “cry for help” scenario by which the plant attracts protective microbes by precise modulation of the composition of its exudates.

Legume-rhizobia symbiosis

Legumes frequently form associations with nitrogen-fixing rhizobia, a symbiosis that can significantly improve productivity. Rhizobia reside within specialized root lateral organs (nodules) that maintain a low-oxygen internal environment required for effective nitrogenase activity. In addition to rhizobia-legume interactions, associations between legumes and arbuscular mycorrhizal fungi also play an important role in nutrient acquisition and plant growth, particularly under impoverished nutrient availability. The establishment of symbioses between microbes and plants requires successful communication whereby chemical signals elicit developmental changes in prospective partners, enabling them to function together as a single entity. Flavonoids, strigolactones and other compounds exuded by plants activate developmental processes in microbes, including the synthesis and export of signal molecules (such as rhizobial nodulation factors). Flavonoids and rhizobial nod factors are then recognised in a highly specific manner by plant-encoded LysM receptor kinases. These receptors act as master regulators of symbiotic interactions, controlling large regulatory networks that reprogramme gene expression in both partners, establishing beneficial nutrient exchange and allowing colonisation to proceed. Even within engaged plant–microbe partnerships, mechanisms can be required to limit the extent of symbiotic root-lateral organ formation.

Nodulation can be curtailed via Autoregulation of Nodulation (AON), a mechanism that functions systemically to balance nodule number with overall plant growth. AON requires the production of a root-derived signal that is triggered by either rhizobia or high levels of soil nitrate. This root signal is consistent with a subset of CLE family peptide hormones that are post-translationally modified and exported into the vascular system, from where they travel to the shoot to suppress additional nodulation. Additional knowledge on the impact of heat stress and the underlying protective mechanism in legumes will help improve heat-resilient legumes in the future. The identification of heat-tolerant genotypes with more stable carbohydrate and lipid composition in reproductive organs and more efficient activation for antioxidants and stress-protective proteins provides a valuable resource for enhancement of legume fertility under heat stress and for exploration of heat-resistance regulatory pathways and associated markers (Foyer *et al.,* 2019). Advanced approaches such as metabolic modelling and metabolic profiling are useful to investigate molecular mechanisms of nutrient exchange among legumes, arbuscular mycorrhizal fungi and rhizobia under nutrient-deficient conditions. Multi-omics will facilitate once land-saving agriculture becomes increasingly important (Liu *et al.,* 2020).

Mycorrhizal associations in stressful environments

Arbuscular mycorrhizal (AM) fungi, together with nitrogen-fixing rhizobia, form the most widespread symbiotic associations in terrestrial ecosystems. AMF penetrate the outer cortex of plant roots and establish a symbiotic relationship with the majority of land plant species (Wang *et al.,* 2024). Within the root, the fungi form highly branched structures termed arbuscules that function as the primary sites of arbuscular mycorrhizal symbiotic nutrient exchange (Volpe *et al.,* 2018). Throughout natural, soils and agricultural plots, plants have evolved a complete plant 6AMF symbiosis system that sustains growth and development under various abiotic stresses. Environmental stress often limits the availability of important plant nutrients, and mechanistic studies of AM symbiosis under abiotic stress conditions can be applied to the development of AMF-mediated strategies for sustainable agriculture that improve plant production and environmental safety. AMF belong to the Glomeromycotina, a group of symbiotic fungi classified in the division Mucoromycota. Typical AMF structures include hyphae, arbuscules, spores and in some species vesicles and auxiliary cells. The hyphal mycelia are gener-ally divided into two types, extraradical and intraradical. Extraradical mycelia emerge from the symbiotic interface to the soil, forming vast networks, whereas intraradical mycelia remain inside the plant root.

Challenges in studying plant–microbe interactions

Many studies on plant–microbe interactions are carried out under controlled laboratory conditions that differ substantially from the complex and fluctuating environments observed in the field, especially under climate change scenarios. Abiotic stresses—such as high and low temperatures, salinity, heavy metal contamination, and drought—have substantial effects on plant–microbe systems. Microbial partners may either positively or negatively influence plant growth under these conditions. Investigations into these interactions benefit from a multidisciplinary approach involving metagenomics, next-generation sequencing (NGS), and imaging techniques. Understanding plant–microbiome relationships offers a promising pathway to enhance crop resilience and to develop cultivars that withstand abiotic and biotic stressors. The rhizosphere plays a pivotal role in plant–microbe symbiosis and warrants particular emphasis to maintain continuity with earlier discussions.

Technical limitations and methodological advances

Across the Earth's terrestrial surface, plants coexist with diverse microbes that collectively form ecological communities, on the surface of plants and inside tissues. The rhizosphere acts as an interface between plants and soils and hosts highly diverse microbes, including actinobacteria, Bacteroidetes, cyanobacteria, Firmicutes, proteobacteria, and fungi. Earlier attempts to characterize the diversity of soil and rhizosphere microbial communities were largely confined to culture-dependent methods, which allowed the identification of less than 1% of the total microbes in soil. Although culture-dependent methods and microscopy-based quantitation gave an overall understanding of microbial diversity in the rhizosphere, culture-independent molecular approaches are widely used to discriminate between the diversity of microbial communities, since many microbial taxa that colonize the rhizosphere are relatively unknown and still await a physiological or functional description. Advances in high-end instrumentation and computational analysis have enabled the deciphering of signal molecules, proteins, genes, and their networks. Multi-omics approaches have emerged as holistic strategies for studying microbial interactions with plants and how they modulate responses to stresses. A large number of metagenomics-, transcriptomics-, and proteomics-based studies on plant-associated microbiota have established the importance of a key class of secondary metabolites in maintaining and regulating stress responses within the phytomicrobiome. Complementary approaches involving metabolomics and other systems biology techniques are needed to understand the interplay between microbes and plants in response to various environmental conditions (Meena *et al.,* 2017).

Ecological complexity and variability

The rhizosphere, a narrow zone of soil encompassing the root surface and inhabited by diverse microbial communities, constitutes the main site of microbial–plant interactions, collectively termed the phytomicrobiome (Shree *et al.,* 2022; Khan, 2023). The phytomicrobiome is considered the second genome of plants and plays a critical role in plant growth, development, and stress adaptation. Recent evidence indicates that the rhizosphere also acts as a hotspot for multicellular eukaryotes such as protists and nematodes, as well as viruses (Beck *et al.,* 2022). Aboveground, plants are associated with a phyllosphere microbiome that interacts with macroorganisms and has a significant impact on plant health. The relative abundance of less abundant phyla such as Verrucomicrobia, Nitrospirae, Cyanobacteria, Bacteroidetes, and Firmicutes is altered under drought stress conditions, and the structure of the active rhizosphere microbiome is reassembled under diverse environmental stressors. Changes in temperature at the plant interface can lead to rearrangements in microbial diversity within the rhizosphere microbiome.

Conclusion

Symbiotic interactions with microbial partners directly influence the host nutrition, growth and health. The understanding of factors controlling the structure, function and diversity of plant vs. microbe symbiosis is an important objective for enabling sustainable agroecosystems and cleaner environments. Since microbes residing in the rhizosphere play an important role in regulating the structural and functional composition of microbial diversity, they ensure the continuous sustainability for the ecosystem functions. The holistic understanding of such an integral process can be achieved through the development of research abilities that combine the data from multiple, disparate sources, including metagenomics methods, to understand the composition and functional potential of the rhizosphere ecosystems (Shree *et al.,* 2022). The information gathered from such investigations is used to develop strategies to exploit this microbial information further, to formulate the sustainable remedial solutions for the productive and environmental welfare of the Earth.

Conflicts of interest

The authors declare that there are no conflicts of interest regarding the publication of this paper.

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