PLANT SCIENCE TODAY
Vol 12(4): 1-19
https://doi.org/10.14719/pst.9052

eISSN 2348-1900

REVIEW ARTICLE

Unlocking the microbiome-mediated mechanism of stress resilience in plants

R Abarna, J P Jinisha Blessie, M S Nandana, Drisya K Anand, N Chitra & K N Anith*

Department of Microbiology, College of Agriculture, Kerala Agricultural University, Vellayani, Thiruvananthapuram 695 522, Kerala, India

*Correspondence email - anith.kn@kau.in

Received: 23 April 2025; Accepted: 30 October 2025; Available online: Version 1.0: 30 December 2025; Version 2.0: 31 December 2025

Cite this article: Abarna R, Jinisha BJP, Nandana MS, Drisya KA, Chitra N, Anith KN. Unlocking the microbiome-mediated mechanism of stress resilience in plants. Plant Science Today. 2025; 12(4): 1-19. https://doi.org/10.14719/pst.9052

Abstract

Plants are continuously challenged by living organisms (biotic stress) and environmental factors (abiotic stress) throughout their lifecycle. Biotic stress factors, such as phytopathogens and pests, along with abiotic challenges like drought, salinity, high temperature and heavy metal contamination, pose significant risk to crop productivity and global food security. These stresses can negatively impact crop growth by altering the rhizosphere environment and disrupting essential cellular and biochemical mechanisms. Understanding the composition, structure and function of the plant microbiome and how it helps plants withstand stress, is crucial. This knowledge could lead to the development of strategies to reduce stress in crops and breed stress-tolerant varieties. Plant-associated microbiomes have the potential to protect plants from biotic and abiotic stresses by enhancing their natural immune responses, either directly or indirectly. They also improve photosynthetic efficiency, promote plant growth, aid in nutrient absorption and synthesize beneficial compounds, hormones and enzymes that increase productivity and stress tolerance in plants. *Pseudomonas* species that produce DAPG have gained significant interest for their effectiveness in suppressing a wide range of soil-borne plant diseases, such as wheat take-all, tobacco black root rot and damping-off in sugar beet. They are also recognized as key contributors to the natural disease-suppressive properties of various soils worldwide. Insights into how the plant microbiome interacts with biotic and abiotic stresses can help in creating innovative bioinoculants. In conclusion, this review highlights the importance of microbial communities in supporting plant health and productivity under stress conditions, showcasing the microbiome-mediated mechanisms that enhance plant resilience to both biotic and abiotic stressors.

Keywords: abiotic stress; biotic stress; microbial communities; plant microbiome; stress mitigation

Introduction

The plant-microbe association has persisted for over 400 million years, as evidenced by the fossil records of plant-fungi associations, particularly arbuscular mycorrhizal symbiosis (1). Plants are associated with various microorganisms, such as bacteria, oomycetes, fungi, archaea and a largely unexplored realm of viruses (2-4). Plants host diverse microorganisms, including bacteria, fungi, oomycetes, archaea and viruses, forming dynamic associations that date back to early plant evolution (5). The concept of the microbiome, defined as the community of resident microorganisms inhabiting a host or environment, highlights the complexity of these interactions. In agriculture, microbes function as biocontrol agents, biofertilizers and biotransformers, supporting plant growth and resilience. The composition of plant microbiota is shaped by both abiotic factors and biotic interactions, with microbes classified as mutualistic, commensal, or pathogenic. Plant structures act as ecosystems containing niches such as the rhizosphere, phylloplane, rhizoplane and endosphere, where microorganisms exert beneficial, neutral, or harmful effects (6-9).

Plant-microbiome interactions play a crucial role in determining plant development, vigour and yield. These interactions vary depending on the specific niche, classifying plant microbial groups into rhizo, endospheric and phyllo regions. Understanding these interactions provides a chance to establish sustainable farming methods. It is essential to unravel the intricate architectural and metabolic diversity of the plant microbiome to harness its enormous prospects in agriculture. The phytomicrobiome contains vast microbial communities that challenge analytical approaches when studying the patterns of plant-microbiome interactions (10). This review article primarily explores the research performed on the aspect of alleviating plant stress through the interaction of the host with its microbiome. Given their numerous benefits, microorganisms are now being utilized as alternatives to chemicals to boost crop yield and act as microbe-based fertilizers and inoculants in agricultural land, thereby enhancing soil fertility and crop production (11). In light of the current climatic conditions, we aim to present a comprehensive overview of how phytomicrobiome can be harnessed to enhance plant resilience and contribute to sustainable agricultural practices that address global food security challenges.

Microbial diversity in plant-microbe association

Plant-microbe associations play a crucial role in the health and productivity of plants. These associations involve a diverse array of microorganisms, including bacteria, fungi and archaea, interacting with plants in various ways. This section discusses the microbial diversity in plant-microbe associations, rhizosphere microbiome, mycorrhizal associations, endophytic microbes, phyllosphere microbiome, plant growth-promoting rhizobacteria (PGPR) and their impact on plant health.

Rhizosphere microbiome

The rhizosphere microbiome refers to the complex community of microorganisms that inhabit the narrow region of soil surrounding plant roots. This microbial community is influenced by interactions between plant roots, soil and various environmental factors. The rhizosphere is primarily inhabited by bacterial groups such as Proteobacteria, Bacteroidetes, Firmicutes, Actinobacteria and Acidobacteria. As for fungi, dominant phyla in the rhizosphere are Ascomycota and Basidiomycota in soil ecosystems (12). Microorganisms inhabiting the rhizosphere can perceive and interpret signals originating from themselves, other microbes and plants and have the ability to impact their plant hosts by emitting signalling molecules. This communication leads to various significant outcomes, including the activation of plant immune response, increased stress adaptability, promotion of overall plant health and physiological functions, optimization of nutrient uptake, regulation of rhizospheric microbiota and improving the soil physiochemical attributes (13). Examples of these molecular signals include “plant-emitted” and “quorum-sensing” molecules such as N-acyl homoserine lactones (AHLs), diffusible signalling compounds, diketopiperazines, molecules mimicking phytohormones and plant-emitted volatile organic compounds (14, 15). Numerous root exudates, released by most plants, have been observed as signals attracting soil microbes. Plants utilize specialized pattern recognition receptors to identify the microbes associated with the rhizosphere (16). Communication through molecules secreted by plants has been demonstrated to play a major role in various beneficial plant-microbe interactions (17). The study of signalling between plants and root-associated microorganisms has primarily concentrated on close interdependent relationships, especially those involving mycorrhizal symbionts and rhizobia (18, 19).

Several flavonoids are known to enhance the growth of AMF hyphae, with the intensity of this response influenced by their specific chemical structure. This stimulatory action becomes more pronounced under CO_2 levels comparable to those naturally present in the rhizosphere. Recent findings further indicate that, during the pre-symbiotic stage as well as in plants inoculated with AMF, flavonoids trigger effects that are specific to the genus and species of the fungal partner (20). When plants encounter nutrient limitations, they deploy specialized chemical signals to recruit beneficial microbes. For instance, under phosphorus or nitrogen deficiency, plants increase the production of strigolactones, which stimulate the branching and growth of arbuscular mycorrhizal fungi (AMF). This interaction enhances fungal colonization and promotes symbiosis, thereby improving nutrient foraging capacity and uptake of immobile nutrients such as phosphorus, helping the plant alleviate nutrient stress (21). Similarly, flavonoids act as key signalling molecules in legume-rhizobium symbiosis by triggering rhizobial chemotaxis, nod gene expression and infection thread formation. This process leads to effective nodule development, enabling legumes to fix atmospheric nitrogen and overcome nitrogen limitation (22). In addition, flavonoids contribute to stress mitigation by mobilizing phosphorus; they can chelate or release mineral-bound phosphates and dissolve mineral-phosphate associations, thereby enhancing phosphorus availability to plants (23, 24). Overall, these compounds-along with a wide array of other root exudates-function as both nutrient sources and signalling molecules in the rhizosphere, allowing plants to recruit beneficial microbial partners and adapt to environmental stress conditions. For example, research indicates that the plant growth-promoting rhizobacteria (PGPR) *Pseudomonas protegens* have four potential chemoreceptors for amino acids, which enhance their ability to move towards them by chemotaxis (25). Root exudates are suggested as a potential agent for shaping the plant microbiota due to their complex chemical profile with signalling role and their ability to impact the composition and activity of the below-ground microbial ecosystem (26).

Mycorrhizal associations

Mycorrhizal associations are symbiotic relationships between certain fungi and the roots of most vascular plants. These associations are mutually beneficial, providing advantages to both the plant and the fungus involved. Mycorrhizal fungal partnerships with plant roots contribute to better nutrient absorption and heightened stress endurance. Mycorrhizae can be classified into four main types - arbuscular mycorrhiza (AM), ectomycorrhiza (EcM), ericoid mycorrhiza (ErM) and orchid mycorrhiza (OM) - each differing in functional morphology and evolutionary ecology (27). Arbuscular mycorrhizal fungi (AMF), belonging to the monophyletic group Glomeromycota, play a vital role in terrestrial ecosystems by forming close symbiotic associations with the roots of most plant species. Through this partnership, plants gain enhanced access to essential soil nutrients such as phosphates and nitrates, while the fungi receive photosynthetically derived carbon compounds, primarily sugars, which support their growth and reproduction (28). Individual genetic strains of mycorrhizal fungi establish common mycelial networks (CMNs) in the soil, linking the rhizosphere structure of both intraspecific and interspecific plants at various growth stages (29). Common mycelial networks (CMNs) between plant species are significantly organized based on the type of mycorrhizal relationship, with association specificity playing a comparatively smaller role in compartmentalization of resources (30). CMNs have the potential to redistribute carbon and nutrients among plants, amplify below-ground signalling by plants and govern competition (31). Mycorrhizal fungi establish communication with plants by utilising plant hormones, organic acids and volatile organic compounds (VOCs) to activate symbiosis development and convey warnings (32). AM and EcM common mycelial networks (CMNs) have been identified as facilitators of belowground signalling between plants and similar processes may theoretically arise by ErM, OM and endophytic engagement as well. AM fungi are capable of transmitting warning signals from plants under attack by pathogens or herbivores to neighbouring healthy plants. This transmission prompts the upregulation of immune-related genes and biosynthesis of stress-responsive compounds, with the signal transfer occurring *via* pathways involving jasmonic acid and salicylic acid (33). Effective signal transmission might be subject to advantageous selection in both plants and fungi as a means to promote environmental homeostasis and ensure sufficient nutrient availability (34). Mycorrhiza can influence plant communities by exerting varying impacts on different plant species. Larger plants that allocate more carbon to mycorrhizal symbionts tend to receive greater benefits from nutrient absorption by these fungi, suggesting a form of nutrient exchange. Plants preferentially allocate carbon to AM fungi that supply higher levels of phosphorus or nitrogen (35). The successful establishment of arbuscular mycorrhizal (AM) plants typically encounters difficulties in areas where there are AM trees of the same species. However, their primary regeneration niche appears to be under ectomycorrhizal (EcM) vegetation, particularly beneath AM plants of different species (36). Common mycelial networks (CMNs) are regarded as one of the most intriguing aspects of mycorrhizal relationships. Numerous studies have explored the redistribution of carbon and nutrients among plants through CMNs, highlighting their crucial role in mycoheterotrophic lifestyles (37). However, the environmental importance of CMNs for autotrophic plants remains a topic of intense debate (38, 39). In modern times, it has been acknowledged that common mycelial networks (CMNs) possess the capability to mediate allelochemical exchange and relay plant signals. In theory, mycelial connections may act as conduits in spreading viruses, considering that multiple phytoviruses are capable of infecting fungal hosts (40).

Endophytic microbes

Endophytes are microorganisms that colonize the internal tissues of plants without causing any apparent harm to their host. These microbes can reside within the roots, stems, leaves, or other plant parts. Endophytic microbes encompass a diverse array of bacteria, fungi and other microorganisms and they play various roles in plant health and ecology. Plants within natural ecosystems form mutually beneficial relationships with endophytic microorganisms, aiding in their growth while also safeguarding them from various environmental pressures, both living and non-living (41). *Trichoderma* species function as potent biocontrol agents that enhance plant tolerance to both biotic factors (such as pests and pathogens) and abiotic challenges (including salinity, temperature extremes, drought and heavy metal stress). They contribute to plant resilience by improving photosynthetic activity, stimulating root development, enhancing uptake of water and nutrients and scavenging reactive oxygen species (ROS). Their mechanisms also involve genetic approaches like chemical mutagenesis or T-DNA mutagenesis, secretion of alamethicins and other metabolites, induction of hydrolytic enzyme genes such as the endochitinase gene (ech33) and the production of trichodermin, a trichothecene-type terpene toxin (42). The key metabolites produced by bacterial endophytes are given in Table 1. Environmental pressures prompt plant cells to generate reactive oxygen species (ROS), encompassing superoxide, hydroperoxyl radicals, hydrogen peroxide and hydroxyl radicals. The emission of ROS within plant tissues and cells can result in oxidative harm to plant proteins, nucleic acids and membranes. Certain endophytes promote stress resilience against both living and non-living stressors (43).

Trichoderma sp., *Xylaria* sp., *Fusarium* sp., *Alternaria* sp. and *Cladosporium* sp. are the predominant fungal endophytes (44). The *Piriformospora indica* (endophytic fungus) has been demonstrated to have the ability to enhance tolerance to various non-living stressors in numerous plant species (45). Chinese cabbage (*Brassica rapa*) infected with the endophytic fungus *Piriformospora indica* and subjected to polyethylene glycol treatment to simulate drought stress showed increased expression of antioxidant enzymes such as superoxide dismutases, peroxidases and catalases in leaf tissues within a day. Additionally, the expression of genes involved in drought tolerance, including *ANAC072*, *RD29A*, *DREB2A* and *CBL1*, was upregulated in the leaves of plants containing the endophyte (46). Utilizing microbial endophytes and soil microbes presents a promising approach to bolstering plant vigour and improving agricultural output. These microorganisms offer benefits such as pathogen suppression, reduction of insect damage and competition with weeds. By harnessing the capabilities of endophytes, it is possible to enhance crop yields without resorting to extensive agrochemical use, thus avoiding potential harm to soil health and food quality. However, integrating these methods into current agricultural practices poses challenges that need to be addressed to ensure sustainable and effective implementation.

Detection of the first discovered seed-endophytic bacterium possessing comprehensive disease-preventing characteristics was made possible through integrated methods. These methods encompassed not only traditional microbiome assessments but also extensive monitoring of disease occurrences on a large scale (47). Initial investigations revealed that various types of bacteria from the *Sphingomonas* genus were gathered and passed down through successive cycles in pathogen-resistant rice seeds. These bacteria provided resistance against disease-causing strains of *Burkholderia plantarii* in susceptible rice plants. Through the integration of high-throughput sequencing (HTS) data, mutagenesis research and molecular docking experiments, *Sphingomonas melonis* strain ZJ26 was identified as a key contributor to this resistance. This discovery shed light on the primary mechanism through which *S. melonis* ZJ26 inhibits the pathogen, which involves the secretion of anthranilic acid, disrupting the pathogens' virulence signalling cascade (47).

Plant growth-promoting rhizobacteria

Plant Growth-Promoting Rhizobacteria (PGPR) are a group of helpful bacteria that live near plant roots in the soil-an area called the rhizosphere. These bacteria support plant health and growth through a variety of actions. Some PGPR are free-living in the soil and interact with plants either directly or indirectly. Their role includes improving how well plants absorb water and nutrients and helping them handle stressful environments like drought or poor soil conditions. They act like natural fertilizers by increasing the surface area of roots for better nutrient uptake, helping fix nitrogen, breaking down phosphorus so plants can use it and even producing compounds like siderophores that bind iron and make it available to plants. Some also release hydrogen cyanide (HCN), which has

Table 1. Key metabolites produced by bacterial endophytes and their roles in stress mitigation.

Bacterial genus/species	Metabolites produced	Function in stress mitigation	References
Pseudomonas spp. (e.g., *P. aeruginosa*, *P. fluorescens*	Pyrrolnitrin, Phenazine-1-carboxylic acid, Pyoleutirin, 2,4-Diacetylphloroglucinol (DAPG), Hydrogen cyanide (HCN)	Strong antifungal activity; inhibits the growth of fungal pathogens; enhances plant defence	(192)
Bacillus spp. (e.g., *B. megaterium*)	Lipopeptides, antibiotics and various biologically active molecules	Suppression of phytopathogens; biological disease control; promotion of plant health	(193)
Enterobacter hormaechei	Bioactive metabolites (not specified)	Improves stress tolerance and enhances plant growth	(193)
Aneurinibacillus aneurinilyticus	Antimicrobial compounds	Enhances plant tolerance to stress and protects against pathogens	(194)

roles in plant protection (48). A well-studied example is the partnership between legume plants and rhizobia bacteria. The plant gives sugar and a low-oxygen environment to the bacteria, which in turn convert nitrogen from the air into a form the plant can use. Other helpful microbes, like phosphate-solubilizing microorganisms (PSMs), release organic acids that detoxify harmful metals in the soil, making nutrients easier for plants to absorb and use (49).

Phytohormones play crucial roles in governing crop growth and structural development. They serve as molecular cues that respond to ecological factors, which could otherwise hinder plant growth or become life-threatening if not properly regulated (50-52). PGPR also produce plant hormones, especially auxins like indole-3-acetic acid (IAA), which are crucial for shaping roots and helping plants grow (53-56). Moreover, PGPR can produce an enzyme called ACC deaminase that reduces ethylene levels in plants. Ethylene can build up during stress and slow growth, so this helps the plant stay healthier (57, 58). They also defend plants against disease by activating internal defences, such as stress-related genes and can "prime" plants for future attacks through a process called Induced Systemic Resistance (ISR) (59, 60). Interestingly, some fungi, like species of *Penicillium*, can boost seed germination and plant health by releasing antimicrobial substances and growing quickly on root surfaces. One such species has even been developed into a commercial bio-product (61, 62).

Phyllosphere microbiome

The phyllosphere refers to the parts of plants above the ground; like leaves, stems, flowers and fruits, with leaves being the most common surface colonized by microbes (63). Microbes that live on leaves must survive harsh conditions such as sunlight, dryness and temperature swings. To do this, they develop traits like UV-protective pigments, sticky substances (polysaccharides) and surfactants that help them cling to the plant surface (64). Some parts of the leaf, like near the veins or stomata (tiny pores), attract more microbes because they leak nutrients and offer shelter (65-67). Among these leaf-dwelling microbes, Methylobacterium and similar bacteria can use methanol or methane as their sole food source and contribute to plant growth (68-70). Fungi and yeasts also exist in the phyllosphere, though they are usually less diverse than bacteria. Still, they play key roles in recycling nutrients and helping plants handle drought or disease (71). Some algae and other microbes are present too, contributing to the ecosystem by providing sugars that other microbes can use. Abiotic stress resistance induced by microalgal applications is largely associated with the modulation of reactive oxygen species (ROS) and enhanced antioxidant defence. In tomato and bean plants, foliar treatment with extracts of *Dunaliella salina* and *Chlorella vulgaris* stimulated the activity of key antioxidant enzymes, including peroxidase (POD), superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX) (72). Various beneficial bacteria found on leaves, such as *Bacillus*, *Pseudomonas* and *Acetobacter*, are known to make phosphate more available to plants, promoting overall plant health (73-75). Plant-microbe associations exert a profound impact on plant health by orchestrating a myriad of beneficial interactions throughout different compartments of the plant and its surrounding environment. Plant-microbe associations exemplify the interconnectedness of microbial communities with plant physiology and ecosystem functioning, underscoring their pivotal role in sustaining plant health and productivity in diverse environments, as depicted in Fig. 1.

Plant stress responses

Plants are under stress when conditions in their environment, like water, temperature, or soil quality, aren't ideal. These stresses affect basic functions such as chlorophyll production and cell division, leading to lower yields (76). Stress can be abiotic (like drought, salt, cold, or nutrient deficiency) or biotic (caused by living things such as pests, pathogens, or weeds) (Fig. 2) (77). Currently, over 45 % of farmland is affected by drought and salinity impacts more than 800 M ha worldwide. Similarly, acidity and flooding are also increasing

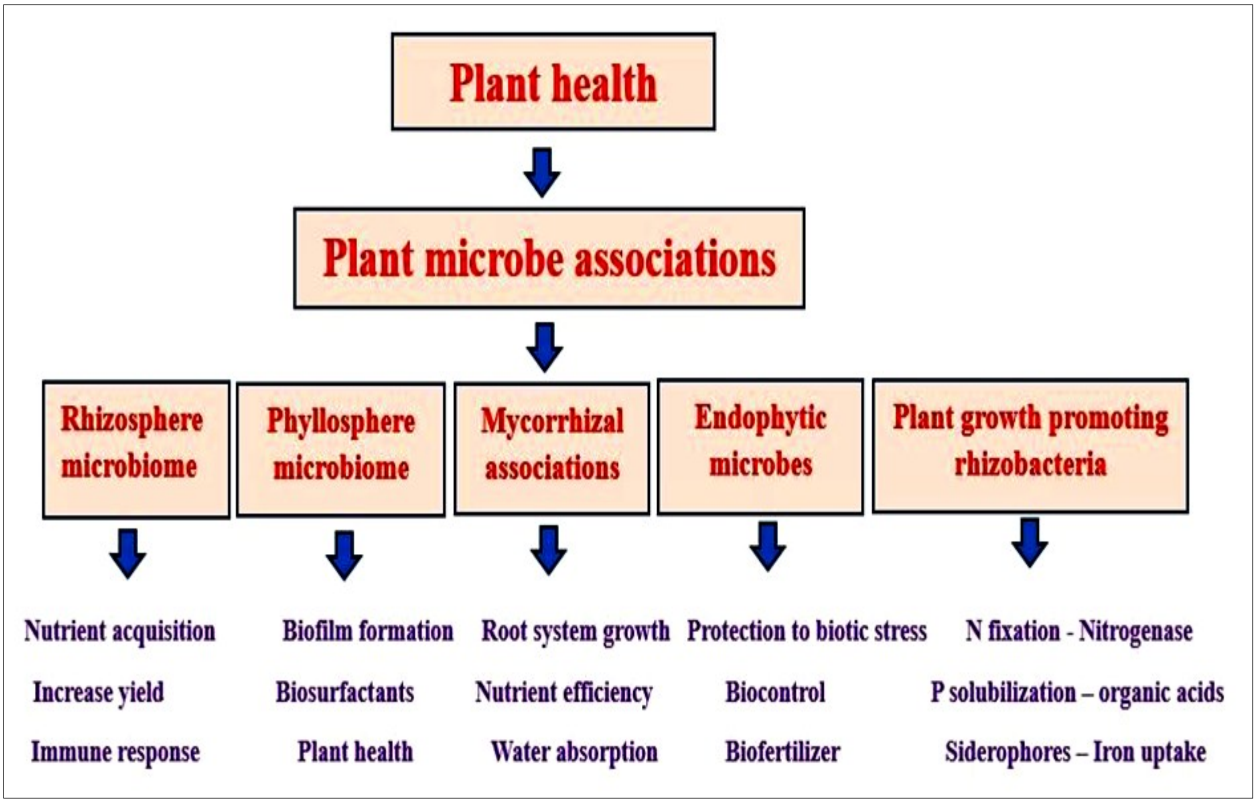

Fig. 1. Impact of plant-microbe associations on plant health.

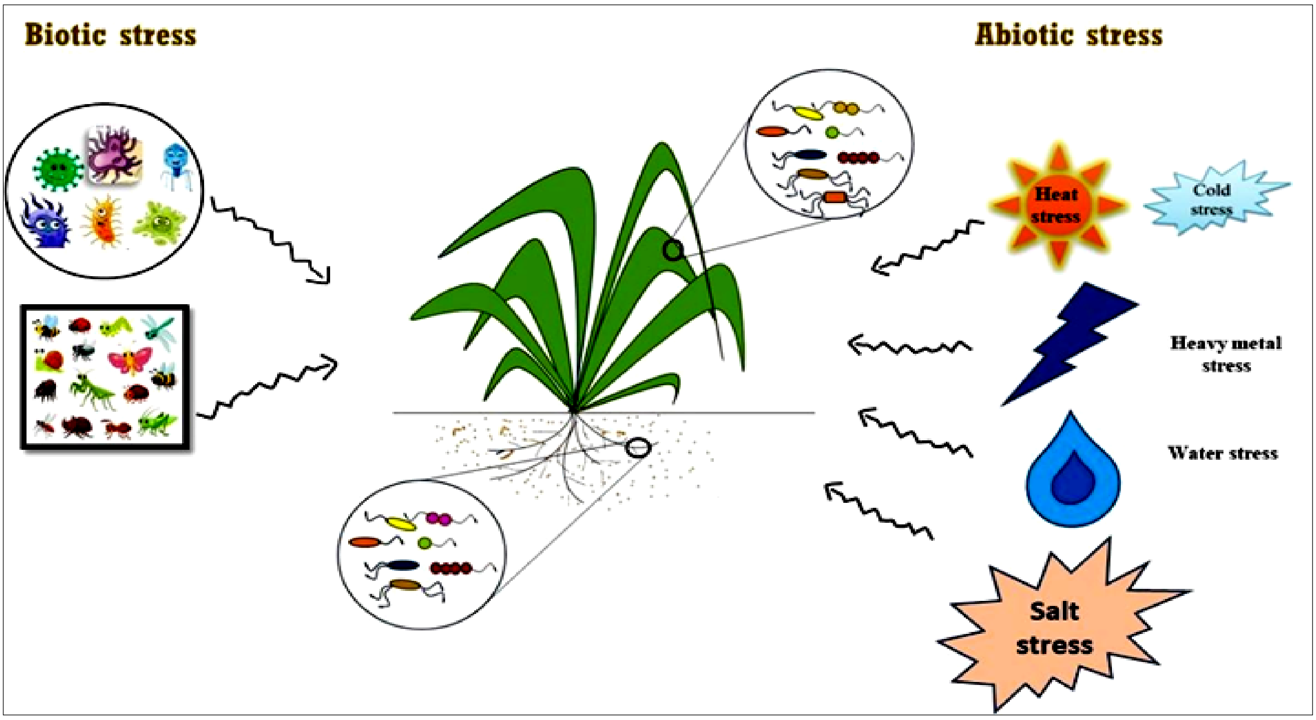

Fig. 2. Various stresses undergone by plants.

concerns (78). More than 6 % of the terrestrial areas and 20 % of irrigated land worldwide are affected by soil salinity (79) and 3950 M ha of arable land are affected by soil acidity (80). Approximately 82 % of the global population and one-third of the Earths' land area are exposed to varying degrees of flood risk. The area of cropland exposed to flood has increased by 7.75 % in the last 10 years (81). The duration, intensity and frequency of cold extremes also affect crop productivity, as in the case of spring frost, affecting 85 % of the wheat sown area globally each year (82, 83). Plants respond to these challenges by changing how their genes and metabolic systems work. For example, salt-tolerant plants store excess salt in vacuoles, while others try to isolate it in older leaves (84, 85). Regardless of the type of stress, plants use a layered defence strategy that includes sensing the problem, signalling within the cell, activating genes and producing protective proteins or metabolites. Biotic stressors such as fungi, bacteria and insects can directly damage crops. Each year, plant diseases and pests cause major yield losses worldwide-up to 40 % in some crops (86). Weeds can also cause yield losses ranging from 10 % to 100 % in various crops, depending on factors such as weed species, crop type and weed management practices (87). To defend themselves, plants detect harmful organisms by sensing molecules they release. These trigger immune responses like PTI (pathogen-triggered immunity) and ETI (effector-triggered immunity) (88) (Fig. 3). Plants also fight herbivores by producing toxic or bitter substances or by attracting other insects that prey on the pests. This is called direct and indirect defence (89) (Fig. 4).

Interestingly, when plants face multiple stresses at once, they can develop cross-tolerance, where one type of stress helps them prepare for another. The interplay between stresses elicits intricate responses in plants. During periods of stress, the accumulation of specific metabolites positively influences the plants' response to both types of stress, protecting them from

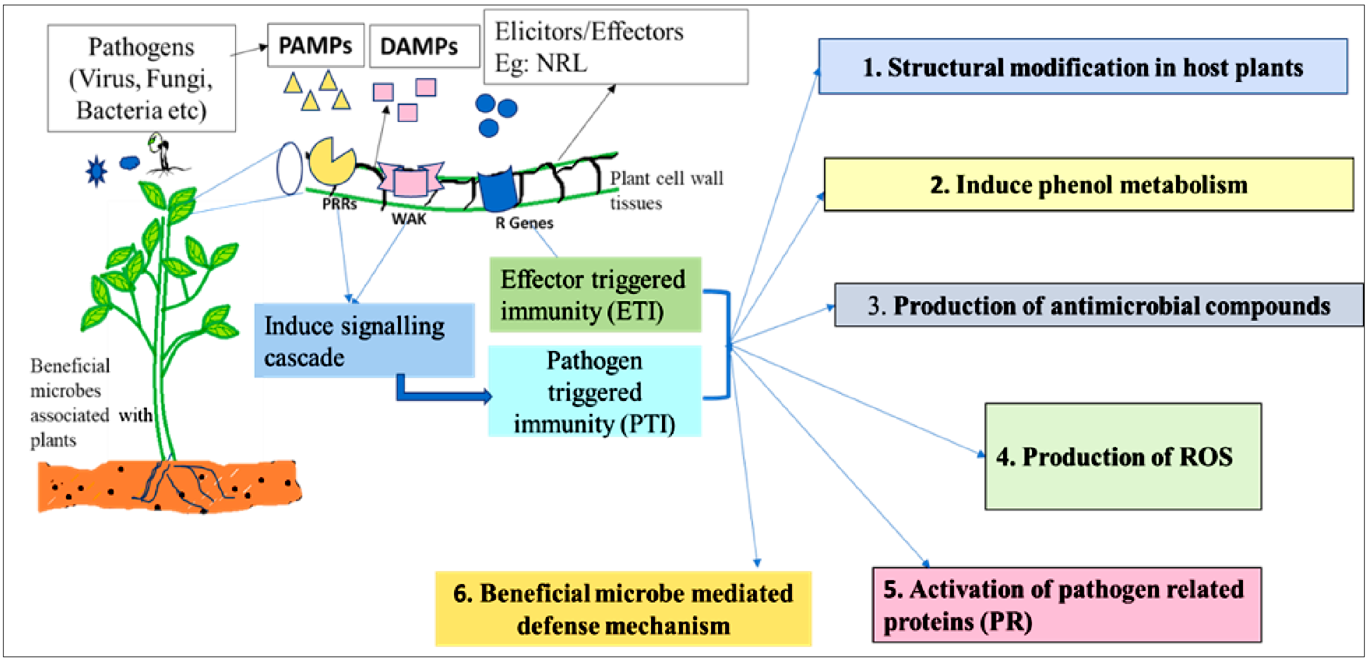

Fig. 3. Schematic diagram of defence response in plant cells in response to various plant pathogens.

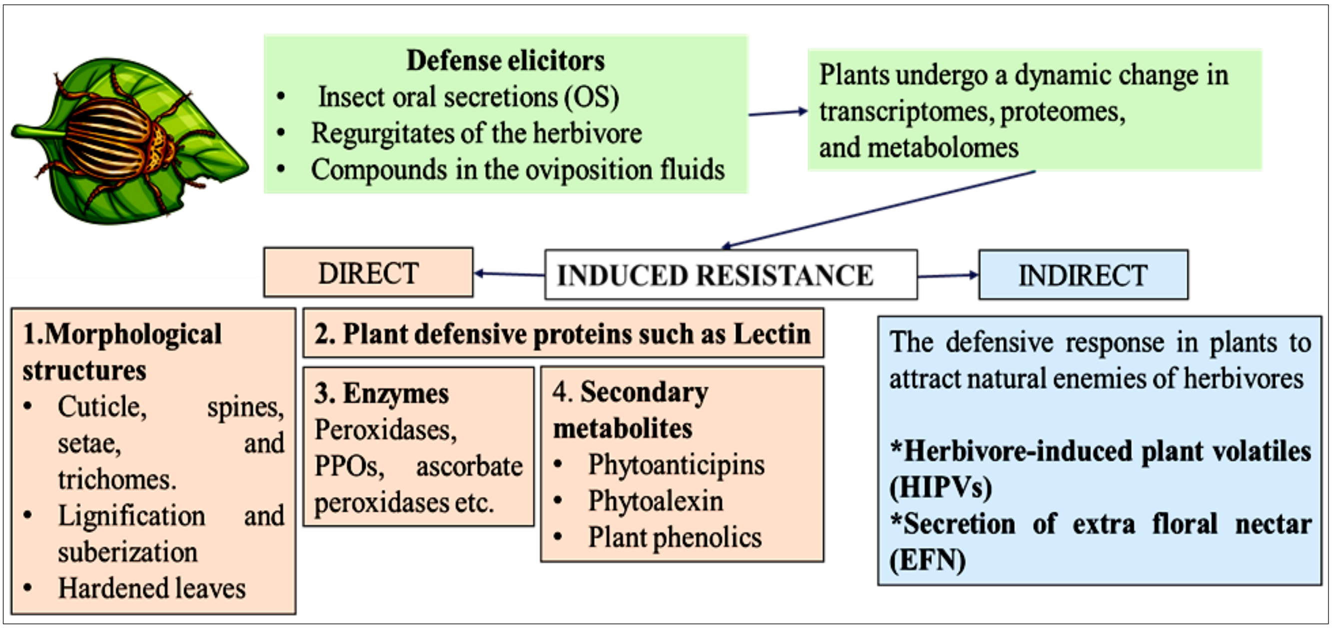

Fig. 4. Schematic diagram of mechanisms of induced resistance in plants in response to herbivory.

multiple threats. Initial responses include callose accumulation, alterations in reactive oxygen species (ROS) and changes in phytohormone levels, all of which trigger signal transduction and metabolic reprogramming toward defence mechanisms (90). Plants, being sessile organisms, are significantly impacted by even minor changes in their immediate environment. They need to fight and survive these conditions by activating a series of complex metabolic pathways at the cellular level. Despite their lack of mobility, plants exhibit a dynamic response to stress tolerance and survival challenges. The pathways involved in defending against abiotic and biotic stress are both unique and interconnected. Therefore, studying these pathways at the molecular level is essential for developing climate-resilient crops, stress-mitigating bioinoculants and other sustainable solutions.

How microbes help plants cope with stress

With the help of advanced tools like DNA sequencing, scientists can now explore how microbial communities influence plant health at the genetic and metabolic level (91). Sophisticated methods such as Illumina-based microbiome analysis assist in studying the microbial community and its dynamic relationships more quickly (92, 93). The plant microbiome plays a significant role in maintaining soil health, supporting plant health and development and controlling plant diseases by interacting with the roots and adjusting the microbiome in the rhizosphere accordingly (94). In the soil, some microbes create "suppressive soils" that naturally protect plants from harmful pathogens. These soils are either broadly or specifically protective, depending on which microbes dominate (95-97). For instance, bacteria like *Pseudomonas* can suppress diseases in crops like tomatoes and cucumbers. Others, such as *Burkholderia* and *Streptomyces*, are also linked to healthier soils (98). Biotic stressors such as viruses, bacteria, fungi, arachnids and nematodes have a substantial impact on the growth, development and productivity of plants. These pathogens disrupt the regular metabolic processes in plants, leading to decreased agricultural production. Worldwide, there is a significant reduction in crop yield ranging from 21 % to 30 %, with a particular focus on the negative effects of plant diseases on cereal crops (99). Instead of relying solely on synthetic pesticides-which can lead to environmental harm and pathogen resistance-using plant-associated microbes offers a more sustainable solution

Table 2. Potential of plant microbiome in biotic stress management.

Biotic stressors	Crop	Microorgansisms	Mechanism	References
Ralstonia solanacearum causing bacterial wilt	Tomato	*Bacillus subtilis* QST713	Antagonism through the production of antifungal metabolites	(195)
		Piriformospora indica	Induced systemic resistance	(196)
Rhizoctonia solani	Cowpea	*Bacillus subtilis*, *B. amyloliquefaciens* and *B. velezensis*	Pathogen suppression	(197)
	Amaranthus	*Bacillus* spp.	Antifungal activity	(198, 199)
F. oxysporum, *R. solani* and *P. capsici*	Black pepper and ginger	*T. asperellum*, *T. brevicompactum* and *T. harzianum*	Antimycotic activity	(200)
Phytophthora capsici	Black pepper	*Alcaligenes* sp. and *T. harzianum*	Antagonistic activity	(201)
		Rhizobium sp. and *Bacillus* sp.	Disease suppression	(202, 203)
		Trichoderma spp. and *Pseudomonas fluorescens*	Biocontrol potential	(204)
Sclerotinia sclerotiorum white mould disease	Cucumber	*Trichoderma asperellum* and *Trichoderma album*	Antifungal activity	(205)
Spodoptera frugiperda	Maize	*Bacillus amyloliquefaciens*	Defensive and antifeeding metabolic activity	(206)
Spodoptera litura	Black gram	*Glomus intraradices* and *Rhizobium*	Defense stimulation	(207)
	Cowpea	*Bacillus subtilis* and *Bacillus velezensis*	Enhanced plant defence	(208)

to control pests and boost plant immunity (Table 2). As pathogens evolve and climate shift, understanding and using beneficial microbes becomes essential for building resilient agricultural system (100, 101).

Microbiome-mediated biotic stress mitigation

The plant microbiome plays a significant role in maintaining soil health, supporting plant health and development and controlling plant diseases by interacting with the roots and adjusting the microbiome in the rhizosphere accordingly (94). Suppressive soils are prime examples of this, acting as the initial line of defence against specific soilborne nematodes and pathogens, or a broader range of them (95). The term suppressiveness can be categorized as either general or specific, depending on whether a wide or particular group of microorganisms, respectively, contributes to the soils' ability to fight off pathogens (96). Variations in soil composition can impact the enhancement of plant defence mechanisms. Disease-suppressive soils tend to activate a higher expression of plant defence genes compared to regular soils, likely due to their unique microbial makeup (97). For example, the increase in *Pseudomonas* spp. was linked to the ability of soils to suppress diseases in apple replants, *Fusarium* wilt in tomatoes, *Pythium* damping-off in wheat and cucumbers, *Aphanomyces* root rot in peas, as well as clubroot diseases in Chinese cabbage (95). *Flavobacterium*, *Chryseobacteria*, *Burkholderia* and non-pathogenic *Streptomyces* strains could potentially be responsible for soil-specific suppression (98).

Biotic stressors such as viruses, bacteria, fungi, arachnids and nematodes have a substantial impact on the growth, development and productivity of plants. These pathogens disrupt the regular metabolic processes in plants, leading to decreased agricultural production. Worldwide, there is a significant reduction in crop yield ranging from 21 % to 30 %, with a particular focus on the negative effects of plant diseases on cereal crops (99). Pesticides and chemical fertilizers are costly and contribute to soil degradation, persisting in the environment and causing pollution. Additionally, prolonged application of these chemical fertilizers has led to the buildup of pathogens. Therefore, studying plant microbiome offers a sustainable approach to effectively manage plant pests and diseases (Table 2). The emergence of new pathogen races and insect biotypes heightens the threat to crop production (100). Plants have various defence mechanisms that are activated in response to pathogens (101).

Plant pathogen interaction

The plants' ability to adapt to diverse environments is enhanced by intricate interactions between its immune system and microbiome, thereby increasing the overall capacity and flexibility of plants (102). Plants engage in a complex and dynamic defence system to counteract pathogens (Fig. 5). This defence mechanism is categorized as innate and systemic plant responses. There are two types of innate immunity in plants: effector-triggered immunity (ETI) and microbial-associated molecular-pattern-triggered immunity (MTI, also known as PTI). Pattern-recognition receptors (PRRs) have developed to identify typical microbial substances, like bacterial flagellin or fungal chitin, known as pathogen- or microbe-associated molecular patterns (PAMPs or MAMPs) (103). Additionally, plants react to signals produced internally due to damage caused by enemy invasion, referred to as damage-associated molecular patterns (DAMPs) (104).

Pattern recognition transforms into an initial defence mechanism known as PAMP-triggered immunity (PTI). Pathogens that thrive have developed strategies to reduce host defence activation and employ pathogenic effector molecules to evade this primary defence. They do so by either inhibiting PTI signalling or avoiding host-mediated detection (105). In response, plants have evolved a secondary resistance mechanism where resistance (R) proteins, specifically Nucleotide binding-leucine rich repeat (NB-LRR) receptor proteins, play a crucial role in identifying effector molecules from attackers. This recognition leads to effector-triggered immunity (ETI), frequently accompanied by programmed cell death at the

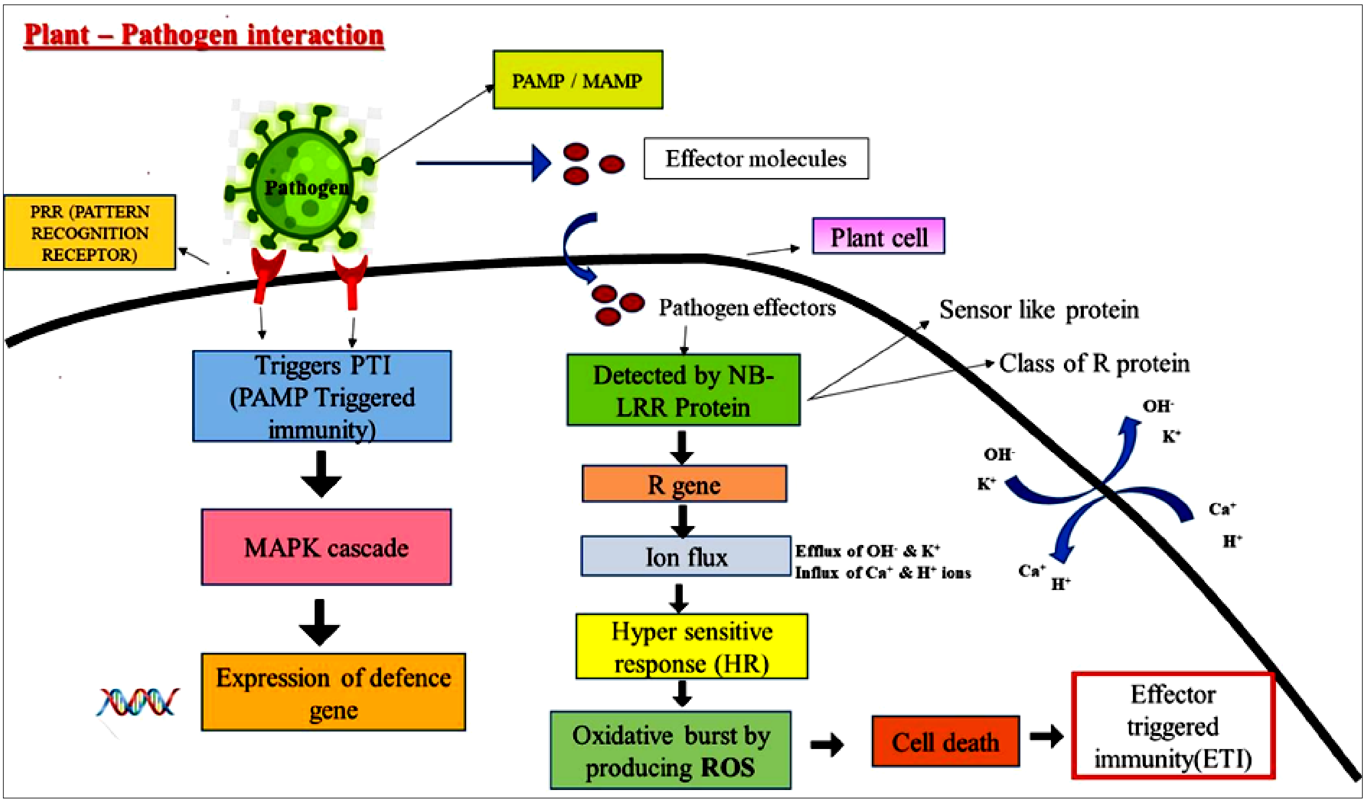

Fig. 5. Plant pathogen interaction.

infection site, preventing the further invasion of biotrophic pathogens thriving on living host tissue (106). The initiation of both PTI and ETI often induces heightened resistance in tissues distant from the infection site (Fig. 5). This process involves one or more long-distance signals propagating an augmented defensive capability in still unaffected parts of the plant (107). Systemic acquired resistance (SAR) is the widely recognized term for this thoroughly characterized type of resistance induced by pathogens (108). The initiation of SAR in response to pathogen attack begins when a PTI or ETI response is locally activated. In distant tissues, SAR is identified by higher concentrations of the salicylic acid (SA) hormone. Moreover, the simultaneous activation of Pathogenesis-Related (PR) genes occurs during SAR and several of these genes code for PR proteins exhibiting antimicrobial effects (109).

Pathogen-induced systemic acquired resistance

The induction of SAR by pathogens occurs when a plant immune response (PTI or ETI) is activated locally. To initiate SAR in distant organs, there is an extended signal transduction within xylem and phloem (108). In this cascade, the membrane lipid carrier protein Defective in induced resistance1 (DIR1) likely functions as a chaperone for the long-distance SAR signals. It is important to note that Salicylic Acid (SA) itself does not function as the systemically moved SAR signal (61). Several metabolites are potentially engaged in remote SAR signalling, such as the diterpenoid dehydroabietinal (DA), methyl ester of SA (MeSA), a factor dependent on pipecolic acid (Pip), azelaic acid (AzA) and glycerol-3-phosphate (G3P) (110). In wheat, *Xanthomonas translucens* pv. *cerealis* and *Pseudomonas syringae* pv. *japonica* have been reported to trigger systemic acquired resistance (SAR) or SAR-like immune responses, which in some cases display regulatory characteristics distinct from those observed in Arabidopsis (111). The infections caused by *Pseudomonas syringae* in both Arabidopsis and wheat activate systemic acquired resistance (SAR). This response is generally mediated by salicylic acid (SA), leading to the increased expression of pathogenesis-related (PR) genes and improved disease resistance throughout the plant (112).

Flavin-dependent monooxygenase 1 (FMO1) plays a crucial role in initiating SAR in tissues throughout the system (113). This function of FMO1 may involve transmitting or enhancing signals over long distances, originating from the initial foliage. The regulation of SAR signalling downstream of Salicylic Acid (SA) is governed by the nonexpressor of PR genes1 (NPR1), a protein responsive to redox changes. Upon induction by SA, NPR1 functions as a transcriptional mediator, influencing many Pathogenesis-Related (PR) genes (113). In cells activated by salicylic acid (SA), NPR1 interacts with TGA family transcription factors. Alongside WRKY transcription factors, they jointly bind to the promoters of defence genes responsive to SA, activating these genes (114). Primed plants adjust their primary metabolic pathways (shifts in malate, oxoglutarate and fumarate levels) and enhance the production of secondary metabolites (Phenylpropanoids and Octadecanoic acids) to strengthen their defence responses (115). Arabidopsis transgenic lines that continuously activate SAR signalling (SA synthase or cpr mutations) experience a notable reduction in yield when grown under non-stress conditions (116).

Herbivore-induced resistance

Research indicates that signalling begins when plant signals (such as DAMPs) and inducers from insect saliva are released at the site of tissue damage known as HAMPs (Herbivore-associated molecular patterns) (117). Moreover, there have been reports of effector molecules from insects that inhibit host immunity (118). As a result, plants might have developed resistance genes (R genes) in response to herbivore effectors, akin to their response to pathogen effectors (119). The rapid detection of elicitors associated with herbivory triggers the quick release of oxylipins derived from membrane lipids. The oxylipin family known as jasmonates (JA) emerges as a pivotal signal, as evidenced by the reduction of herbivore-induced resistance in JA biosynthesis and signalling mutants (120). The physiologically active signal, Jasmonoyl-isoleucine (JA-Ile), is identified and recognized by a coreceptor assembly composed of the Jasmonate Zim-domain (JAZ) proteins and the F-box protein coronatine insensitive1 (COI1). COI1-JAZ coreceptor recognition of JA-Ile leads to the proteasomal breakdown of JAZ proteins, which in non-stimulated cells inhibit promoters of JA-mediated defence responses, including the transcription factors MYC2, 3 and 4 (121). In JA-stimulated cells, the JA signalling pathway is upregulated, resulting in the initiation of numerous JA-responsive genes (122).

Induced resistance by beneficial microorganisms

Like pathogens, beneficial microbes must successfully evade plant defence pathways to establish a long-term and close symbiotic association with the host. The mechanisms and molecules adopted by pathogens to evade host immunity are also employed by microbes in the soil that induce ISR (61). It is possible that the invasion of roots necessitates the local suppression of PTI (Pattern-triggered immunity) to shield PGPR (plant growth-promoting rhizobacteria) from MAMP (Microbe-associated molecular pattern)-triggered antimicrobial compound production (123). The signalling components within the plant root that are crucial for initiating ISR include the R_2R_3-type MYB transcription factor gene MYB72, identified as one of the significantly induced genes (124). MYB transcription factors represent one of the largest families in plants, functioning in growth regulation and stress adaptation by binding to MYB-specific cis-elements in the promoters of target genes. Among them, MYB15 and MYB37 contribute positively to abscisic acid (ABA) signalling and drought resistance. Their expression is markedly upregulated by ABA and plants overexpressing these genes exhibit enhanced drought tolerance through stimulation of ABA-mediated stomatal closure (125). The root transcriptional responses associated with MYB72 in ISR-inducing rhizobacteria are mainly linked to genes involved in the iron deprivation response. Interestingly, these genes are also induced by VOCs produced by ISR -inducing PGPR and Plant Growth-Promoting Fungi (PGPF) (126). Therefore, the iron-deprivation response is triggered even when plants are not experiencing iron limitation (127).

ISR can be triggered by non-pathogenic microbes in the rhizosphere. Initially, rhizobacteria-mediated ISR was thought to have mechanistic similarities with pathogen-induced SAR due to its broad-spectrum effectiveness (123). However, it was later discovered that rhizobacteria-mediated ISR and SA-dependent SAR are controlled by distinct signalling pathways (128). SAR refers to resistance induced by a pathogen that is SA-dependent, whereas ISR refers to resistance induced by a beneficial microbe that is SA-independent. The regulation of systemic resistance independent of SA by symbiotic soil microbes is primarily orchestrated by JA (Jasmonic Acid) and ET (Ethylene) (123).

Mechanism of microbiome-mediated biotic stress mitigation

Survival depends on defence strategies within an environmental ecosystem. To thrive in this interconnected system, organisms, especially plants, employ various mechanisms to fend off threats, such as pathogens (129). This defence involves the production of secondary metabolites, specifically phytoalexins or phytoanticipins. When an infection occurs, defence signals are activated in response to the presence of microbes, triggering protective reactions against the invader and other pathogens (61, 130). Plants significantly influence their rhizosphere microbiome by releasing specific exudates into the rhizosphere. This process plays a central role in selecting, initiating and attracting potential microbes. These recruited microbes, whether beneficial or antagonistic, interact with plant receptors, priming the plants' immune system. This priming of defence genes in response to inducers, such as microbes or elicitors, is known as induced systemic resistance (131). Plants selectively recruit beneficial microbes via root exudates, initiating ISR by priming plant immune responses. The production of phytoalexins and signalling compounds enables systemic defence responses even before actual pathogen invasion. The root microbiome shapes immunity through coumarin release, promoting the establishment of ISR-inducing bacterial communities (132).

Abiotic stress

Plants necessitate an abiotic environment to facilitate their physiological and developmental processes (133). An unfavourable abiotic environment comprises various stress conditions that limit plant growth and development (134). Plants exhibit the ability to sense and respond to stresses through diverse mechanisms, thereby enhancing their nutritional support (135). Abiotic stress is a major constraint on global crop production, with stresses like high salinity, extreme temperatures and water scarcity (drought or dehydration), posing challenges to plant well-being (136). These stressors disrupt normal plant metabolic processes, leading to compromised growth and development (137). Microorganisms can withstand harsh environmental conditions and can help other biological entities cope with such stress to some extent (138). Through the induction of systemic tolerance, alteration of plant defence pathways and improving nutrition and growth, microorganisms effectively reduce the impact of stress (Table 3). Employing plant growth-promoting bacteria (PGPB) and mycorrhizal fungi is a viable strategy to counteract the effects of abiotic stress and help plants survive under challenging conditions (139).

The effective application of diazotrophic bacteria has enhanced crop yields in Brazil (140). During the 2019/2020 cultivation period, approximately 37 M ha of cultivated soybeans in Brazil yielded an average of 3.4 t/ha. Since soybeans typically need about 80 kilograms of nitrogen per ton of grain and considering that nitrogen fertilizer efficiency is usually below 50 % due to processes like denitrification, volatilization and leaching (141, 142). A total of around 20 million tons of nitrogen would be required to sustain Brazilian soybean plantations without biological nitrogen fixation. This nitrogen requirement is equivalent to roughly 43 million tons of urea processes (143). Additionally, replacing chemical fertilizers with nitrogen-fixing microbes significantly reduces greenhouse gas emissions.

Microbiome-mediated abiotic stress mitigation

The microbiome holds significant importance in aiding plants to alleviate abiotic stress through the utilization of their metabolic and genetic capabilities (144). Rhizobacteria-induced drought endurance and resilience (RIDER) involve a spectrum of changes in phytohormone concentrations, defence-associated proteins and enzymes, antioxidants and exopolysaccharides. These alterations serve as indicators of plant responses mediated by microbes and such adaptive strategies enhance the resilience of plants against

Table 3. Major abiotic stresses affecting plants, their effects and typical defence mechanisms to the stress.

Stress and its effects on plants	Effects on plants	Mechanism for stress mitigation	Reference
Heat stress	Affect seed germination Reduce plant growth Induce production of ROS Reduction in photosynthesis	Adaptation by avoidance and tolerance Avoidance of extreme heat Tolerance-producing osmoprotectants, antioxidant enzymes Upregulating heat shock genes	(8, 209-210)
Drought stress	Photosynthetic and transpiration rate decreases	Physical mechanisms - closure of stomata to prevent transpirational water loss Functional protein - Protects the cells like channel proteins, Late embryogenesis abundant protein (LEA), OSM protein, etc. Regulatory protein - Indirectly protects cells through calcium-dependent protein kinases, calmodulin, etc.	(211, 212)
Edaphic stresses	Inhibition in photosynthesis Excessive ROS production leads to membrane damage	Reducing the osmotic potential of cells Ion compartmentation by storing absorbed salts in vacuoles (halophytes) Signal transduction pathways - Ca^{2+} dependent-SOS pathway, Abscisic acid pathway and CDPK pathway - Independent-Mitogen-activated protein kinase (MAPK) pathway	(213-216)
Cold stress	Ice formation in the extracellular space of plant tissue Punctures cells, leading to cytosol outflow and finally leading to death	Accumulation of cryoprotective polypeptides and osmolytes Production of antifreeze proteins NIA genes initiate nitric oxide, which signals cold stress pathways and events Gene-regulated pathways like ICE-CBF-COR regulate the Cold response gene (COR), which initiates various mechanisms to defend against cold stress	(217-219)
Flood/Waterlogging	Soil redox potential (Eh) declines Soil pH increases	Morphological modifications like suberized exodermis, Hypertrophied lenticels and Adventitious root production due to auxin-ethylene interaction Accumulation of ethylene in the root initiates the formation of aerenchyma Anaerobic stress proteins enable anaerobic pathways like ethanolic and lactic fermentation in plant cells Genes like HKI 1105 induce programmed cell death that precedes aerenchyma formation	(220, 221)

various abiotic stresses (145). PGP bacteria can induce systemic tolerance (IST), manifesting as a multitude of physicochemical modifications in plant cells that enhance their ability to withstand abiotic stress (146). Recent research demonstrates the efficacy of microbe-driven abiotic stress tolerance in diverse conditions such as heat, salinity, metal toxicity, chilling injury and drought. When exposed to salt stress, various microorganisms synthesize osmoprotectants in response, exopolysaccharides during water stress, heat-shock proteins at elevated temperatures and cold-shock proteins at low temperatures (147).

Salinity

Salinity is a prevalent issue in global soil degradation. The presence of soil salinity has the potential to hinder optimal vegetative growth and diminish microbial dynamics in soil (148). Microbes capable of thriving in saline conditions fall into two categories: halophiles and halotolerant organisms. Bacteria, within this classification, are known to secrete unique enzymes characterized by polyextremophilic traits. These enzymes include cellulases, xylanases, proteases, amylases, lipases and gelatinases (149). It is plausible to categorize these enzymes as haloenzymes or halozymes, given their inherent salt-tolerant catalytic properties. Halotolerant microbes secrete haloenzymes and osmolytes. The secretion of enzymes by halophiles plays a pivotal role in plant microbiome interactions and contributes to sustaining soil integrity, as emphasized in the work of (143). Notably, salt-resistant plants develop a supportive microbiome within their root zone, a phenomenon explored (150). This microbiome assumes a vital role in both plant enhancement and protection against soil salinity. Microorganisms employ both direct and indirect strategies to enhance plant tolerance. The direct approach encompasses the synthesis of phytohormones, mobilization of nutrients, nitrogen fixation, production of siderophores and ACC deaminase activity by rhizobacteria (151). Rhizobitoxine, an enzyme, plays a crucial role in inhibiting ethylene production (152).

Microorganisms aid in enhancing salinity tolerance by facilitating the cytoplasmic retention of osmolytes. These osmolytes act as effective agents against the osmoprotective regulator, thereby preserving cellular turgor pressure and ultimately boosting plant growth. *Bacillus* species improve ion homeostasis and hormone production. In addition to their osmoregulatory functions, specific bacterial strains, such as *Bacillus pumilus* and *Bacillus subtilis*, contribute to salinity stress resilience by stimulating various defence mechanisms. *Bacillus pumilus* is involved in the production of indole-3-acetic acid (IAA), while *Bacillus subtilis* releases hydrogen cyanide and ammonia and facilitates phosphate solubilization. These concerted actions further enhance the plants' ability to cope with salinity stress, underscoring the multifaceted contributions of microbial interactions in promoting sustainable plant growth (153).

Drought

Microorganisms play a pivotal role in mitigating drought stress and promoting plant resilience. They possess the ability to endure desiccation-induced stress and simultaneously influence plant growth and development. Under adverse conditions, microbes employ adaptive strategies such as the formation of resilient cellular barriers, synthesis and accumulation of osmolytes and induction of dormancy to counteract environmental stress (154). Specific microbial species, including *Pseudomonas putida*, *Azospirillum brasilense*, *Pseudomonas aeruginosa*, *Alcaligenes faecalis* and *Bacillus thuringiensis*, have been shown to alleviate the effects of drought (155, 156). Arbuscular mycorrhizal fungi (AMFs) can enhance plant performance during drought by improving nutrient acquisition and stomatal conductance, ultimately increasing water-use efficiency (157). Studies have also highlighted the enrichment of Actinobacteria in the root microbiota of drought-stressed rice (*Oryza sativa*) and sorghum (*Sorghum bicolor*) and a survey across 30 plant species identified Streptomyces sp. as prevalent in the root endosphere, with its abundance correlating with enhanced plant drought tolerance (158). Leveraging the potential of plant-associated microbiota offers a cost-effective and environmentally friendly strategy to enhance drought resilience in agriculture (159). Plant microbiomes are characterized by rapid growth, high population density, physiological robustness, metabolic versatility and broad ecological distribution, which enable them to thrive under adverse environmental conditions (160). Consequently, there is growing global interest in harnessing plant-microbe interactions to improve crop stress tolerance (161).

Plants, in turn, respond to drought stress through a range of morphological, physiological and molecular adaptations. Drought reduces cell size, compromises membrane integrity, induces leaf senescence and increases reactive oxygen species (ROS), ultimately decreasing plant productivity (162). It also disrupts biological and genetic processes, alters pigment composition and impairs the photosynthetic system (163). To counter these effects, plants synthesize compatible osmolytes, such as betaine, proline, spermidine and soluble sugars, to maintain cell turgor and preserve cellular integrity during prolonged water deficit (164). Additionally, they deploy efficient antioxidant systems to scavenge ROS and other radicals (165). Plants further adapt by modulating gene transcription and protein synthesis for signal perception and intracellular signalling, alongside upregulation of drought-responsive genes, collectively enhancing their tolerance mechanisms (166).

Temperature stress

Climate change has the potential to alter the intensity of temperature-induced stress experienced by plants. Plants exhibit resilience to extreme temperature conditions, including stress from both high temperatures and cold conditions. The impact of temperature stress is evident through changes in the plasma membrane, photosynthetic activity, cell division and overall plant growth. Heat stress leads to increased fluidity in plants, while cold stress reduces fluidity (167). Exposure to heat stress triggers the production of reactive oxygen species, prompting the activation of antioxidant defence mechanisms in plants. Enzymes like peroxidase (POX), ascorbate peroxidase (APX), glutathione reductase (GR), superoxide dismutase (SOD) and catalase (CAT) are upregulated in response. SOD transforms the superoxide anion radical into H_2O_2 and O_2, which is then converted to oxygen and water by CAT and APX. GR plays a crucial role in regenerating reduced glutathione, a vital antioxidant. These detoxification systems play a key function in maintaining cellular balance, promoting plant growth and facilitating development under conditions of heat stress (168). Microbes that promote plant growth can trigger thermotolerance in plants by synthesising heat shock proteins and causing structural modifications in plants (138). Furthermore, PGPM mediates plant hormone production, nutrient availability and nitrogen fixation. Rhizospheric microorganisms produce and release phytohormones such as indole-3-acetic acid (IAA), gibberellins and cytokinins. Endophytic microorganisms intricately regulate the levels of ABA, SA and JA (169). Auxins are essential for cell division, differentiation, root and shoot development and seed germination. Gibberellins influence embryogenesis, stem elongation, flowering and fruit ripening, whereas abscisic acid regulates cell division and fruit maturation (170). Cytokinins contribute to seed germination and the growth of roots and shoots, while ethylene plays a role in abscission, senescence and reproductive processes. PGPM-derived gibberellins have been shown to enhance plant growth and stress tolerance (171). Plant-associated microbes, known for their production of exopolysaccharides, create biofilms around plant roots, forming a protective shield and aiding nutrient availability (172). The EPS producing *Bacillus cereus* has been reported to improve root and shoot length, boost chlorophyll content, increase water uptake and enhance flowering and fruit production in tomatoes (173). Low-temperature stress significantly limits crop productivity by negatively affecting plant growth and development. Inoculation of grapevines with *B. phytofirmans* PsJN has been shown to enhance tolerance to low nonfreezing temperatures and bolster resistance against grey mould, underscoring its potential to mitigate the detrimental impact of such stressors (174).

Heavy metal stress

The progress in agricultural techniques and industrialization has led to the contamination of soil with heavy metals (175). Lead (Pb), among all the metallic elements with substantial density, is widely distributed and known to hinder root growth by causing dysfunction in cells near the roots (176). Various physicochemical and biological methods designed for contaminant removal have proven unsuccessful, due to high costs, environmental hazards and lack of public acceptance (177). Phytoremediation, which uses plants to remove soil contaminants, is a cost-effective and environmentally sustainable technology that is widely accepted by the public (178, 179). Additionally, plant microbiota play a crucial role in alleviating trace metal toxicity in plants by protecting mechanisms such as heavy metal sequestration, nutrient translocation, bio-solubilization and detoxification, as well as contributing to stress tolerance induction in plants (138). Isolates of *Pseudomonas fluorescens* and *Trichoderma* sp. were obtained from soil contaminated with heavy metals and showed effectiveness in enhancing the chickpea growth and yield by reducing cadmium (Cd) uptake (180). Research indicates that the rhizobacterial strains from mining sites contaminated with heavy metals, focusing on their application to enhance the growth of *Sulla spinosissima* L. in severely contaminated and toxic soil (181). They found that strains such as LMR283 (*Pseudomonas brassicacearum*), LMR340 (*Rhodococcus qingshengii*), LMR249 (*Pseudarthrobacter phenanthrenivorans*) and LMR291 (*Pseudarthrobacter oxydans*) significantly improved various growth parameters in Sulla plants and positively impacted light-harvesting pigments and antioxidant enzymatic functions.

Microorganisms utilize mechanisms such as efflux discharge, evaporation, metal complexation and biochemical detoxification to mitigate stress induced by heavy metals, contributing to enhanced plant growth through the release of plant growth regulators like IAA and ACC. Plant-associated microbes also play a crucial role in reducing ethylene concentration, promoting optimal plant development in the presence of metal stress (182). The living and non-living microbial biomass can effectively eliminate heavy metals from plants, with bacterial and fungal cell walls playing a substantial role in this process (8). Research indicated the pivotal involvement of diverse microorganisms, including proteobacteria, firmicutes and actinobacteria, in the effective mitigation of Pb, As and Mn from the soil (63). While copper accumulation led to growth diminution in Vicia faba, the deleterious effects of copper were effectively mitigated through inoculation with rhizobia and PGPR (183).

Microbial genetic engineering for heavy metal detoxification

Using CRISPR/Cas9 to modify microbial genomes, such as *Mesorhizobium huakuii*, has enhanced cadmium (Cd) detoxification by boosting the synthesis of metal-binding peptides like phytochelatins, which significantly improve both metal uptake and tolerance in polluted environments (184). In addition, genetically engineered microbes can be programmed to alter transporter genes and efflux pathways, improving their ability to bind and export metals. Synthetic microbial communities further combine the strengths of bacteria and fungi, enabling the removal of a wider range of contaminants. Customized rhizobacteria can therefore be developed not only to detoxify Cd more efficiently but also to withstand and remediate multiple pollutants at once, as demonstrated by recombinant strains capable of simultaneously clearing Cd and organic xenobiotics (185).

Genetic and molecular aspects of microorganism-induced stress tolerance in plants

Stress tolerance in plants induced by microorganisms involves complex genetic and molecular mechanisms. The interactions between plants and microorganisms, ranging from beneficial symbioses to antagonistic confrontations, have profound implications for plant health, growth and stress tolerance. The genetic and molecular aspects of microorganism-induced stress tolerance in plants reveal a fascinating realm where intricate signalling pathways, gene regulation mechanisms and microbial interactions converge to shape the plants' ability to withstand environmental challenges. Understanding the genetic and molecular aspects underlying these interactions is crucial for harnessing the full potential of microorganisms in agriculture and sustainable crop production. Tomato plants treated with *Trichoderma asperellum* SL2 showed, through RNA-seq analysis, a marked increase in the expression of genes related to photosynthesis, stress signalling and antioxidant defences, indicating that the fungus triggers transcriptional changes that enhance drought and salt tolerance (186). Exposure of rice seedlings to the microbial volatile compound 3-methylbutanal (3-MB) vapour produced a unique transcriptomic response, as revealed by RNA-seq, with increased expression of salt stress-related genes involved in compatible solute production and redox detoxification (187). Defence responses triggered by a biostimulant in Arabidopsis: RNA-seq analysis revealed that treatment with an Ascophyllum nodosum-based biostimulant ("SuperFifty") quickly activated a range of stress-responsive genes, notably those encoding heat shock proteins and ROS-detoxifying enzymes, providing molecular evidence for enhanced tolerance to abiotic stress (188).

Challenges and prospects in microbe-mediated plant stress management

Microorganisms offer promising solutions for managing plant stress and enhancing agricultural productivity. However, several challenges must be addressed to effectively harness the full potential of microbial-based strategies. Additionally, exploring prospects can guide research and application efforts toward sustainable agricultural practices. Understanding the dynamics of plant-associated microbial communities is crucial for optimising microbial-based strategies for stress management. Long-term field studies and multi-omics approaches are needed to elucidate how microbiomes respond to environmental perturbations and contribute to plant health and stress tolerance (189). Metagenomics and metatranscriptomics reveal the composition and activity of plant-associated microbes under stress, while metabolomics links microbial and plant metabolic changes, including stress-alleviating compounds. Integrating these approaches provides insights into microbial mechanisms that enhance plant stress tolerance. This multi-omics strategy supports the identification of beneficial microbes for developing bioinoculants to improve crop resilience in the field (138). Integrating multi-omics approaches, computational modelling and functional genomics can facilitate the elucidation of these networks. Moreover, studying the cross-talk between genetic, epigenetic and metabolic pathways will provide insights into the molecular basis of microbial-induced stress tolerance in plants. Computational modelling and network analysis techniques can help decipher the hierarchical organization and cross-talk between signalling pathways, transcriptional regulators and metabolic processes involved in stress tolerance.

Innovative delivery methods, such as encapsulation, carrier-based formulations and biofilm coatings, can enhance microbial survival, adhesion and colonization on plant surfaces (190). Biodegradable materials and eco-friendly formulations should be used to minimize environmental impact and ensure product safety. Understanding the factors influencing microbial survival and activity in soil, such as pH, moisture and temperature, can help optimize application timing and dosage for maximum efficacy under field conditions. Scaling up microbial-based interventions for large-scale agricultural use requires addressing logistical, economic and regulatory challenges (191). Establishing cost-effective production methods, quality control measures and distribution networks is essential for making microbial products accessible and affordable to farmers. Collaborative partnerships between research institutions, industry stakeholders and government agencies are needed to support research and development efforts, streamline regulatory approvals and facilitate technology transfer.

Conclusion

Microorganisms that interact with plants play a vital role in supporting plant growth and resilience. They assist plants by facilitating nutrient availability, producing growth-promoting hormones and generating organic compounds that enhance development. These microbes also stimulate plant defence mechanisms, helping plants withstand various stresses. By influencing hormone levels, defence proteins, enzymes and secondary metabolites, they contribute to stress signalling and overall plant health. Plant growth-promoting microbes employ diverse strategies, such as solubilizing phosphorus and other minerals, fixing atmospheric nitrogen, producing siderophores and aiding nutrient uptake, making them key contributors to sustainable agriculture. Despite their potential, challenges remain in effectively applying microbial inoculants, including variability in strain survival, compatibility with different plants, environmental influences and interactions with native soil microbiomes. Limited shelf-life and formulation issues can further reduce their consistency in field conditions. To ensure safe and effective use, long-term field validation and robust regulatory frameworks are essential. Reports such as the FAOs' 2023 guidelines emphasize the importance of quality control, reliable formulation techniques, risk assessment and monitoring of microbial persistence and soil interactions to maximize benefits while avoiding unintended consequences. Addressing these factors will allow the full potential of beneficial microbes to be harnessed for sustainable crop production and future food security.

Acknowledgements

Authors are grateful to the Kerala Agricultural University for providing facilities for carrying out the research.

Authors' contributions

KNA carried out the finalization and submission of manuscript. RA carried out the conception, design, preparation of draft of the manuscript. JPJB, MSN and DKA participated in the literature survey, analysis, writing the original draft. KNA and NC did revision and editing. All authors contributed to the article and approved the submitted version.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

References

1. Chialva M, Lanfranco L, Bonfante P. The plant microbiota: composition, functions and engineering. Curr Opin Biotechnol. 2022;73:135-42. https://doi.org/10.1016/j.copbio.2021.07.003
2. Agler MT, Ruhe J, Kroll S, Morhenn C, Kim ST, Weigel D, et al. Microbial hub taxa link host and abiotic factors to plant microbiome variation. PLoS Biol. 2016;14:e1002352. https://doi.org/10.1371/journal.pbio.1002352
3. Santoyo G. How plants recruit their microbiome? New insights into beneficial interactions. J Adv Res. 2022;40:45-58. https://doi.org/10.1016/j.jare.2021.11.020
4. Trivedi P, Leach JE, Tringe SG, Sa T, Singh BK. Plant–microbiome interactions: from community assembly to plant health. Nat Rev Microbiol. 2020;18:607-21. https://doi.org/10.1038/s41579-020-0412-1
5. Dolatabadian A. Plant-microbe interaction. Biol (Basel). 2020;10:15. https://doi.org/10.3390/biology10010015
6. Lederberg J, McCray A. 'Ome Sweet' Omics - A genealogical treasury of words. The Scientist. 2001;15:7-8.
7. Koul B, Chopra M, Lamba S. Microorganisms as biocontrol agents for sustainable agriculture. In: Samuel J, Kumar A, Singh J, editors. Relationship between microbes and the environment for sustainable ecosystem services. Vol. 1. Elsevier; 2022. p. 45-68. https://doi.org/10.1016/B978-0-323-89938-3.00003-7
8. Rodriguez PA, Rothballer M, Chowdhury SP, Nussbaumer T, Gutjahr C, Falter-Braun P. Systems biology of plant-microbiome interactions. Mol Plant. 2019;12:804-21. https://doi.org/10.1016/j.molp.2019.05.006

9. Suman J, Rakshit A, Ogireddy SD, Singh S, Gupta C, Chandrakala J, et al. Microbiome as a key player in sustainable agriculture and human health. Front Soil Sci. 2022;2:821589. https://doi.org/10.3389/fsoil.2022.821589
10. Zhang L, Zhou J, George TS, Limpens E, Feng G. Arbuscular mycorrhizal fungi conducting the hyphosphere bacterial orchestra. Trends Plant Sci. 2022;27:402-11. https://doi.org/10.1016/j.tplants.2021.10.008
11. Gupta R, Anand G, Gaur R, Yadav D. Plant–microbiome interactions for sustainable agriculture: a review. Physiol Mol Biol Plants. 2021;27(1):165-79. https://doi.org/10.1007/s12298-021-00927-1
12. Nosheen S, Ajmal I, Song Y. Microbes as biofertilizers, a potential approach for sustainable crop production. Sustainability. 2021;13:1868. https://doi.org/10.3390/su13041868
13. Mohanram S, Kumar P. Rhizosphere microbiome: revisiting the synergy of plant-microbe interactions. Ann Microbiol. 2019;69:307-20. https://doi.org/10.1007/s13213-019-01448-9
14. Varghese EM, Manirajan BA, Anith KN, Jisha MS. Physicochemical properties of acid sulphate soil profoundly influence the composition of rhizobacterial community of rice (*Oryza sativa* L.). Rhizosphere. 2024;32:100971. https://doi.org/10.1016/j.rhisph.2024.100971
15. Kakkar A, Nizampatnam NR, Kondreddy A, Pradhan BB, Chatterjee S. Xanthomonas campestris cell–cell signalling molecule DSF (diffusible signal factor) elicits innate immunity in plants and is suppressed by the exopolysaccharide xanthan. J Exp Bot. 2015;66(21):6697-714. https://doi.org/10.1093/jxb/erv377
16. Xu J, Zhou L, Venturi V, He YW, Kojima M, Sakakibari H, et al. Phytohormone-mediated interkingdom signaling shapes the outcome of rice-*Xanthomonas oryzae* pv. *oryzae* interactions. BMC Plant Biol. 2015;15:10. https://doi.org/10.1186/s12870-014-0411-3
17. Venturi V, Keel C. Signaling in the rhizosphere. Trends Plant Sci. 2016;21:3. https://doi.org/10.1016/j.tplants.2016.01.005
18. Mhlongo MI, Piater LA, Madala NE, Labuschagne N, Dubery IA. The chemistry of plant–microbe interactions in the rhizosphere and the potential for metabolomics to reveal signaling related to defense priming and induced systemic resistance. Front Plant Sci. 2018;9:112. https://doi.org/10.3389/fpls.2018.00112
19. Hassan S, Mathesius U. The role of flavonoids in root–rhizosphere signalling: opportunities and challenges for improving plant–microbe interactions. J Exp Bot. 2012;63(9):3429-44. https://doi.org/10.1093/jxb/err430
20. Scervino JM, Ponce MA, Erra-Bassels R, Vierheilig H, Ocampo JA, Godeas A. Arbuscular mycorrhizal colonization of tomato by *Gigaspora* and *Glomus* species in presence of root flavonoids. J Plant Physiol. 2005;162:625-33.
21. Kiers ET, Duhamel M, Beesetty Y, Mensah JA, Franken O, Verbruggen E, et al. Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. Science. 2011;333(6044):880-2. https://doi.org/10.1126/science.1208473
22. Aliche EB, Screpanti C, De Mesmaeker A, Munnik T, Bouwmeester HJ. Science and application of strigolactones. New Phytol. 2020;227:1001-17. https://doi.org/10.1111/nph.16489
23. Fadiji AE, Barmukh R, Varshney RK, Singh BK. Exploring the connectivity between rhizosphere microbiomes and the plant genes: A way forward for sustainable increase in primary productivity. J Sustain Agric Environ. 2023;2:424-43. https://doi.org/10.1002/sae2.12081
24. Cesco S, Mimmo T, Tonon G, Tomasi N, Pinton R, Terzano R, et al. Plant-borne flavonoids released into the rhizosphere: impact on soil bio-activities related to plant nutrition. Biol Fertil Soils. 2012;48:123-49. https://doi.org/10.1007/s00374-011-0653-2
25. Hida A, Oku S, Miura M, Matsuda H, Tajima T, Kato J. Characterization of methyl-accepting chemotaxis proteins (MCPs) for amino acids in plant-growth-promoting rhizobacterium *Pseudomonas protegens* CHA0 and enhancement of amino acid chemotaxis by MCP genes overexpression. Biosci Biotechnol Biochem. 2020;84(9):1948-57. https://doi.org/10.1080/09168451.2020.1780112
26. Jacoby RP, Chen L, Schwier M, Koprivova A, Kopriva S. Recent advances in the role of plant metabolites in shaping the root microbiome. F1000Research. 2020;9:F1000. https://doi.org/10.12688/f1000research.21796.1
27. Brundrett MC, Tedersoo L. Evolutionary history of mycorrhizal symbioses and global host plant diversity. New Phytol. 2018;220:1108-15. https://doi.org/10.1111/nph.14976
28. Bonfante P, Genre A. Mechanisms underlying beneficial plant-fungus interactions in mycorrhizal symbiosis. Nat Commun. 2010;1:48.
29. Rillig MC, Lehmann A, Lanfranco L, Caruso T, Johnson D. Clarifying the definition of common mycorrhizal networks. Funct Ecol. 2025;39:1411-7. https://doi.org/10.1111/1365-2435.14545
30. Põlme S, Bahram M, Jacquemyn H, Kennedy P, Kohout P, Moora M, et al. Host preference and network properties in biotrophic plant-fungal associations. New Phytol. 2018;217:1230-9. https://doi.org/10.1111/nph.14895
31. Leake J, Johnson D, Donnelly D, Muckle G, Boddy L, Read D. Networks of power and influence: the role of mycorrhizal mycelium in controlling plant communities and agroecosystem functioning. Can J Bot. 2004;82(8):1016-45. https://doi.org/10.1139/b04-060
32. Werner S, Polle A, Brinkmann N. Belowground communication: impacts of volatile organic compounds (VOCs) from soil fungi on other soil-inhabiting organisms. Appl Microbiol Biotechnol. 2016;100:8651-65. https://doi.org/10.1007/s00253-016-7792-1
33. Johnson D, Gilbert L. Interplant signalling through hyphal networks. New Phytol. 2015;205(4):1448-53. https://doi.org/10.1111/nph.13115
34. Gorzelak MA, Asay AK, Pickles BJ, Simard SW. Inter-plant communication through mycorrhizal networks mediates complex adaptive behaviour in plant communities. AoB Plants. 2015;7:plv050. https://doi.org/10.1093/aobpla/plv050
35. Bever JD. Preferential allocation, physio-evolutionary feedbacks and the stability and environmental patterns of mutualism between plants and their root symbionts. New Phytol. 2015;205:1503-14. https://doi.org/10.1111/nph.13239
36. Kadowaki K, Yamamoto S, Sato H, Tanabe AS, Hidaka A, Toju H. Mycorrhizal fungi mediate the direction and strength of plant–soil feedbacks differently between arbuscular mycorrhizal and ectomycorrhizal communities. Commun Biol. 2018;1(1):196. https://doi.org/10.1038/s42003-018-0201-9
37. Martin FM, van Der Heijden MG. The mycorrhizal symbiosis: research frontiers in genomics, ecology and agricultural application. New Phytol. 2024;242:1486-506. https://doi.org/10.1111/nph.19541
38. Klein T, Siegwolf RT, Körner C. Belowground carbon trade among tall trees in a temperate forest. Science. 2016;352(6283):342-4. https://doi.org/10.1126/science.aad6188
39. Wagg C, Veiga R, van der Heijden MGA. Facilitation and antagonism in mycorrhizal networks. In: Horton T, editor. Mycorrhizal networks. Ecological studies. Vol. 224. Dordrecht: Springer; 2015. p. 93-113. https://doi.org/10.1007/978-94-017-7395-9_7
40. Roossinck MJ. Evolutionary and ecological links between plant and fungal viruses. New Phytol. 2019;221:86-92. https://doi.org/10.1016/j.molp.2019.05.006
41. Johnston-Monje D, Lundberg DS, Lazarovits G, Reis VM, Raizada MN. Bacterial populations in juvenile maize rhizospheres originate from both seed and soil. Plant Soil. 2016;405:337-55. https://doi.org/10.1007/s11104-016-2826-0
42. Sharma R, Joshi A, Dhaker R. A brief review on mechanism of Trichoderma fungus use as biological control agents. Int J Innov Bio-Sci. 2012;96(2):190-4.
43. Bastias DA, Martínez-Ghersa MA, Ballaré CL, Gundel PE. Epichloë

fungal endophytes and plant defenses: not just alkaloids. Trends Plant Sci. 2017;22:939-48. https://doi.org/10.1016/j.tplants.2017.08.005

44. Mousa WK, Shearer CR, Limay-Rios V, Ettinger CL, Eisen JA, Raizada MN. Root-hair endophyte stacking in finger millet creates a physicochemical barrier to trap the fungal pathogen *Fusarium graminearum*. Nat Microbiol. 2016;1:16167. https://doi.org/10.1038/nmicrobiol.2016.167

45. Mutungi PM, Wekesa VW, Onguso J, Kanga E, Baleba SB, Boga HI. Culturable bacterial endophytes associated with shrubs growing along the draw-down zone of Lake Bogoria, Kenya: assessment of antifungal potential against *Fusarium solani* and induction of bean root rot protection. Front Plant Sci. 2022;12:796847. https://doi.org/10.3389/fpls.2021.796847

46. Gupta S, Pandey S, Sharma S. Decoding the plant growth promotion and antagonistic potential of bacterial endophytes from *Ocimum sanctum* Linn. against root rot pathogen *Fusarium oxysporum* in *Pisum sativum*. Front Plant Sci. 2022;13:813686. https://doi.org/10.3389/fpls.2022.813686

47. Lata R, Chowdhury S, Gond SK, White JJF. Induction of abiotic stress tolerance in plants by endophytic microbes. Lett Appl Microbiol. 2018;66(4):268-76. https://doi.org/10.1111/lam.12855

48. Datta D, Behera L, Chaudhary V, Kumar S, Bisen K. Endophytes: rendering systemic resistance to plants. In: Singh UB, Sahu PK, Singh HV, Sharma PK, Sharma SK, editors. Rhizosphere microbes. Microorganisms for sustainability. Vol. 40. Singapore: Springer; 2022;40:175-95. https://doi.org/10.1007/978-981-19-5872-4_9

49. Rajput S, Sengupta P, Kohli I, Varma A, Singh PK, Joshi NC. Role of *Piriformospora indica* in inducing soil microbial communities and drought stress tolerance in plants. In: Singh H, Vaishnav A, editors. New and future developments in microbial biotechnology and bioengineering. Elsevier; 2022. p. 93-110. https://doi.org/10.1016/B978-0-323-85163-3.00003-X

50. Sun C, Johnson JM, Cai D, Sherameti I, Oelmüller R, Lou B. *Piriformospora indica* confers drought tolerance in Chinese cabbage leaves by stimulating antioxidant enzymes, the expression of drought-related genes and the plastid-localized CAS protein. J Plant Physiol. 2010;167:1009-17. https://doi.org/10.1016/j.jplph.2010.02.013

51. Pii Y, Mimmo T, Tomasi N, Terzano R, Cesco S, Crecchio C. Microbial interactions in the rhizosphere: beneficial influences of plant growth-promoting rhizobacteria on nutrient acquisition process. A review. Biol Fertil Soils. 2015;51:403-15. https://doi.org/10.1007/s00374-015-0996-1

52. Ahemad M. Phosphate-solubilizing bacteria-assisted phytoremediation of metalliferous soils: a review. 3 Biotech. 2015;5:111-21. https://doi.org/10.1007/s13205-014-0206-0

53. Fahad S, Hussain S, Bano A, Saud S, Hassan S, Shan D, et al. Potential role of phytohormones and plant growth-promoting rhizobacteria in abiotic stresses: consequences for changing environment. Environ Sci Pollut Res. 2015;22:4907-21. https://doi.org/10.1007/s11356-014-3754-2

54. Gupta G, Parihar SS, Ahirwar NK, Snehi SK, Singh V. Plant growth promoting rhizobacteria (PGPR): current and future prospects for development of sustainable agriculture. J Microb Biochem Technol. 2015;7:96-102. https://doi.org/10.5772/intechopen.1004252

55. Vacheron J, Desbrosses G, Bouffaud ML, Touraine B, Moenne-Loccoz Y, Muller D, et al. Plant growth-promoting rhizobacteria and root system functioning. Front Plant Sci. 2013;4:356. https://doi.org/10.3389/fpls.2013.00356

56. Ahemad M, Kibret M. Mechanisms and applications of plant growth-promoting rhizobacteria: current perspective. J King Saud Univ Sci. 2014;26:1-20. https://doi.org/10.1016/j.jksus.2013.05.001

57. Glick BR. Bacteria with ACC deaminase can promote plant growth and help to feed the world. Microbiol Res. 2014;169:30-9. https://doi.org/10.1016/j.micres.2013.09.009

58. Vejan P, Abdullah R, Khadiran T, Ismail S, Nasrulhaq Boyce A. Role of plant growth promoting rhizobacteria in agricultural sustainability-a review. Molecules. 2016;21:573. https://doi.org/10.3390/molecules21050573

59. Lugtenberg B, Kamilova F. Plant-growth-promoting rhizobacteria. Annu Rev Microbiol. 2009;63:541-56. https://doi.org/10.1146/annurev.micro.62.081307.162918

60. Pieterse CM, Zamioudis C, Berendsen RL, Weller DM, Van Wees SC, Bakker PA. Induced systemic resistance by beneficial microbes. Annu Rev Phytopathol. 2014;52:347-75. https://doi.org/10.1146/annurev-phyto-082712-102340

61. Gómez-Munõz B, Jensen LS, de Neergaard A, Richardson AE, Magid J. Effects of *Penicillium bilaii* on maize growth are mediated by available phosphorus. Plant Soil. 2018;431(1):159-73. https://doi.org/10.1007/s11104-018-3756-9

62. Raymond NS, Gómez-Muñoz B, van der Bom FJT, Nybroe O, Jensen LS, Müller-Stöver DS. Phosphate-solubilising microorganisms for improved crop productivity: a critical assessment. New Phytol. 2021;229:1268-77. https://doi.org/10.1111/nph.16924

63. Vorholt JA. Microbial life in the phyllosphere. Nat Rev Microbiol. 2012;10:828-40. https://doi.org/10.1038/nrmicro2910

64. Helfrich EJ, Vogel CM, Ueoka R, Schäfer M, Ryffel F, Müller DB, et al. Bipartite interactions, antibiotic production and biosynthetic potential of the Arabidopsis leaf microbiome. Nat Microbiol. 2018;3(8):909-19. https://doi.org/10.1038/s41564-018-0200-0

65. Remus-Emsermann MN, Schlechter RO. Phyllosphere microbiology, at the interface between microbial individuals and the plant host. New Phytol. 2018;218:1327-33. https://doi.org/10.1111/nph.15054

66. Van Der Wal A, Leveau JHJ. Modelling sugar diffusion across plant leaf cuticles, the effect of free water on substrate availability to phyllosphere bacteria. Environ Microbiol. 2011;13:3. https://doi.org/10.1111/j.1462-2920.2010.02382.x

67. Knief C, Delmotte N, Chaffron S, Stark M, Innerebner G, Wassmann R, et al. Metaproteogenomic analysis of microbial communities in the phyllosphere and rhizosphere of rice. ISME J. 2012;6(7):1378-90. https://doi.org/10.1038/ismej.2011.192

68. Mizuno M, Yurimoto H, Iguchi H, Tani A, Sakai Y. Dominant colonization and inheritance of *Methylobacterium* sp. strain OR01 on Perilla plants. Biosci Biotechnol Biochem. 2013;77:1533-8. https://doi.org/10.1271/bbb.130207

69. Krishnamoorthy R, Kwon SW, Kumutha K, Senthilkumar M, Ahmed S, Sa T, et al. Diversity of culturable methylotrophic bacteria in different genotypes of groundnut and their potential for plant growth promotion. 3 Biotech. 2018;8:1-11. https://doi.org/10.1007/s13205-018-1291-2

70. Kalyuzhnaya MG, Gomez OA, Murrell JC. The methane-oxidizing bacteria (methanotrophs). In: McGenity T, editor. Taxonomy, genomics and ecophysiology of hydrocarbon-degrading microbes. Handbook of hydrocarbon and lipid microbiology. Cham: Springer; 2019. p. 1-34. https://doi.org/10.1007/978-3-319-60053-6_10-1

71. Guerreiro MA, Brachmann A, Begerow D, Peğsoh D. Transient leaf endophytes are the most active fungi in 1-year-old beech leaf litter. Fungal Divers. 2018;89(1):237-51. https://doi.org/10.1007/s13225-017-0390-4

72. Arroussi HE, Benhima R, Elbaouchi A, Sijilmassi B, Mernissi NE, Aafsar A, et al. *Dunaliella salina* exopolysaccharides: a promising biostimulant for salt stress tolerance in tomato (*Solanum lycopersicum*). J Appl Phycol. 2018;30:2929-41. https://doi.org/10.1007/s10811-017-1382-1

73. Kumar V, Singh P, Jorquera MA, Sangwan P, Kumar P, Verma AK, et al. Isolation of phytase-producing bacteria from Himalayan soils and their effect on growth and phosphorus uptake of Indian mustard (*Brassica juncea*). World J Microbiol Biotechnol. 2013;29:1361-9. https://doi.org/10.1007/s11274-013-1299-z

74. Souza R, Beneduzi A, Ambrosini A, Costa PB, Meyer J, Vargas LK, et al. The effect of plant growth-promoting rhizobacteria on the growth of rice (*Oryza sativa* L.) cropped in southern Brazilian fields. Plant Soil. 2013;366:585-603. https://doi.org/10.1007/s11104-012-1430-1

75. Verma P, Yadav AN, Kazy SK, Saxena AK, Suman A. Evaluating the diversity and phylogeny of plant growth promoting bacteria associated with wheat (*Triticum aestivum*) growing in central zone of India. Int J Curr Microbiol Appl Sci. 2014;3:5.

76. Zhang H, Zhu J, Gong Z, Zhu J. Abiotic stress responses in plants. Nat Rev Genet. 2022;23:104-19. https://doi.org/10.1038/s41576-021-00413-0

77. Cramer GR, Urano K, Delrot S, Pezzotti M, Shinozaki K. Effects of abiotic stress on plants: a systems biology perspective. BMC Plant Biol. 2011;11:163. https://doi.org/10.1186/1471-2229-11-163

78. Rojas O. Agricultural extreme drought assessment at global level using the FAO-Agricultural Stress Index System (ASIS). Weather Clim Extrem. 2020;27:100184. https://doi.org/10.1016/j.wace.2018.09.001

79. Qadir M, Quillérou E, Nangia V, Murtaza G, Singh M, Thomas RJ, et al. Economics of salt-induced land degradation and restoration. Nat Resour Forum. 2014;38:282-95. https://doi.org/10.1111/1477-8947.12054

80. Bian M, Zhou M, Sun D, Li C. Molecular approaches unravel the mechanism of acid soil tolerance in plants. Crop J. 2013;1:91-104. https://doi.org/10.1016/j.cj.2013.08.002

81. Osei BK, Ahenkorah I, Ewusi A, Fiadonu EB. Assessment of flood prone zones in the Tarkwa mining area of Ghana using a GIS-based approach. Environ Chall. 2021;3:100028. https://doi.org/10.1016/j.envc.2021.100028

82. Augspurger CK. Reconstructing patterns of temperature, phenology and frost damage over 124 years: Spring damage risk is increasing. Ecology. 2013;94:41-50. https://doi.org/10.1890/12-0200.1

83. Yue Y, Zhou Y, Wang J, Ye X. Assessing wheat frost risk with the support of GIS: An approach coupling a growing season meteorological index and a hybrid fuzzy neural network model. Sustainability. 2016;8:1308. https://doi.org/10.3390/su8121308

84. Chaudhry S, Sidhu GPS. Climate change regulated abiotic stress mechanisms in plants: A comprehensive review. Plant Cell Rep. 2022;41:1-31. https://doi.org/10.1007/s00299-021-02759-5

85. Ganie SA, Molla KA, Henry RJ, Bhat KV, Mondal TK. Advances in understanding salt tolerance in rice. Theor Appl Genet. 2019;132:851-70. https://doi.org/10.1007/s00122-019-03301-8

86. Jones JD, Dangl JL. The plant immune system. Nature. 2006;444(7117):323-9. https://doi.org/10.1038/nature05286

87. FAO. Managing salt-affected soils for a sustainable future: proceedings of the second meeting of the International Network of Salt-Affected Soils (INSAS). Rome; 2023. Available from: https://openknowledge.fao.org [Accessed 14 October 2024].

88. Kaur S, Samota MK, Choudhary M, Choudhary M, Pandey AK, Sharma A. How do plants defend themselves against pathogens - Biochemical mechanisms and genetic interventions. Physiol Mol Biol Plants. 2022;28(2):485-504. https://doi.org/10.1007/s12298-022-01146-y

89. War AR, Paulraj MG, Ahmad T, Buhroo AA, Hussain B, Ignacimuthu S, et al. Mechanisms of plant defense against insect herbivores. Plant Signal Behav. 2012;7:10. https://doi.org/10.4161/psb.21663

90. Ben Rejeb I, Pastor V, Mauch-Mani B. Plant responses to simultaneous biotic and abiotic stress: molecular mechanisms. Plants. 2014;3:458-75. https://doi.org/10.3390/plants3040458

91. Khosravi H, Dolatabad HK. Identification and molecular characterization of *Azotobacter chroococcum* and *Azotobacter salinestris* using ARDRA, REP, ERIC and BOX. Mol Biol Rep. 2020;47(1):307-16. https://doi.org/10.1007/s11033-019-05133-7

92. Blaustein RA, Lorca GL, Meyer JL, Gonzalez CF, Teplitski M. Defining the core citrus leaf- and root-associated microbiota: Factors associated with community structure and implications for managing huanglongbing (citrus greening) disease. Appl Environ Microbiol. 2017;83:e00210-7. https://doi.org/10.1128/AEM.00210-17

93. Tkacz A, Pini F, Turner TR, Bestion E, Simmonds J, Howell P, et al. Agricultural selection of wheat has been shaped by plant-microbe interactions. Front Microbiol. 2020;11:132. https://doi.org/10.3389/fmicb.2020.00132

94. Lebeis SL, Paredes SH, Lundberg DS, Breakfield N, Gehring J, McDonald M, et al. Salicylic acid modulates colonization of the root microbiome by specific bacterial taxa. Science. 2015;349(6250):860-4.

95. Schlatter D, Kinkel L, Thomashow L, Weller D, Paulitz T. Disease suppressive soils: new insights from the soil microbiome. Phytopathology. 2017;107:1284-97. https://doi.org/10.1094/PHYTO-03-17-0111-RVW

96. Weller DM, Raaijmakers JM, Gardener BBM, Thomashow LS. Microbial populations responsible for specific soil suppressiveness to plant pathogens. Annu Rev Phytopathol. 2002;40:1. https://doi.org/10.1146/annurev.phyto.40.030402.110010

97. Chialva M, Salvioli di Fossalunga A, Daghino S, Ghignone S, Bagnaresi P, Chiapello M, et al. Native soils with their microbiotas elicit a state of alert in tomato plants. New Phytol. 2018;220:1296-308.

98. Gómez Expósito R, De Bruijn I, Postma J, Raaijmakers JM. Current insights into the role of rhizosphere bacteria in disease suppressive soils. Front Microbiol. 2017;8:2529. https://doi.org/10.3389/fmicb.2017.02529

99. Savary S, Willocquet L, Pethybridge SJ, Esker P, McRoberts N, Nelson A. The global burden of pathogens and pests on major food crops. Nat Ecol Evol. 2019; 3:430-9. https://doi.org/10.1038/s41559-018-0793-y

100. Khanna K, Kohli SK, Sharma N, Kour J, Devi K, Bhardwaj T, et al. Phytomicrobiome communications: Novel implications for stress resistance in plants. Front Microbiol. 2022;13:912701. https://doi.org/10.3389/fmicb.2022.912701

101. Kannojia P, Sharma P, Kashyap AK, Manzar N, Singh UB, Chaudhary K. Microbe-mediated biotic stress management in plants. In: Singh D, Singh H, Prabha R, editors. Plant-microbe interactions in agro-ecological perspectives. Vol. 2. Singapore: Springer; 2017. p. 627-48. https://doi.org/10.1007/978-981-10-6593-4_26

102. Teixeira PJP, Colaianni NR, Fitzpatrick CR, Dangl JL. Beyond pathogens: microbiota interactions with the plant immune system. Curr Opin Microbiol. 2019;49:7-17. https://doi.org/10.1016/j.mib.2019.08.003

103. Nishad R, Ahmed T, Rahman VJ, Kareem A. Modulation of plant defense system in response to microbial interactions. Front Microbiol. 2020;11:1298. https://doi.org/10.3389/fmicb.2020.01298

104. Boller T, Felix G. A renaissance of elicitors: perception of microbe-associated molecular patterns and danger signals by pattern-recognition. Annu Rev Plant Biol. 2009;60:379-406. https://doi.org/10.1146/annurev.arplant.57.032905.105346

105. Pel MJ, Pieterse CM. Microbial recognition and evasion of host immunity. J Exp Bot. 2013;64:1237-48. https://doi.org/10.1093/jxb/ers262

106. Ding LN, Li YT, Wu YZ, Li T, Geng R, Cao J, et al. Plant disease resistance-related signaling pathways: recent progress and future prospects. Int J Mol Sci. 2022;23:16200. https://doi.org/10.3390/ijms232416200

107. Dempsey DMA, Klessig DF. SOS - too many signals for systemic acquired resistance? Trends Plant Sci. 2012;17:538-45. https://doi.org/10.1016/j.tplants.2012.05.011

108. Zeier J. Metabolic regulation of systemic acquired resistance. Curr Opin Plant Biol. 2021;62:102050. https://doi.org/10.1016/j.pbi.2021.102050

109. Van Loon LC, Rep M, Pieterse CM. Significance of inducible defense-related proteins in infected plants. Annu Rev Phytopathol. 2006;44:6. https://doi.org/10.1146/annurev.phyto.44.070505.143425

110. Shah J, Zeier J. Long-distance communication and signal amplification in systemic acquired resistance. Front Plant Sci. 2013;4:30. https://doi.org/10.3389/fpls.2013.00030

111. Zhao S, Li M, Ren X, Wang C, Sun X, Sun M, et al. Enhancement of broad-spectrum disease resistance in wheat through key genes involved in systemic acquired resistance. Front Plant Sci. 2024;15:1355178. https://doi.org/10.3389/fpls.2024.1355178

112. Yu Y, Gui Y, Li Z, Jiang C, Guo J, Niu D. Induced systemic resistance for improving plant immunity by beneficial microbes. Plants. 2022;11:386. https://doi.org/10.3390/plants11030386

113. Mishina TE, Zeier J. The *Arabidopsis* flavin-dependent monooxygenase FMO1 is an essential component of biologically induced systemic acquired resistance. Plant Physiol. 2006;141:1666-75. https://doi.org/10.1104/pp.106.081257

114. Caarls L, Pieterse CM, Van Wees SC. How salicylic acid takes transcriptional control over jasmonic acid signaling. Front Plant Sci. 2015;6:170. https://doi.org/10.3389/fpls.2015.00170

115. Tugizimana F, Mhlongo MI, Piater LA, Dubery IA. Metabolomics in plant priming research: the way forward? Int J Mol Sci. 2018;19:6. https://doi.org/10.3390/ijms19061759

116. Derbyshire MC, Newman TE, Thomas WJ, Batley J, Edwards D. The complex relationship between disease resistance and yield in crops. Plant Biotechnol J. 2024;22:9. https://doi.org/10.1111/pbi.14373

117. Heil M. Damaged-self recognition in plant herbivore defence. Science. 2009;14(7):356-63. https://doi.org/10.1016/j.tplants.2009.04.002

118. Hogenhout SA, Bos JI. Effector proteins that modulate plant–insect interactions. Curr Opin Plant Biol. 2011;14(4):422-8. https://doi.org/10.1016/j.pbi.2011.05.003

119. Wang H, Shi S, Hua W. Advances of herbivore-secreted elicitors and effectors in plant-insect interactions. Front Plant Sci. 2023;14:1176048. https://doi.org/10.3389/fpls.2023.1176048

120. Dave A, Graham IA. Oxylipin signaling: a distinct role for the jasmonic acid precursor cis-(+)-12-oxo-phytodienoic acid (cis-OPDA). Front Plant Sci. 2012;3:42. https://doi.org/10.3389/fpls.2012.00042

121. Sheard LB, Tan X, Mao H, Withers J, Ben-Nissan G, Hinds TR, et al. Jasmonate perception by inositol-phosphate-potentiated COI1–JAZ co-receptor. Nature. 2010;468:400-5. https://doi.org/10.1038/nature09430

122. Memelink J. Regulation of gene expression by jasmonate hormones. Phytochemistry. 2009;70:1560-70. https://doi.org/10.1016/j.phytochem.2009.09.004

123. Sharma S, Rana VS, Sharma U, Sharma S, Likhita J, Sharma N, et al. Appraisal of arbuscular mycorrhiza fungi in fruit production and mitigation against stress: current insights and prospects. Rev Agric Sci. 2025;13(4):1-29. https://doi.org/10.7831/ras.13.4_1

124. Van der Ent S, Verhagen BW, Van Doorn R, Bakker D, Verlaan MG, Pel MJ, et al. MYB72 is required in early signaling steps of rhizobacteria-induced systemic resistance in *Arabidopsis*. Plant Physiol. 2008;146:3. https://doi.org/10.1104/pp.107.113829

125. Yu YT, Wu Z, Lu K, Bi C, Liang S, Wang XF, et al. Overexpression of the MYB37 transcription factor enhances abscisic acid sensitivity and improves both drought tolerance and seed productivity in *Arabidopsis thaliana*. Plant Mol Biol. 2016;90:267-79. https://doi.org/10.1007/s11103-015-0411-1

126. Zhang H, Kim MS, Krishnamachari V, Payton P, Sun Y, Grimson M, et al. Rhizobacterial volatile emissions regulate auxin homeostasis and cell expansion in *Arabidopsis*. Planta. 2007;226:4. https://doi.org/10.1007/s00425-007-0530-2

127. Riaz N, Guerinot ML. All together now: regulation of the iron deficiency response. J Exp Bot. 2021;72:2045-55. https://doi.org/10.1093/jxb/erac450

128. Choudhary DK, Prakash A, Johri BN. Induced systemic resistance (ISR) in plants: mechanism of action. Indian J Microbiol. 2007;47:289-97. https://doi.org/10.1007/s12088-007-0054-2

129. Enebe MC, Babalola OO. The impact of microbes in the orchestration of plants' resistance to biotic stress: a disease management approach. Appl Microbiol Biotechnol. 2019;103:9-25. https://doi.org/10.1007/s00253-018-9433-3

130. Cho MH, Lee SW. Phenolic phytoalexins in rice: biological functions and biosynthesis. Int J Mol Sci. 2015;16:29120-33. https://doi.org/10.3390/ijms161226152

131. Berendsen RL, Pieterse CM, Bakker PA. The rhizosphere microbiome and plant health. Trends Plant Sci. 2012;17:478-86. https://doi.org/10.1016/j.tplants.2012.04.001

132. Vannier N, Agler M, Hacquard S. Microbiota-mediated disease resistance in plants. PLoS Pathog. 2019;15(6):e1007740. https://doi.org/10.1371/journal.ppat.1007740

133. Crane TA, Roncoli C, Hoogenboom G. Adaptation to climate change and climate variability: The importance of understanding agriculture as performance. NJAS Wageningen J Life Sci. 2011;57:179-85. https://doi.org/10.1016/j.njas.2010.11.002

134. Ahmad P, Hashem A, Abd-Allah EF, Alqarawi AA, John R, Egamberdieva D, et al. Role of *Trichoderma harzianum* in mitigating NaCl stress in Indian mustard (*Brassica juncea* L) through antioxidative defense system. Front Plant Sci. 2015;6:868. https://doi.org/10.3389/fpls.2015.00868

135. Jiang QY, Zhuo F, Long SH, Zhao HD, Yang DJ, Ye ZH, et al. Can arbuscular mycorrhizal fungi reduce Cd uptake and alleviate Cd toxicity of *Lonicera japonica* grown in Cd-added soils? Sci Rep. 2016;6(1):21805. https://doi.org/10.1038/srep21805

136. Yadav S, Modi P, Dave A, Vijapura A, Patel D, Patel M. Effect of abiotic stress on crops. In: Shankar S, editor. Sustainable crop production. 1st ed. IntechOpen; 2020. p. 1-10. Available from: https://doi.org/10.5772/intechopen.88434

137. Kuppusamy P, Bagul SY, Das S, Chakdar H. In: Varma A, Tripathi S, Prasad R, editors. Microbe-mediated abiotic stress alleviation. In: Varma A, Tripathi S, Prasad R, editors. Molecular and biochemical basis. Cham: Springer International Publishing; 2019. p. 263-81. https://doi.org/10. 1007/978-3-030-26657-8_16

138. Singh A, Mazahar S, Chapadgaonkar SS, Giri P, Shourie A. Phyto-microbiome to mitigate abiotic stress in crop plants. Front Microbiol. 2023;14:1210890. https://doi.org/10.3389/fmicb.2023.1210890

139. Meena KK, Sorty AM, Bitla UM, Choudhary K, Gupta P, Pareek A, et al. Abiotic stress responses and microbe-mediated mitigation in plants: the omics strategies. Front Plant Sci. 2017;8:172. https://doi.org/10.3389/fpls.2017.00172

140. Santos LF, Olivares FL. Plant microbiome structure and benefits for sustainable agriculture. Curr Plant Biol. 2021;26:100198. https://doi.org/10.1016/j.cpb.2021.100198

141. HUNGRIA M, Mendes I, Campo R. A importância do processo de fixação biológica do nitrogênio para a cultura da soja: componente essencial para a competitividade do produto brasileiro; 2007. Available from: http://www.infoteca.cnptia.embrapa.br/infoteca/handle/doc/468512

142. Lassaletta L, Billen G, Grizzetti B, Anglade J, Garnier J. 50 year trends in nitrogen use efficiency of world cropping systems: the relationship between yield and nitrogen input to cropland. Environ Res Lett. 2014;9(10):105011. https://doi.org/10.1088/1748-9326/9/10/105011

143. Zhang J, Wang LH, Yang JC, Liu H, Dai JL. Health risk to residents and stimulation to inherent bacteria of various heavy metals in soil. Sci Total Environ. 2015;508:29-36. https://doi.org/10.1016/j.scitotenv.2014.11.064

144. Zhang H, Kim MS, Sun Y, Dowd SE, Shi H, Pare PW. Soil bacteria confer plant salt tolerance by tissue-specific regulation of the sodium transporter HKT1. Mol Plant Microbe Interact. 2008;21:6. https://doi.org/10.1094/MPMI-21-6-0737

145. Kaushal M, Wani SP. Plant-growth-promoting rhizobacteria: drought stress alleviators to ameliorate crop production in drylands. Ann Microbiol. 2016;66:35-42. https://doi.org/10.1007/s13213-015-1112-3

146. Yang J, Kloepper JW, Ryu CM. Rhizosphere bacteria help plants tolerate abiotic stress. Trends Plant Sci. 2009;14:1-4. https://doi.org/10.1016/j.tplants.2008.10.004

147. Tripathi P, Singh PC, Mishra A, Srivastava S, Chauhan R, Awasthi S, et al. Arsenic tolerant *Trichoderma* sp. reduces arsenic induced stress in chickpea (*Cicer arietinum*). Environ Pollut. 2017;223:137-45. https://doi.org/10.1016/j.envpol.2016.12.073

148. Otlewska A, Migliore M, Dybka-Stępień K, Manfredini A, Struszczyk-Świta K, Napoli R, et al. When salt meddles between plant, soil and microorganisms. Front Plant Sci. 2020;11:1429. https://doi.org/10.3389/fpls.2020.553087

149. Chirakkara RA, Cameselle C, Reddy KR. Assessing the applicability of phytoremediation of soils with mixed organic and heavy metal contaminants. Rev Environ Sci Biotechnol. 2016;15:299-326. https://doi.org/10.1007/s11157-016-9391-0

150. Fatnassi IC, Chiboub M, Saadani O, Jebara M, Jebara SH. Impact of dual inoculation with *Rhizobium* and PGPR on growth and antioxidant status of *Vicia faba* L. under copper stress. C R Biol. 2015;338:241-54. https://doi.org/10.1016/j.crvi.2015.02.001

151. Hayat R, Ali S, Amara U, Khalid R, Ahmed I. Soil beneficial bacteria and their role in plant growth promotion: a review. Ann microbiol. 2010;60:579-98. https://doi.org/10.1007/s13213-010-0117-1

152. Vardharajula S, Zulfikar Ali S, Grover M, Reddy G, Bandi V. Drought-tolerant plant growth promoting *Bacillus* spp.: effect on growth, osmolytes and antioxidant status of maize under drought stress. J Plant Interact. 2011;6:1. https://doi.org/10.1080/17429145.2010.535178

153. Damodaran T, Sharma DK, Mishra VK, Jha SK, Kannan R, Sah V, et al. Isolation of salt-tolerant endophytic and rhizospheric bacteria by natural selection and screening for promising plant growth-promoting rhizobacteria (PGPR) and growth vigor in tomato under sodic soil. Afr J Microbiol Res. 2013;7:5082-9. https://doi.org/10.5897/AJMR2013.6003

154. Porcel R, Zamarreño ÁM, García-Mina JM, Aroca R. Involvement of plant endogenous ABA in *Bacillus megaterium* PGPR activity in tomato plants. BMC Plant Biol. 2014;14:1-12. https://doi.org/10.1186/1471-2229-14-36

155. Naseem H, Bano A. Role of plant growth-promoting rhizobacteria and their exopolysaccharide in drought tolerance of maize. J Plant Interact. 2014;9:689-701. https://doi.org/10.1080/17429145.2014.902125

156. Ortiz N, Armada E, Duque E, Roldán A, Azcón R. Contribution of arbuscular mycorrhizal fungi and/or bacteria to enhancing plant drought tolerance under natural soil conditions: effectiveness of autochthonous or allochthonous strains. J Plant Physiol. 2015;174:87-96. https://doi.org/10.1016/j.jplph.2014.08.019

157. Yadav J, Verma JP, Jaiswal DK, Kumar A. Evaluation of PGPR and different concentration of phosphorus level on plant growth, yield and nutrient content of rice (*Oryza sativa*). Ecol Eng. 2014;62:123-8. https://doi.org/10.1016/j.ecoleng.2013.10.013

158. Hilker M, Schwachtje J, Baier M, Balazadeh S, Bäurle I, Geiselhardt S, et al. Priming and memory of stress responses in organisms lacking a nervous system. Biol Rev. 2016;91(4):1118-33. https://doi.org/10.1111/brv.12215

159. Jiao W, Tian C, Chang Q, Novick KA, Wang L. A new multi-sensor integrated index for drought monitoring. Agric For Meteorol. 2019;268:74-85. https://doi.org/10.1016/j.agrformet.2019.01.008

160. Caddell DF, Deng S, Coleman-Derr D. Role of the plant root microbiome in abiotic stress tolerance. In: Verma S, White Jr J, editors. Seed endophytes. Cham: Springer; 2019. p. 273-311. https://doi.org/10.1007/978-3-030-10504-4_14

161. Liu H, Brettell LE, Qiu Z, Singh BK. Microbiome-mediated stress resistance in plants. Trends Plant Sci. 2020;25:733-43. https://doi.org/10.1016/j.tplants.2020.03.014

162. Tiwari R, Rana CS. Phytomedicine for diabetes: a traditional approach. Ann Phytomed. 2015;4:108-110.

163. Lata C, Prasad M. Role of DREBs in regulation of abiotic stress responses in plants. J Exp Bot. 2011;62(14):4731-48. https://doi.org/10.1093/jxb/err21

164. Siddique Z, Jan S, Imadi SR, Gul A, Ahmad P. Drought stress and photosynthesis in plants. In: Ahmad P, editor. Water stress and crop plants: a sustainable approach. Vol. 1. New York: Wiley; 2016. p. 1-11. https://doi.org/10.1002/9781119054450.ch1

165. Kaur H, Kohli SK, Khanna K, Bhardwaj R. Scrutinizing the impact of water deficit in plants: Transcriptional regulation, signaling, photosynthetic efficacy and management. Physiol Plant. 2021;172(2):935-62. https://doi.org/10.1111/ppl.13389

166. Fang Y, Xiong L. General mechanisms of drought response and their application in drought resistance improvement in plants. Cell Mol Life Sci. 2015;72:673-89. https://doi.org/10.1007/s00018-014-1767-0

167. Zgadzaj R, Thiergart T, Bozsoki Z, Garrido-Oter R, Radutoiu S, Schulze-Lefert P. *Lotus japonicus* symbiosis signaling genes and their role in the establishment of root-associated bacterial and fungal communities. bioRxiv. 2019;547687. https://doi.org/10.1101/547687

168. Zandi P, Schnug E. Reactive oxygen species, antioxidant responses and implications from a microbial modulation perspective. Biology. 2022;11:155. https://doi.org/10.3390/biology11020155

169. Saeed Q, Xiukang W, Haider FU, Kučerik J, Mumtaz MZ, Holatko J, et al. Rhizosphere bacteria in plant growth promotion, biocontrol and bioremediation of contaminated sites: A comprehensive review of effects and mechanisms. Int J Mol Sci. 2021;22:10529. https://doi.org/10.3390/ijms221910529

170. Sosnowski J, Truba M, Vasileva V. The impact of auxin and cytokinin on the growth and development of selected crops. Agriculture. 2023;13:724. https://doi.org/10.3390/agriculture13030724

171. Hakim S, Naqqash T, Nawaz MS, Laraib I, Siddique MJ, Zia R, et al. Rhizosphere engineering with plant growth-promoting microorganisms for agriculture and ecological sustainability. Front Sustain Food Syst. 2021;5:617157. https://doi.org/10.3389/fsufs.2021.617157

172. Li Y, Narayanan M, Shi X, Chen X, Li Z, Ma Y. Biofilms formation in plant growth-promoting bacteria for alleviating agro-environmental stress. Sci Total Environ. 2024;907:167774.

173. Mukhtar T, Rehman SU, Smith D, Sultan T, Seleiman MF, Alsadon AA, et al. Mitigation of heat stress in *Solanum lycopersicum* L. by ACC-deaminase and exopolysaccharide producing *Bacillus cereus*: effects on biochemical profiling. Sustainability. 2020;12:2159. https://doi.org/10.3390/su12062159

174. Hussain SS, Mehnaz S, Siddique KHM. Harnessing the plant microbiome for improved abiotic stress tolerance. In: Egamberdieva D, Ahmad P, editors. Plant microbiome: stress response. Singapore: Springer; 2018. p. 21-43. https://doi.org/10.1007/978-981-10-5514-0_2

175. Khanna K, Kohli SK, Sharma N, Kour J, Devi K, Bhardwaj T, et al. Phytomicrobiome communications: Novel implications for stress resistance in plants. Front Microbiol. 2022;13:912701. https://doi.org/10.3389/fmicb.2022.912701

176. Zia R, Nawaz MS, Siddique MJ, Hakim S, Imran A. Plant survival under drought stress: Implications, adaptive responses and integrated rhizosphere management strategy for stress mitigation. Microbiol Res. 2021;242:126626. https://doi.org/10.1016/j.micres.2020.126626

177. Spoel SH, Dong X. Salicylic acid in plant immunity and beyond. Plant Cell. 2024;36:1451-64. https://doi.org/10.1093/plcell/koad329

178. Beskoski VP, Gojgic-Cvijovic G, Milic J, Ilic M, Miletic S, Solevic T, et al. Ex situ bioremediation of a soil contaminated by mazut (heavy residual fuel oil)-A field experiment. Chemosphere. 2011;83:34-40. https://doi.org/10.1007/s10532-011-9481-1

179. Hadi F, Bano A. Effect of diazotrophs (*Rhizobium* and *Azatebactor*) on growth of maize (*Zea mays* L.) and accumulation of lead (Pb) in different plant parts. Pak J Bot. 2010;42(6):4363-70.

180. Syed A, Elgorban AM, Bahkali AH, Eswaramoorthy R, Iqbal RK, Danish S, et al. Metal-tolerant and siderophore-producing *Pseudomonas fluorescens* and *Trichoderma* spp. improved the growth, biochemical features and yield attributes of chickpea by lowering Cd uptake. Sci Rep. 2023;13:4471. https://doi.org/10.1038/s41598-023-31330-3

181. Oubohssaine M, Sbabou L, Aurag J. Native heavy metal-tolerant plant growth promoting rhizobacteria improves *Sulla spinosissima* (L.) growth in post-mining contaminated soils. Microorganisms. 2022;10:838. https://doi.org/10.3390/microorganisms10050838

182. Munir N, Hanif M, Abideen Z, Sohail M, El-Keblawy A, Radicetti E, et al. Mechanisms and strategies of plant microbiome interactions to mitigate abiotic stresses. Agronomy. 2022;12:2069. https://doi.org/10.3390/agronomy12092069

183. Zarraonaindia I, Owens SM, Weisenhorn P, West K, Hampton-Marcell J, Lax S, et al. The soil microbiome influences grapevine-associated microbiota. MBio. 2015;6:2. https://doi.org/10.1128/mbio.02527-14

184. Saxena S. The role of CRISPR-Cas9 in environmental restoration: evidence on CRISPR-edited *Mesorhizobium* for cadmium detoxification and broader applications of genetic engineering in enhancing microbial phytoremediation. Int J Res Appl Sci Eng Technol (IJRASET). 2025;13:1. https://doi.org/10.22214/ijraset.2025.66660

185. Misra SK, Kumar A, Pathak K, Kumar G, Virmani T. Role of genetically modified microorganisms for effective elimination of heavy metals. BioMed Res Int. 2024;2024:1. https://doi.org/10.1155/2024/9582237

186. Garcha S, Tohani S. Omics in plant science for improved stress tolerance. J Pure Appl Microbiol. 2025;19(3):1733. https://doi.org/10.22207/JPAM.19.3.41

187. Nguyen DK, Nguyen TP, Lin CC, Ly TT, Li YR, Chang CH, et al. Transcriptome analysis reveals the role of microbial volatile 3-methyl-1-butanol-induced salt stress tolerance in rice (*Oryza sativa* L.) seedlings through antioxidant defense system. Plant Physiol Biochem. 2025;223:109830. https://doi.org/10.1016/j.plaphy.2025.109830

188. Gechev T. Genomics control of biostimulant-induced stress tolerance and crop yield enhancement. Plant J. 2025;123(2):e70382. https://doi.org/10.1111/tpj.70382

189. Mengelkoch S, Gassen J, Lev-Ari S, Alley JC, Schüssler-Fiorenza Rose SM, Snyder MP, et al. Multi-omics in stress and health research: study designs that will drive the field forward. Stress. 2024;27 (1):2321610. https://doi.org/10.1080/10253890.2024.2321610

190. Pandey T, Pandey V. Microbial assistance in nano-carrier development: Innovative strategies in drug delivery. J Drug Deliv Sci Technol. 2024;105:105607. https://doi.org/10.1016/j.jddst.2024.105607

191. Westermann O, Förch W, Thornton P, Körner J, Cramer L, Campbell B. Scaling up agricultural interventions: Case studies of climate-smart agriculture. Agric Syst. 2018;165:283-93. https://doi.org/10.1016/j.agsy.2018.07.007

192. Bastias DA, Martínez-Ghersa MA, Ballaré CL, Gundel PE. Epichloë fungal endophytes and plant defenses: not just alkaloids. Trends Plant Sci. 2017;22:939-48. https://doi.org/10.1016/j.tplants.2017.08.005

193. Mutungi PM, Wekesa VW, Onguso J, Kanga E, Baleba SB, Boga HI. Culturable bacterial endophytes associated with shrubs growing along the draw-down zone of Lake Bogoria, Kenya: assessment of antifungal potential against *Fusarium solani* and induction of bean root rot protection. Front Plant Sci. 2022;12:796847. https://doi.org/10.3389/fpls.2021.796847

194. Gupta S, Pandey S, Sharma S. Decoding the plant growth promotion and antagonistic potential of bacterial endophytes from *Ocimum sanctum* Linn. against root rot pathogen *Fusarium oxysporum* in *Pisum sativum*. Front Plant Sci. 2022;13:813686. https://doi.org/10.3389/fpls.2022.813686

195. Ni L, Punja ZK. Management of fungal diseases on cucumber (*Cucumis sativus* L.) and tomato (*Solanum lycopersicum* L.) crops in greenhouses using *Bacillus subtilis*. In: Islam M, Rahman M, Pandey P, Boehme M, Haesaert G, editors. Bacilli and agrobiotechnology: phytostimulation and biocontrol. Bacilli in climate resilient agriculture and bioprospecting. Cham: Springer; 2019. p. 1-28. https://doi.org/10.1007/978-3-030-15175-1_1

196. Athira S, Anith KN. Plant growth promotion and suppression of bacterial wilt incidence in tomato by rhizobacteria, bacterial endophytes and the root endophytic fungus *Piriformospora indica*. Indian Phytopathol. 2020;73:629-42.

197. Siva M, Sreeja SJ, Susha ST, Heera G, Anith KN. Endophytic *Bacillus* spp. suppress *Rhizoctonia solani* web blight of bush cowpea. Rhizosphere. 2023;25:100682. https://doi.org/10.1016/j.rhisph.2023.100682

198. Yashaswini MS, Nysanth NS, Anith KN. Endospore-forming phyllosphere bacteria from *Amaranthus* spp. suppress leaf blight (*Rhizoctonia solani* Kuhn) disease of *Amaranthus tricolor* L. J Trop Agric. 2022;60:95-108.

199. Yashaswini MS, Nysanth MS, Anith KN. Endospore-forming bacterial endophytes from *Amaranthus* spp. improve plant growth and suppress leaf blight (*Rhizoctonia solani* Kühn) disease of *Amaranthus tricolor* L. rhizosphere. 2021;19:100387. https://doi.org/10.1016/j.rhisph.2021.100387

200. Das MM, Haridas M, Sabu A. Biological control of black pepper and ginger pathogens, *Fusarium oxysporum*, *Rhizoctonia solani* and *Phytophthora capsici*, using *Trichoderma* spp. Biocatal Agric Biotechnol. 2019;17:177-83. https://doi.org/10.1016/j.bcab.2018.11.021

201. Anith KN and Manomohandas TP. Combined application of *Trichoderma harzianum* and *Alcaligenes* sp. strain AMB 8 for controlling nursery rot disease of black pepper. Indian Phytopathol. 2001;54:335-9. https://doi/full/10.5555/20023011338

202. Kollakkodan N, Anith KN, Nysanth NS. Endophytic bacteria from *Piper colubrinum* suppress *Phytophthora capsici* infection in black pepper (*Piper nigrum* L.) and improve plant growth in the nursery. Arch Phytopathol Plant Prot. 2021;54:86-108. https://doi.org/10.1080/03235408.2020.1818493

203. Kollakkodan N, Anith KN, Radhakrishnan NV. Diversity of endophytic bacteria from *Piper* spp. with antagonistic property against *Phytophthora capsici* causing foot rot disease in black pepper (*Piper nigrum* L.). J Trop Agric. 2017;55:63-70.

204. Nysanth NS, Divya S, Nair CB, Anju AB, Praveena R, Anith KN. Biological control of foot rot (*Phytophthora capsici* Leonian) disease in black pepper (*Piper nigrum* L.) with rhizospheric microorganisms. Rhizosphere. 2022;23:100578. https://doi.org/10.1016/j.rhisph.2022.100578

205. Ahmed GA, Makhlouf AH, Selim ME. Efficacy of compost and some biocontrol agents in controlling cucumber white mould disease under protected house conditions. Alexandria Sci Exch J. 2021;42:495-507. https://doi.org/10.21608/asejaiqjsae.2021.178433

206. Sellappan Selvaraj A, Thangavel K, Uthandi S. Arbuscular mycorrhizal fungi (*Glomus intraradices*) and diazotrophic bacterium (*Rhizobium* BMBS) primed defense in blackgram against herbivorous insect (*Spodoptera litura*) infestation. Microbiol Res.

2020;231:126355. https://doi.org/10.1016/j.micres.2019.126355

207. Selvaraj A, Thangavel K, Uthandi S. Arbuscular mycorrhizal fungi (*Glomus intraradices*) and diazotrophic bacterium (*Rhizobium* BMBS) primed defense in blackgram against herbivorous insect (*Spodoptera litura*) infestation. Microbiol Res. 2020;231:126355. https://doi.org/10.1016/j.micres.2019.126355
208. Rajeshwaran B, Faizal MH, Themuhi M, Anith KN. Harnessing endophytic allies: Defense priming in *Vigna unguiculata* (L.) Walp. against *Spodoptera litura* (Fabricius) by bacterial endophytes. Symbiosis. 2025;95:125-40. https://doi.org/10.1007/s13199-025-01034-5
209. Chang HC, Tang YC, Hayer-Hartl M, Hartl FU. SnapShot: molecular chaperones, Part I. Cell. 2007;128:212-e1. https://doi.org/10.1016/j.cell.2007.01.001
210. Hasanuzzaman M, Nahar K, Alam MM, Roychowdhury R, FujitaM. Physiological, biochemical and molecular mechanisms of heat stress tolerance in plants. Int J Mol Sci. 2013;14(5):9643-84. https://doi.org/10.3390/ijms14059643
211. Santos VAHFD, Ferreira MJ, Rodrigues JVFC, Garcia MN, Ceron JVB, Nelson BW, et al. Causes of reduced leaf-level photosynthesis during strong El Niño drought in a Central Amazon forest. Glob Chang Biol. 2018;24:4266-79. https://doi.org/10.1111/gcb.14293
212. Yang X, Lu M, Wang Y, Wang Y, Liu Z, Chen S. Response mechanism of plants to drought stress. Horticulturae. 2021;7:3. https://doi.org/10.3390/horticulturae7030050
213. Acosta-Motos JR, Ortuño MF, Bernal-Vicente A, Diaz-Vivancos P, Sanchez-Blanco MJ, Hernandez JA. Plant responses to salt stress: adaptive mechanisms. Agronomy. 2017;7:18. https://doi.org/10.3390/agronomy7010018
214. Du YT, Zhao MJ, Wang CT, Gao Y, Wang YX, Liu YW, et al. Identification and characterization of GmMYB118 responses to drought and salt stress. BMC Plant Biol. 2018;18:1-18. https://doi.org/10.1186/s12870-018-1551-7
215. Ganie SA, Molla KA, Henry RJ, Bhat KV, Mondal TK. Advances in understanding salt tolerance in rice. Theor Appl Genet. 2019;132:851-70. https://doi.org/10.1007/s00122-019-03301-8
216. Hao S, Wang Y, Yan Y, Liu Y, Wang J, Chen S. A review on plant responses to salt stress and their mechanisms of salt resistance. Horticulturae. 2021;7(6):132. https://doi.org/10.3390/horticulturae7060132
217. Ritonga FN, Chen S. Physiological and molecular mechanism involved in cold stress tolerance in plants. Plants. 2020;9:560. https://doi.org/10.1111/1365-2435.14545
218. Shi Y, Ding Y, Yang S. Molecular regulation of CBF signaling in cold acclimation. Trends Plant Sci. 2018;23:623-37. https://doi.org/10.1016/j.tplants.2018.04.002
219. Tolosa LN, Zhang Z. The role of major transcription factors in Solanaceous food crops under different stress conditions: Current and future perspectives. Plants. 2020;9:56. https://doi.org/10.3389/fmicb.2020.00132
220. Daniel K, Hartman S. How plant roots respond to waterlogging. J Exp Bot. 2024;75:511-25. https://doi.org/10.1093/jxb/erad332
221. Parent C, Capelli N, Berger A, Crèvecoeur M, Dat JF. An overview of plant responses to soil waterlogging. Plant Stress. 2008;2:20-7.

Additional information

Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

Reprints & permissions information is available at https://horizonepublishing.com/journals/index.php/PST/open_access_policy

Publisher's Note: Horizon e-Publishing Group remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Indexing: Plant Science Today, published by Horizon e-Publishing Group, is covered by Scopus, Web of Science, BIOSIS Previews, Clarivate Analytics, NAAS, UGC Care, etc
See https://horizonepublishing.com/journals/index.php/PST/indexing_abstracting

Publisher information: Plant Science Today is published by HORIZON e-Publishing Group with support from Empirion Publishers Private Limited, Thiruvananthapuram, India.