PLANT SCIENCE TODAY
ISSN 2348-1900 (online)
Vol x(x): xx–xx
https://doi.org/10.14719/pst.4342

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REVIEW ARTICLE

Phytomicrobiome –Resilience to climate change

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OPEN ACCESS

ARTICLE HISTORY
Received: 14 July 2024
Accepted: 21 October 2024
Available online
Version 1.0 : 21 November 2024

Check for updates

Additional information

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

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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

CITE THIS ARTICLE
Sankareswari R U, Prabhaharan J, Devi T S. Phytomicrobiome –Resilience to climate change. Plant Science Today (Early Access). https://doi.org/10.14719/pst.4342

Abstract

The abnormal change in weather has resulted in rise in global temperature and the frequency as well as intensity of abiotic factors like drought has a negative influence on agricultural production in many areas. These aspects are mainly related to nutrient acquisition and stress tolerance. Changing the phytomicrobiome or its interactions can improve both of these parameters. "Phytomicrobiome" refers to the microbes that are associated with plants, including bacteria, archaebacteria, fungi, and viruses. It is a community of microorganisms that establish essential ecological relationships with the host plant. This community has the potential to protect the plant against abiotic stresses such as drought, heat, and salinity by producing antioxidant enzymes, plant growth hormones, bioactive compounds, and by detoxifying harmful chemicals, Reactive Oxygen Species (ROS), and free radicals. The abiotic factors have significantly impacted the diversity of microbiome in rhizosphere, phyllosphere and endophytes. To cope with adverse conditions, phytomicrobiomes enables the plants to develop sophisticated mechanisms to sense the stress signals to ensure optimal growth responses. The phytomicrobiome has played a crucial role in creating new bioinoculants, Plant Growth Promoting Rhizobacteria (PGPR) formulations, biofertilizers, biostimulants and biocontrol agents being effective alternatives to chemical fertilizers in future for specific crops, contributing to sustainable agricultural productivity for farmers and society. This article mainly emphasizes on the phytomicrobiome interactions for plant health and how environmentally friendly methods can be used to maximize the agricultural productivity as well as how the phytomicrobiome can be used to reduce the effect of drought stress on plants and boost crop productivity.

Keywords

Climate change; stress resistance; nutrients; phytomicrobiome; bioinoculants

Introduction

According to the Intergovernmental Panel on Climate Change, carbon dioxide (CO_2) in the atmosphere absorbs solar radiation, a process that may raise global temperatures. The weather can change significantly as a result of this process, which is known as global climate change. Greenhouse gas (GHG) emissions have caused climate change, which has an effect on soil systems, natural plant productivity, and human health (1). The primary causes of the increase in atmospheric CO_2 are the patterns of natural resource consumption, extensive industrialization, and urbanization, which result in disruptive natural balance system (2). The concentration of CO_2 in the atmosphere has increased by a staggering 40%, currently at around 414.72 parts per million, surpassing the levels of the pre-industrial era. This alarming increase has caused significant and undeniable impacts on global rainfall, temperature patterns, and soil chemistry, which have gravely affected natural bioresources such as plants and microbes. Moreover, floods, salt stress, and trace elements have been analyzed that the productivity of crop may be reduced by 51-82% and this may led to threaten the food security for future human generations.

Reacting to biotic and abiotic stressors, crops have sophisticated mechanisms. Many signaling pathways, including variations in intracellular calcium levels, the synthesis of secondary signaling molecules like inositol phosphate and reactive oxygen species (ROS), and the activation of kinase cascades which might be responsible for initiating these responses. In addition to serving as Ca^{2+} sensors, calcium-binding proteins are in charge of identifying an increase in intracellular calcium levels in response to unfavorable environmental circumstances. Following activation, Ca^{2+} sensors have two possible mode of action: they can interact with DNA-binding proteins that regulate these genes or bind to cis-elements in the promoters of crucial stress-responsive genes. High Ca^{2+} levels activate Calcium Dependent Protein Kinase (CDPKs), Calcium & Calmodulin dependent Protein Kinase (CCaMK) and phosphatases that phosphorylate/dephosphorylate transcription factors. This regulates stress-responsive gene expression (3). ROS like H_2O_2, $^1O_2$, hydroxyl, and superoxide mediate signaling functions with Ca^{2+} (4). Plants respond to stress through complex pathways, activated by hormones that control physiological processes.

A phytomicrobiome is the microbial community that develops with in plants. Although a great deal of research has been done on bacteria and fungi, little is known about the functional roles that viruses, oomycetes, protozoa, algae, and nematodes play in the phytomicrobiome. A sustained microbial consortium for plant development and output under abiotic stress is provided by the phytomicrobiome, which responds to the genotype and stress tolerance of the plant (5). Plant growth in a particular environmental system has been found to be highly associated with the various qualitative and quantitative microbiomes (6,7).

To fully understand the intricate and dynamic relationship between plants and bacteria, more fundamental information is necessary. As of 2022, for example, there were more than 5,000 reports on the human microbiome. There is comparatively little research in plant sciences (around 800 in Sci. Finder). The fields of biotechnology, genetics, microbiology, crop physiology, food sciences, agriculture, bio economy, bio informatics, and medical sciences are all included in the phytomicrobiome. While the application of a comprehensive microbiome approach is growing, the idea and associated knowledge are still developing. The transition from amplicon-based community analysis to in-depth molecular processes has been brought about by advances in sequencing technologies and machine learning techniques. Meta-transcriptomics, genome-resolved ecogenomics, whole genome association, microbial genomes reconstructed from metagenomics sequencing data, and gene alteration for artificial communities are among the tactics that have garnered interest recently (6,8).To achieve stress tolerance and plant growth to be enhanced, phytomicrobiome diversity utilization for sustainable agriculture is crucial (9).

Diversity of phytomicrobiome

In the phytomicrobiome, various microbes such as bacteria, fungi, archaea, protozoa, oomycetes, viruses, nematodes, and algae play a crucial role for plant growth. The diversity of microbiome, both within species (alpha) and between species (beta), is also important (10).

Microbes in the phytomicrobiome perform a wide range of intricate and interconnected tasks, including the synthesis of numerous classes of small molecules and enzymes, carbohydrates, peptides, lipids, nucleotides, amino acids, and organic substances, as well as the uptake and cycling of nutrients, reproduction, and metabolism related processes (5). Diversity and function possess a considerable and mutualistic relationship in typical circumstances (Fig.1.). Microbe diversity is greater in the rhizosphere compartment compared with the phyllosphere, and the surroundings can have a major effect on both diversity and function. The acquisition and colonization behavior of microbiome species can be profoundly affected by all biological variables, including water, light, pH, and temperature. So, the structure that constitutes the phytomicrobiome has a direct relationship with any abiotic variables stressful events, long-term or short-term, mild to severe. Exploration of a rare treasure of natural reservoir distributed across large community of living organisms is required to generate more fundamental ideas and efficient microbes for abiotic stress tolerance (11).

Rhizosphere Bacteria

The word "rhizosphere" was introduced by Lorenz Hiltner to denote the impact of root exudates on microorganisms within and surrounding the soil. The rhizosphere has the largest impact on plant nutrition and growth, making it the most complex niche (12).

Plant roots interact with microbial communities in their niche, impacting their growth and stress resistance (13) and jointly form the root plant microbiome (14). Based on the plant species, genotypes, and ages, high-performance techniques have revealed that there are up to 1011 bacterial cells per gram of root and at least 30,000 prokaryotes (15).

The rhizosphere microbiota comprises of bacteria, fungus, actinomycetes, and nematodes and is present in complex habitats like the rhizosphere, rhizoplane, and endosphere, is greatly influenced by plants in natural settings. Root exudates are of low molecular weight metabolites like sweeteners, hydrocarbons especially amino compounds, and dead border cells like mucilage, all together release gas such as methane and other gas. The percentage of crop emissions is likely to be 10–20 percent (16).

Root lesions, which are organic compounds secreted by plant roots, have the ability to modify the physical

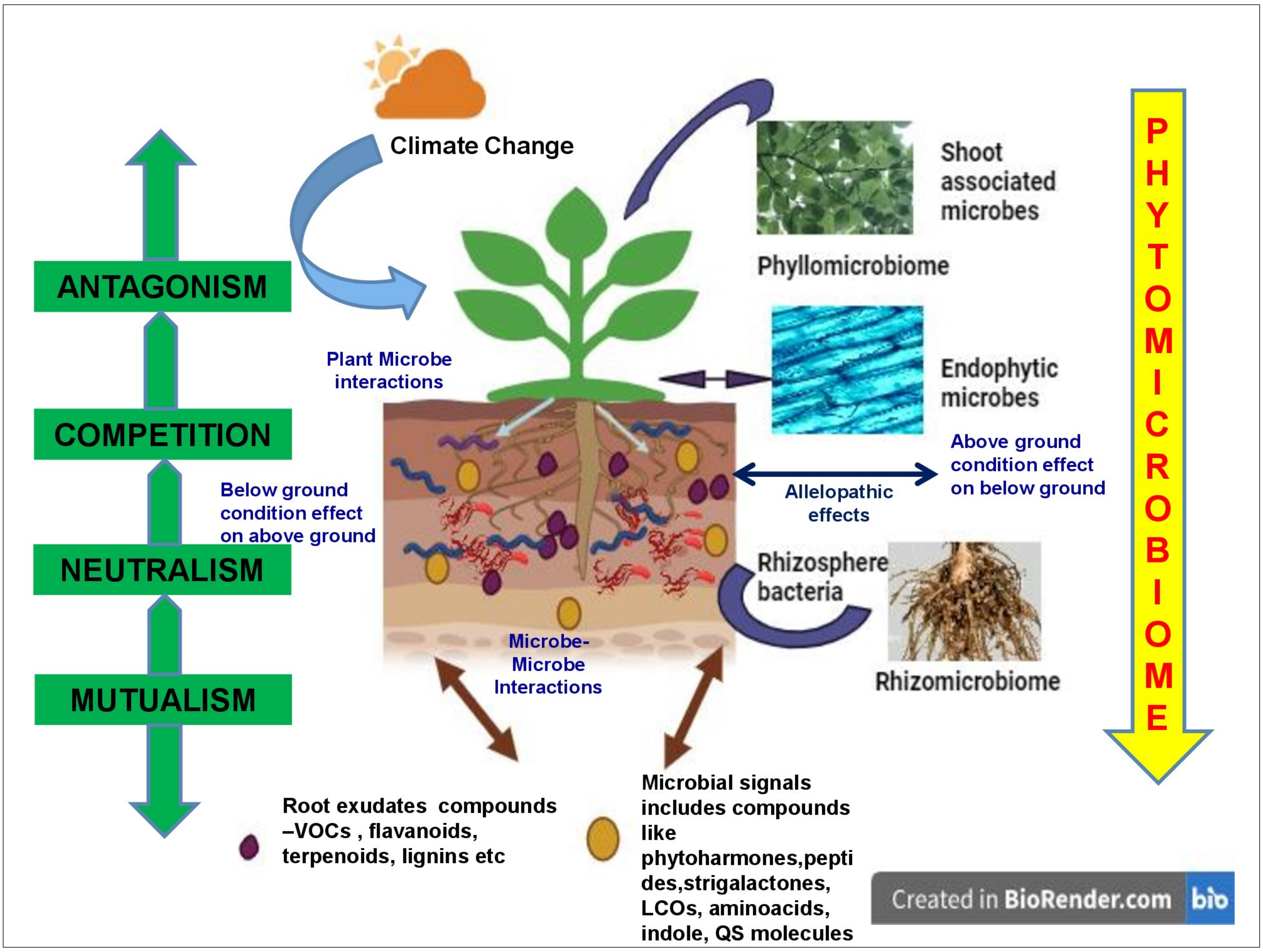

Fig. 1. Overview of Phytomicrobiome.

and chemical properties of soil. This modification creates a suitable environment for the proliferation of microorganisms (17).

Furthermore, different experiments were undertaken to analyze the mechanisms underlying biofilm formation as well as the factors involved in utilizing the substrate and root excretions on it. These studies provide evidence that the composition of rhizosphere microbes is influenced by both the plant species and the exudates released by their roots (18, 15). Bacterial endophyte colonization depends on plant resources and colonization capabilities. The diversified bacterial taxa in rhizosphere microbiome namely Bradyrhizobiaceae, Proteobacteria, Actinobacteria, Acidobacteria, Chloroflexi, Verrucomicrobia, Planctomycetes, Firmicutes, Bacteroidetes, and Gemmatimonatedes (19).

Phyllosphere bacteria

Microbial organisms are ubiquitous in all biomes of the Earth, and they always coexist with plants and their microbiomes. Although microbial densities are generally lower in the 'phyllosphere' (the above-ground part of a plant), it is not safe to assume that the associations between microbes and plants at the apical contact are less significant.

"Phyllosphere" refers to the microorganisms that live on plant leaves. Jakoba Ruinen called it an "ecologically neglected milieu" in 1961. The natural process of moistening and the drying process particularly affect the biological makeup of the phyllosphere population and thereby determine which type of organisms can survive in.

The plant phyllosphere is a niche where a variety of prokaryotes, eukaryotes, and viruses live and interact with one another (20). Particularly, it has been noted that the majority of leaf microbiomes contain Firmicutes, Bacteroidetes, Actinobacteria, and Proteobacteria (21). On the surface of rice leaves, bacterial communities from the genera B*urkholderia, Pseudomonas, and Xanthomonas* were found to be the most prevalent (21). Nevertheless, because *Xanthomonas* is harmful, its application to enhance plant health is uncertain. Also, it was discovered that *Sphingomonas* and *Methylobacterium* dominated the microbial communities of maize leaves (22). The diversity of plant species has a major impact on microbial diversity in the phyllosphere as well (23). Due to their genetic and metabolic variety, different plant species that share the same habitat and environment may have diverse microbial communities (24). One of the main causes of microbial colonization of the phyllosphere is the origin of the microorganisms. The presence of a particular microbial community in an isolated location does not preclude the possibility that its propagules will travel through a variety of vectors, such as wind, rain, insects, pollen, etc., and infect the plant's aerial parts through vectors that will undergo a horizontal transformation within the microbial cells during co-evolution (25).

One of the most well-known functions of phyllosphere microorganisms, according to (26), is fixing atmospheric nitrogen. In humid tropical ecosystems, the main mechanism for supplying nitrogen is phyllosphere nitrogen fixation (27). Due to the higher temperatures and moisture content of the leaf surface, these essential bacteria can flourish in tropical environments and supply the necessary nitrogen to leaf surfaces (28). The phyllosphere of plants in tropical forests is dominated by nitrogen-fixing cyanobacterial species such as *Stygonema, Microcoleus, Oscillatoria,* and *Frischberg* (29). However, research has also shown the importance of cyanobacteria, as well as α-, β-, and γ-proteobacteria, as nitrogen fixers in the phyllosphere (30).

Numerous studies have shown that nitrifying bacteria are present in the phyllosphere of a number of temperate plants in addition to tropical forests (31). In contrast, tropical forests fix nitrogen at a higher rate than temperate plants do (32). Similar findings of nitrogen-fixing microbes in the phyllosphere of other important crop plants, such as rice, wheat, tomatoes, potatoes, mustard, bananas, sugarcane, and jute, have also been reported (33).

The phyllosphere acts as a media that supports the survival or proliferation of diverse microorganisms that are epiphytes, saprophytes and pathogens. Some phyllospheric microorganisms complete their life cycle along with the plant's growth. On the contrary, pathogens enter the leaf and multiply in the interior leaf tissue. Natural surface openings, such as stomata, are important entry ports for microorganisms. Stomata are the key organ for water transpiration and gaseous exchange. This activity is important for plant's growth. Recent studies show that stomata can limit pathogen entry as part of the plant innate defence process. Some plant pathogens have developed counter defence system. For example, the plant pathogen *Pseudomonas syringae* produces coronatine which suppress plant's stomata-based defence system (34).

Through transpiration and photosynthetic processes, phyllosphere microbiomes are essential in regulating the growth and development of plants. The ability of the leaf microbial communities to modify its essential characteristics helps to ensure that the plant is shielded from the effects of changing weather and climate. Crop output, the safety of horticultural products for human consumption, and the fitness of plants in natural environments are all potentially impacted by microbial interactions in the phyllosphere. Apart from the physical and chemical properties of leaves, the structure of phyllosphere communities reflects the movement, endurance, and growth of microbial colonies, which are impacted by several environmental factors as heat and precipitation (35). Plants inevitably face varying levels of UV radiation, causing a broad spectrum of lethal effects, including the generation of intracellular reactive oxygen species (ROS) causing developmental and genetic impairments (36).

As a common hazardous pollutant in Earth's lower atmosphere, ozone has the potential to be remedied by the phyllosphere and its microbiome for air pollution. While ozone phylloremediation has been studied for its effectiveness and mechanism, little is known about the phyllosphere microbiome's response and role. In this study, they revealed *Euonymus japonicus* to varying ozone levels and identified the microbial successions and roles of the phyllosphere microbiome during the exposure (37).

The microbiota of host plants and its mutualistic interactions may confer disease resistance. Although the rhizosphere has received the majority of attention in studies, it is unknown how the microbiome connected to a plant's aerial surface guards against infection. In order to protect rice against *Ustilaginoidea virens*, a phytopathogen that causes false-smut disease and is widely distributed throughout the world, they have discovered a metabolic defense mechanism that underlies the mutualistic interaction between the panicle and the resident microbiota in rice (38).

Plants with fragile, oily leaves frequently have lower microbial loads than those in other environments, according to prior studies (39). It was also shown that microbial communities are linked to various plant environments, most likely as a result of changes in humidity, light and/or UV intensity, airflow rate, and other factors. For instance, bacterial species that produce pigments are typically found on the epiphytic zone, whereas those that use minerals and humic acid are found in the rhizosphere.

Many pigment-producing bacteria like *Methylobacterium, Pseudomonas, and Sphingomonas* are present in the phyllosphere (40). Phyllosphere microbes can also provide tolerance to desiccation and osmotic stress by producing phytohormones like IAA and gibberellic acid and osmoprotectants like proline, choline, soluble sugars, *etc*. (41).

The structures of bacteria and fungi community of the phyllosphere are clearly impacted by global warming (42,43), as does drought (44), suggesting a role for phyllobiomonitoring in gathering and interpreting data that can be put into prediction models for climate warming systems.

Moreover, an effective method for assessing the microbial diversity of the host plant's entire phyllosphere, endosphere, and the root zone must be developed. Identification of the principal microbial populations linked with different places may be useful in the development of techniques for boosting crop output and encouraging sustainable agriculture.

Fungi

Fungi play a crucial role in ecosystem functions, particularly in soil processes (45).They break down organic matter for energy and nutrients while releasing CO_2 (46). Additionally, fungi contribute to soil carbon storage by producing long-lasting organic residues (47). Also, revealed that the enzymes are released by them that break down substances into smaller forms, assisting in the nitrogen and phosphorus cycles (48).

Certain fungi form partnerships with plants, boosting primary productivity. Fungi dominate soil communities contributing 55-89% of microbial biomass (49).With a significant presence in soil communities, fungi heavily influence global biogeochemical cycles.

The wide variety of functions within ecosystems is mirrored by the extensive diversity of fungi in terms of taxonomy, physiology, and morphology. Despite the fact, millions of fungus species are thought to exist in the world (50,51), only a fraction of them have been identified, with even fewer being ecologically characterized, particularly in natural environments (52). Nonetheless, certain distinct fungal lifestyles exist, each associated with specific functional traits that significantly impact ecosystem processes. For example, yeasts would thrive on simple substances like glucose, decomposer fungi are known to break down complex materials like lignin, cellulose, and chitin (53). Furthermore, mycorrhizal fungi form beneficial relationships with plant roots, mostly using the carbon of their host crops as opposed to natural organic components (54). Depending on their composition and roles, those numerous fungal categories are anticipated to have distinct effects on carbon dynamics. Therefore, shifts in fungal communities due to environmental changes, like increased droughts linked to climate change, could alter ecosystem functions, highlighting the importance of understanding fungal diversity and its implications on ecosystem stability (55). However, the correlation of feedback depends on the strength of the relationship between various traits. An important factor is the relationship between specialization in simple carbon molecules and adaptations to drought for particular species of fungi, especially yeasts.

Understanding which physiological and morphological characteristics contribute to drought tolerance and how these traits impact ecosystem functions is crucial. Recently, researchers have started constructing models centered on microbial characteristics to enhance predictions of ecosystem functions (55). These models, including those focused on distinct functional groups of microbes (56, 57) can effectively address ecosystem feedback triggered by changes in microbial communities, thereby enhancing predictive accuracy (58). For characteristics-based models, an extensive knowledge of the correlations across attributes within different fungal species, and for function-based models, the varied distribution of these characteristics across different fungal species, is vital for improving these models.

Fungal Characteristics Associated with Ecosystem Functions

The exploration of fungal characteristics associated with key terrestrial ecosystem functions, including organic carbon decomposition, nitrogen and phosphorus transformations, and soil carbon sequestration. These processes are vital for fungi as they strive to acquire carbon while simultaneously obtaining nitrogen and phosphorus through mineralization, depolymerization, and nutrient immobilization. Fungi's ability to handle unfavorable conditions also plays a crucial role in determining the impact of these processes amidst changing environmental conditions. Additionally, specific stress tolerance traits like melanin or ß 1, 3 - glucan production can directly influence soil carbon storage. We outline the costs and benefits for fungi, the broader implications for ecosystem dynamics and global biogeochemistry, and variations in the capability to execute these processes across different fungal species.

Cellulose decomposition

The most common biopolymer on land and a major component of plant cell walls is cellulose (59). It consists of glucose units that fungi can utilize for energy. Fungi consume glucose for both growth (anabolic processes) and respiration (catabolic processes), producing CO_2 as a by-product.

Lignin decomposition

To access cellulose, nitrogen, and other resources guarded by lignin in plant waste, fungi employ extracellular peroxidases that break down lignin (60).Since lignin is the second most common biopolymer on land (61), its breakdown significantly impacts carbon cycling (62). Additionally, because lignin is frequently mixed with other substances in plant litter, the breakdown of lignin by fungi promotes the breakdown of these substances and quickens the turnover of litter in ecosystems. Fungi are usually regarded as the predominant decomposers of lignin, while certain bacteria can also break down lignin.

Fungi breakdown lignin by utilizing high-oxidation-potential peroxidases like lignin peroxidases (LiP), manganese peroxidases (MnP), and versatile peroxidases (VPLs) for lignin (63, 64). These enzymes are encoded by genes found in only a fraction of fungal taxa, mainly within the Agaricomycetes class of Basidiomycota (60).

Transformation of Phosphorus and Nitrogen

Microorganisms play a crucial part in the process of plant P acquisition because they help plants absorb P outside of the rhizosphere and convert hard-to-utilize P to accessible P (65). Phosphorus Solubilizing Microrganisms (PSMs) can create organic acids and iron carriers, control plant hormone levels, fix nitrogen, and have P-solubilizing effects in addition to promote the uptake and growth of rice nutrients (66).

PSMs can synthesize 1-aminocyclopropane-1-carboxylate (ACC) deaminase to improve phosphorus absorption and disease resistance, thereby increasing plant growth and yield. They can also secrete plant hormones such as auxins, cytokinins, and gibberellins, as well as antifungal compounds and volatile bactericidal metabolites (67). In order to shield plants from several soil-borne diseases and encourage plant growth, PSMs can also release lyases, antibiotics, and iron transporters (69).

Furthermore, some strains have varying capacities to withstand abiotic stress. For example, *Streptomyces laurentii* EU-LWT3-69 can withstand drought stress (70), and *Pseudomonas* PGERs17 can withstand cold stress (71).

According to (72), phosphates like calcium, magnesium, iron, and aluminum phosphates are classified as insoluble P. On the other hand, soluble P primarily takes the form of hydrogen phosphate and dihydrogen phosphate ions (HPO_4^{2-} and $H_2PO_4^-$) (73-74). According to (75), organic P mostly refers to P-containing organic compounds such phosphonates, orthophosphate diesters, monoesters, and organic polyphosphates.

The cycling of inorganic and organic phosphorus in soil depends on the phosphatases and organic acids that microorganisms produce (76).

Enzymatic hydrolysis is the primary process utilized to dissolve the organic forms of P, whereas organic acids are primarily responsible for dissolving insoluble inorganic P. The primary mechanism by which organic acids dissolve insoluble inorganic P is as follows: complex metal ions like iron, aluminum, and calcium in soil release bound phosphate ions; lowering the pH of the medium facilitates the dissolution of insoluble inorganic P; and organic acid anions compete with phosphate ions for binding sites on soil particles, reducing soil adsorption of phosphate ions. In addition to increasing the solubility of insoluble P, such as calcium phosphate and apatite, PSM-secreted organic acids also chelate with cations, such as Ca^{2+}, Fe^{3+}, Al^{3+}, and Mg^{2+}. Furthermore, organic acid anions physically or electrostatically compete with inorganic P for the same adsorption sites in the soil, releasing phosphate ions and raising the effective P content (68).

The types, amounts, and phosphate solubility of organic acids produced by PSM differ (77). But according to (78), *Trichoderma* sp. produces a variety of organic acids, including as lactic acid, fuzzy acid, ascorbic acid, isocitric acid, malic acid, citric acid, and phytic acid.

Among the several organic acids produced by bacteria that have been the subject of in-depth research is glutamic acid, which is regarded as a common and significant organic acid (79). Through the combined action of glucose dehydrogenase (GDH), which dissolves insoluble phosphate, and pyrroloquinoline quinine (PQQ), glucose can generate gluconic acid (80).In order to improve phosphate fertilizer management in contemporary agriculture, *Pseudomonas* creates gluconic acid, which increases phosphate solubility (81,82).

Before being used by plants, organic P must first be converted into inorganic P. Plants are unable to absorb organic P directly. When there is little accessible P content, the primary method of mineralizing organic P is by enzymatic hydrolysis. PSMs can hydrolyze organic P using biological enzymes such phosphatase, phytase, and C-P lyase (83). PSM mineralization is significantly influenced by the hydrolytic enzymes phosphatase and phytase (37).

PSMs generate phosphatase in addition to secreting phytase, which is needed to mineralize organic P. Phosphatases are classified as alkaline phosphatase (ALP) and acid phosphatase (ACP), and the environment's acidity and alkalinity have a major impact on each enzyme's ability to exist. According to (84) and (85), ALP predominates in neutral and alkaline soils, whereas ACP is more prevalent in acidic soils.

Furthermore, phosphatase activity is influenced by temperature, and a rise in temperature might boost the activity of phosphatases released by PSMs (86). With the exception of phytase, phosphatases are responsible for mineralizing about 90% of the organic P in soils (87). Phosphatases are produced by a wide variety of bacteria and fungi, such as *Bacillus, Aspergillus, and Pseudomonas* (88).

AMF mineralization in soil

The process of mineralization through which a colony of beneficial organisms travels on the surface of fungal hyphae of Arbuscular Mycorrhiza to reach an organic patch in the form of a biofilm. We postulated that: (i) AM fungal hyphae create distinct chemical (by releasing exudates) and physical (by forming water films) environments that facilitate bacterial migration to the organic phosphorus patch; and (ii) bacterial migration will stimulate the growth of PSB and AM fungi in the organic phosphorus patch, thereby augmenting the organic phosphorus's mineralization (89).

AMF emit substances such glomalin, a glycoprotein generated by hyphae and spores of the AMF, and increase the absorption area of the roots, hence improving nutrient absorption. Soil globulin facilitates the intake of hard-to-dissolve elements like iron and phosphorus (90). Because P is rapidly absorbed from soil particles, areas free of Pi quickly grow around the roots. Beyond these P-depleted zones, mycorrhizal roots' extraradical hyphae absorb the bioavailable Pi that would otherwise be unavailable to plants.

Nitrogen depolymerization

Extracellular chitinase plays a significant role in breaking down chitin found in fungi cell walls and arthropod exoskeletons. This enzyme is crucial for converting chitin into glucosamine, which fungi can then use as a nutrient source. The process of breaking down large N-containing polymers into smaller, easily absorbable compounds is essential in the nitrogen cycle (91). Several types of fungi have been confirmed to produce extracellular chitinase and can thrive solely on chitin as a source of nitrogen or carbon (92).

(93-95) suggested that extracellular enzymes called proteases and peptidases which have been played a crucial role in breaking down protein compounds in the soil, releasing nitrogen that fungi can absorb. Fungi utilize these enzymes to break down proteins into smaller peptides and amino acids, which they can then absorb using specific membrane transport proteins (96). Particularly, mycorrhizal fungi are known for their ability to efficiently degrade proteins as a nitrogen source.

Stress Tolerance Traits

ß 1, 3-glucan, trehalose, RNA helicase, melanin, and budding development are some of the characteristics that enable fungus to continue growing in extraordinarily dry, hot, or cold environments. Each of these features is discussed here because, according to (97), they can act as "response" traits that could influence changes in the makeup of fungal communities in response to environmental conditions. Melanin and ß 1, 3-glucan may also act as impact traits by causing the deposition of fungus-derived carbon in the soil, which could directly affect ecosystem function. Considering that microbial leftovers may account for up to 50% of the organic carbon in soils, this process is crucial (98).

(99) Research indicated that ß1, 3 - Glucan is an important component of fungal cell walls, enhancing their strength and integrity by forming cross-linkages with chitin. Research suggests that fungal cell walls primarily consist of chitin, with some species also including ß 1, 3-Glucan (100). This carbohydrate can make up a significant portion of the fungal cell wall's dry weight and plays a crucial role in protecting against environmental stresses like drought .Additionally, the presence of ß1,3-Glucan may contribute to the resistance of fungal cell walls to decomposition, potentially influencing soil carbon storage in response to various stress factors.

Trehalose is a beneficial compound that enhances stress tolerance in fungi through various mechanisms (101). It helps by replacing water molecules in cell membranes, safeguarding them from dehydration and freezing injury. Additionally, trehalose aids in improving heat tolerance by stabilizing proteins under heat stress (102). Moreover, it functions as an osmolyte in fungi (103). Studies have shown an increase in trehalose levels in fungi when exposed to environmental stress. Although trehalose concentrations vary and have been predominantly studied in yeasts, it plays a significant role in fungi, requiring resources that could otherwise support growth or metabolism. This high-energy compound can constitute up to 20% of fungal biomass (104). According to research findings, an ecological system's annual gross primary productivity may be negatively impacted by the carbon expenditure generated by producing stress-resistant chemicals like trehalose during only one dry period (105).

In colder temperatures, RiboNucleicAcid (RNA) helicase assists molecular RNA by connecting to or unfolding them, allowing translation to continue (106). Fungi with these helicases exhibit improved cold tolerance and can thrive in colder environments (107) and generated during stress response (108). Melanin, a protective pigment found in fungi, offers defense against various environmental stresses, making melanized fungi common in extreme environments like the Antarctic (109). Melanin-containing fungi are resistant to decomposition and store carbon in soils. This suggests that melanin production in fungi could play a critical role in connecting environmental stress to ecosystem function. Melanized fungi such as Dothideomycetes / Chaelothyriales) exist within the Ascomycota (110), yeast (111), Mycorrhiza (112), free living filamentous groups (113,114).

Endophytes

Endophytic microorganisms reside within plant tissues without causing disease symptoms (115). The classification of endophytic fungi is based on a lineage, host spectrum, tissue colonisation degree, and method of transmission (116).

The transmission of endophytes is crucial for establishing and sustaining endophytic communities over time and space. Horizontal transmission is responsible for a continuous supply of endophytes from the adjacent plant setting, whereas upward transfer fosters the transfer of endophytic populations from mother plants to their offspring *via* embryos. This method also helps to maintain the endophytic microbiome composition across generations (117,118).

Abundant literature suggests that fungal endophytes can enhance plant growth and improve their resilience to various stressors in exchange for nutrients and shelter (119,120).

There is evidence to suggest that fungal endophytes rely on bioactive molecules to induce growth of plants and participate in reactions of adaptation or immunity (121). Also, a few literatures suggest that seed-borne endophytic fungi might encourage germination of seeds and initial emergence of seedlings, and potentially influence the crop's overall growth and response to external indications.

Fungal endophytes have a diverse chemical repertoire shaped by their environment within the plant, making them an exceptional source of bioactive molecules. There is an ample literature that reports how fungal endophytes can improve plant growth and tolerance towards biotic and abiotic stresses, in exchange for nutrients and shelter.

Stress signaling pathways in plants

Plant harmones

Plants, being immobile organisms, are frequently subjected to a diverse range of environmental stresses, both abiotic and biotic in nature. Abiotic stressors consist of heat, cold, salt stress, and drought, whereas biotic stressors are mostly caused by bacteria, fungi, viruses, nematodes, and insects. In order to adapt to such adverse circumstances, crops have evolved sophisticated mechanisms to detect warning signs of stress to initiate optimal growth responses. Plant hormones are key players in enhancing crops to make themselves to adjust to unfavorable environmental conditions.

Plants have complex signalling pathways that respond to abiotic and biotic stresses. These mechanisms include modifications in the intracellular Ca^{2+} concentration, kinase cascade activation, and the synthesis of secondary signaling substances such as reactive oxygen species (ROS). Calcium binding proteins function as Ca^{2+} sensors that can activate stress-responsive genes or interact with DNA-binding proteins to regulate their expression. Ca^{2+} also works with other second messengers like ROS. Under stressful conditions, the body experiences an uptick in ROS production, commonly referred to as 'the oxidative burst' (4). These reactive oxygen species (ROS) molecules, which included superoxide anion radical (SOA), hydroxyl radical, singlet oxygen ($^1O_2$), and hydrogen peroxide (H_2O_2), were essential to signalling processes. For example, H_2O_2 in *Arabidiopsis* triggers the cascade of mitogen-activated protein kinase (MAPK), which in turn causes the overexpression of particular genes linked to stress, so illuminating the ROS-mediated stress response (122).

The stress-response mechanism in plants is a highly intricate process that involves the activation of several integrated pathways in response to external stresses (Fig. 2.). Plant harmones act as mediator for stress responsiveness due to microbial communities interactions within the crop and they could have the ability to control a wide range of physiological processes. Auxins, gibberellins, cytokinins, abscisic acid, ethylene, salicylic acid, jasmonates, brassinosteroids, and strigolactones are the most important hormones that plants produce. There are nine different categories of plant hormones. Among them, the five plant harmones *viz.,* abscisic acid, brassinosteroids, salicylic acid, jasmonates, and ethylene are recognized to be important mediators of the plant defense mechanism against environmental stresses and infections. The signaling pathways of these hormones are strongly linked together, permitting the formation of a complex and effective stress mechanism (123).

Heat stress

Plant defend against heat stress

In the last century, there has been a noticeable shift in the average temperature worldwide, and this trend is expected to persist at an accelerated pace (124). These fluctuations in temperature patterns can lead to harsher winters and scorching summers, directly impacting the growth and sustainability of plant communities (125). Temperature affects physiological and biochemical processes in plants, especially photosynthesis, growth, and respiration, when outside of normal ranges. Various biochemical changes occur within the cell membrane, resulting in modifications to its viscosity, permeability, and fluidity, as has been demonstrated through research (126). Furthermore, enzymatic studies have shown that enzymes such as Ribulose-1, 5-bisphosphate carboxylase/ oxygenase (RuBisCO), phosphoenol pyruvate carboxylase (PEP-case), pyruvate phosphate dikinase (PPDK), adenosine triphosphate (ATP) synthase, and antioxidant enzymes may experience alterations or inhibition. These findings highlight the complex nature of cellular biochemistry and the importance of understanding the underlying mechanisms that govern enzymatic activity. Therefore, further research is necessary to investigate the impact of these changes and their potential implications in various biological contexts (127).

Heat stress is a well-defined phenomenon that occurs due to prolonged temperatures above a particular limit, which permanently impairs the proliferation and developmental processes of plants.

Both day time and night time temperatures have been identified as major limiting factors for plant growth. Previous studies have shown that night time temperatures can play a critical role in a plant's response to heat stress. The term "thermotolerance" refers to a plant's capacity to withstand high temperatures and still generate a useful crop. Even a slight increase in the average atmospheric

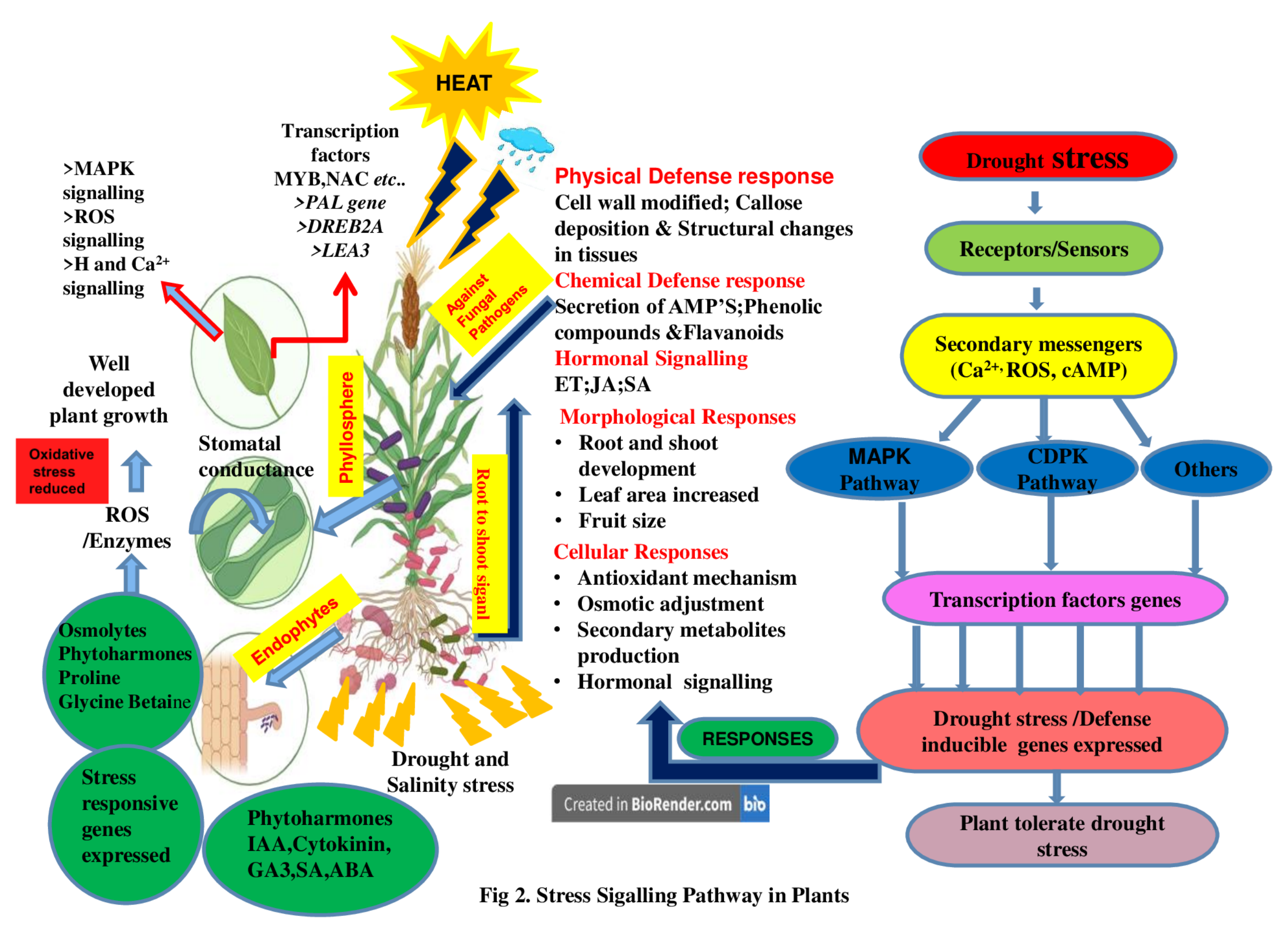

Fig. 2. Stress signalling pathway in plants.

temperature beyond the particular limit can be gravely endangered in many parts of the world.

Tomato (*Solanum lycopersicum* L.) belongs to the family Solanaceae, and it is a widely cultivated crop. Mexico, Brazil, Spain, and Italy are the major tomato producing countries where as Belgium and Netherlands lead in yield per hectare (128). Tomato fruit production is significantly impacted by high temperature stress. Even though tomato plants are capable of growing in variable climates, there would be rise in day time as well as evening temperatures exceeding 26 and 20 °C, respectively, can have a significant impact on fruit setting and yield (129).

According to research conducted by (130), numerous plant species have evolved defense mechanisms to combat challenging conditions. This is due to their exposure to various stresses throughout their evolutionary history. One such survival strategy against heat stress employed by plants is the accumulation of sugars, amino acids, and betaines (131).

High temperatures also affect the process of photosynthesis, altering how the membranes move and upsetting the overall stability of metabolic processes. This leads to an excess of unstable oxygen species formation and oxidative damage (132).

(133) Observed a notable alteration in phenolics content of and it's enzymatic activity under drought stress in tomatoes. Also, found that a deduction in total biomass led to an increase in the concentration of soluble phenolics, as well as a decrease in peroxidase and polyphenol oxidase enzyme activity under heat stress at 35 °C.

Polyamines (PAs) are little, widely dispersed molecules which acts as a crucial players for regulating physiological processes and various stress responses in plants; they accumulate during abiotic stress, such as heat stress (134,135). Through osmosis modifications, PAs improve ecological stress tolerance, maintain membrane balance, and control stomatal activities in plants.

Stress affects fatty acids, which in turn affects photosynthetic function, enclosed by a membrane proteins, and respiration of mitochondria in autopsies (136). They studied how photosynthesis in autopsies plants with altered fluidity in their membranes and Nabisco activation was affected by temperature. They also discovered that (135) highlighted the role that Glycine Betaine (GB) plays in improving resistance to heat stress. GB is an essential molecule that enhances plant thermotolerance by activating hips during heat shock.

(137) mentioned that GB activated Club (HASP100), aiding in protein disaggregation under heat shock. Salicylic acid (SA), also known as 2-hydrocarbon acid, is necessary for acute reactions, systematic resistance, and acquired temperature tolerance (138).

(139,140) discovered that SA boosted induced HASP accumulation in plants. Additionally, (141) noted that SA enhanced the stress response under high temperature shock in tomato plants. In Silvia militarize cell culture; salicylic acid treatment improved the activity of antioxidant enzymes and phenolic compounds (141).

Endogenous proline accumulation levels increase in maize roots under low water potential, serving as a tolerance mechanism against osmotic stress (142). Additionally, the application of exogenous accumulation of proline in maize plants can induce antioxidant activity, improve survivability in plants, and minimize transpiration during osmotic stresses induced by heat and salt stress (143,144).

Polyethylene glycol (PEG)-induced increase in osmotic potential hinders upward shoot growth but promotes the development of lateral roots, indicating a possible strategy employed by maize plants to cope with water scarcity (145).

Recently, there has been an increase in the usage of plant growth promoting compounds, like naturally occurring organic acid that aid in the plant development, is acetic acid, and it has been used to relieve osmotic stress in plants. By speeding up metabolism and enhancing food and water absorption, it has been demonstrated to enhance plant growth and stress tolerance (146)

Myo-inositol accumulation, a crucial point of intersection for biotic and abiotic stress responses, is favorably correlated with plants' ability to withstand abiotic stress (147). Gamma-aminobutyric acid (GABA) accumulation was higher in many plants during osmotic, saline, and drought, because it controls effector proteins (148).

Exogenous GABA decreased H_2O_2 production and increased the activity of enzymes such Catalase (CAT), Peroxidase (POD), Ascorbate Peroxidase (APX), MonoDehydroAscorbate Reducatase (MDHAR), and Glutathione Reductase (GR), which enabled plants to withstand drought (149). However, in perennial ryegrass planted in drought-prone or well-irrigated areas, GABA treatment did not significantly change superoxide dismutase and catalase enzymatic activity (150). These results suggest that GABA activates the glyoxalase and antioxidant enzymatic pathways, increasing tolerance to oxidative stress caused by abiotic conditions such as dryness

Salinity stress

Salinity is recognized as a highly damaging environmental stress that significantly reduces the productivity and quality of crops worldwide. More than twenty per cent of the global agricultural land is stressed by salt, and due to human and natural activity, these prone areas are constantly growing. However, this challenge has intensified significantly in dry and semi-dry areas in the past two decades because of the growing need for irrigation water (151).

Stress by salt is one major climatic factor that influences the proliferation and progression of vegetation. It can raise osmotic pressure, and result in hazardous salt accumulation (152). Crop development and growth are negatively impacted by salt stress,and it throws biological and physiological equilibrium off, causes ion toxicity, oxidative stress, and osmotic stress, and increases plant susceptibility to infection. Plants can be harmed or killed by salt stress in three main ways.

Electrical conductivity and permeability would be altered if the soil has higher concentrations of salt, which lowered the soil's water-holding capacity and causes a shortage of water. Eventually, this leads to biological conditions like drought, interruption of the cell membrane itself, and knocking down of protein due to different ions' toxic effects (mostly Na+).

In addition to the impacts stated above, salt-related stress causes a variety of biophysical and chemical changes in plants, which have an impact on the cycle of photosynthesis other biosynthesis processes, seed development behaviour, and survival. Different crops react differently to salinity; halophytes can easily reproduce and survive in brackish circumstances, while glycophytes, typically exhibit lower growth and overall output. Because of the buildup of sodium and chlorine in the leaf, increased osmotic concentrations at the root-soil interface have a slow effect. Along with decreased spread of leaves and the inhibition of lateral sprout generation, this results in decreased shoot growth.

Plant cells can adjust to low soil water potential by amassing suitable solutes and dispersing ions in response to salt stress. In addition, under salt stress circumstances, the naturally generated abscisic acid (ABA) concentration increases, causing variations in the expression of genes. Additionally, by upsetting the ion balance and restricting access to essential nutrients required for vegetative development and functioning, high concentrations of ions such as Na+, Cl^- displace other mineral nutrients in crops. Secondary stressors that may restrict seedling germination, improvement, and development are produced when osmotic imbalance and toxicity from ions are combined (153).

Water deficit situations brought on by salt decrease stomatal conductance, a phenomenon that lowers the rate of photosynthesis in plants and promotes the accumulation of reactive oxygen species (ROS). These comprise highly reactive and often deadly radicals composed of oxygen and its derivatives, such as hydroxyl radicals (OH-), singlet oxygen ($^1O_2$), hydrogen peroxide (H_2O_2), and radicals including superoxide (O_2^-). They have the potential to disrupt various cellular components like proteins, lipids, and nucleic acids, as well as compromise the plant strength (154).

On the other hand, NaCl can also act as an elicitor (155), applying a natural elicitor in the form of NaCl to increase the generation and buildup of secondary phenolic substances in Melissa officinalis L. Pots containing solutions containing 50 or 100 mM sodium chloride were added to stress the plants to prepare them for salt stress. Plants seemed to develop less when exposed to NaCl treatments, whereas total phenol compounds, bioavailable flavonols, anthocyanins, and phenolic acids seemed to build up more quickly. The effect was most noticeable at 100 mM NaCl. However, the salt stress did not affect the proper functioning of the PS II photosystem or the build-up of photosynthetic pigments.

In nature, plants produce secondary metabolites as a defense mechanism against environmental stresses. NaCl boosts the biosynthesis of phenolic secondary metabolites in *Melissa officinalis* L. Eliciting plants with NaCl (0, 50 or 100Mm) offers a convenient and cost-effective way to enhance the quality of lemon balm, potentially increasing health-promoting phytochemical levels in herbal products.

Plants have to evolve efficient adaptation mechanisms to withstand high salinity because they are immobile. Crops use a variety of strategies to adjust for salt related stress, including ion equilibrium control, osmotic stress response network activation, phytohormone signalling mediation, cytoskeleton stability, and cell wall composition. Gaining insight into the processes underlying these physical and biochemical reactions to salt stress could assist in developing effective methods for raising crop yields in agriculture. Plants therefore adapt physically to deal with these conditions.

A rise in apoplastic water content, which maintains leaf turgidity and helps counteract the effects of salinity, is one common response seen in species subjected to salt stress, along with changes in cell wall flexibility and higher osmotic adjustment. Many substances are now widely recognized to play a role in the water balance of plants. These include organic acids (malate as well as oxalate) and nitrogen-based compounds (such as proteins, betaine, glutamate, aspartate, glycine, proline, choline, and 4-gamma aminobutyric acid) and a few carbohydrate compounds encompass sucrose, sorbitol, mannitol, glycerol, and pinitol. The two most important effective compatible solutes among the organic osmolytes that may assist in alleviate the effects of salt stress and enhance the development of crop are proline (Pro) and glycine betaine (GB).

Microbial inoculants for sustainable agriculture

Numerous studies have indicated that Plant Growth Promoting Rhizobacteria (PGPR), biofertilizers, bio-inoculants, biostimulants, and bio-control agents can be effective alternatives to chemical fertilizers, thereby enhancing sustainable agricultural productivity (156).

Several products are currently available in the market to improve the availability of nitrogen and phosphorus for crop uptake. Culturable Plant Growth Promoting Rhizobacteria (PGPR) and endophytes demonstrate significant potential in increasing agricultural production and are expected to play a crucial role in reducing reliance on chemical fertilizers in the future. However, the inconsistent efficacy poses a primary challenge in utilizing Plant Growth Promoting Rhizobacteria (PGPR), often due to factors such as lack of competitiveness with native soil microflora, limited root colonization ability, and insufficient desired activities. Adhering to recommended protocols in field applications, along with addressing issues related to bioformulation preparation in unsuitable carrier materials and survival in diverse soil types, contribute to the effectiveness of Plant Growth Promoting Rhizobacteria (PGPR) (157).

Many microbial formulations are developed by various biofertilizer companies, introducing strains from different agroclimatic zones that may not be locally adapted. To overcome these challenges, it is crucial to develop locally adapted Plant Growth Promoting Rhizobacteria (PGPR) inoculants tailored to specific crops, using suitable carrier materials to enhance their longevity and effectiveness, ultimately contributing to sustainable agricultural productivity for farmers and society (158).

Recent studies suggest that challenges in plant-microbe interactions can be addressed by utilizing synthetic communities composed of endophytes and organic materials. Microbial inoculants from the phytomicrobiome, particularly the core microbiome, show promise in overcoming these challenges by capitalizing on their co-evolution with plants to effectively colonize plant tissues and enhance plant traits (158).

Leveraging endophytic core microbiome members can reduce competition with soil microbiota by colonizing plant tissues internally, providing protection (159). Modifying the phytomicrobiome on-site to adjust its composition and functions based on plant requirements presents opportunities for optimization. For example, boosting the population and roles of core microbiome members that enhance plant resistance to pests and diseases could significantly enhance agricultural productivity. Some studies have proven the efficiency of such approaches, like using 1 - Amino Cyclopropane -1- Carboxylate (ACC) deaminase to regulate the rhizosphere microbiome and mitigate stress caused by high soil salinity (160).

Continuous advancements in bioinoculant technologies are essential for long-term success and improved effectiveness. These advancements involve utilizing consortia, synthetic communities instead of individual isolates, endophytic microbes, and innovative formulation techniques. The future of microbial strategies depends on our capacity to manage the native phytomicrobiome within the plant environment to enhance the performance of advantageous microbiota. Although strides have been taken in phytomicrobiome research, critical knowledge gaps exist, such as understanding the process of microbial colonization in plant tissues, identifying chemical and molecular signals that attract beneficial microbes in the root zone and interior of plants, and discerning the pivotal plant-associated microbiota and their reactions to agricultural methods and climate variations and it seems closely related to the studies of 161,162. By systematically addressing these gaps, novel phytomicrobiome tools could be developed to significantly increase agricultural output and environmental sustainability. In the future, phytomicrobiome applications could emerge as more efficient resources as bio inoculants and bio pesticide aswellas bio insecticide agents for supporting vegetation development under various climatic challenges, potentially leading to the creation of tailored endophytic consortia for fostering sustainable agriculture.

Future perspectives

The agricultural microbial sector is experiencing rapid growth, with microbial amendments emerging as a key driver exceeding the agrochemical market. However, addressing technical and translational challenges is necessary to further propel this growth. Studying the intricate relationship between plants and their microbiomes requires substantial extensive intiatives, including understanding the ecological processes and factors that influence the functions of the phytomicrobiome.

Phytomicrobiomes are essential for plant well-being and soil health, as they impact resource distribution, pest management, and the production and modulation of organic compounds in the soil. Yet, the intricate nature of these interactions, involving physiological, molecular, and environmental factors, remains incompletely understood.

Researchers are exploring the potential of incorporating genetic traits from other environmental microbes to enhance plant growth and colonization. However, technical challenges in transferring multiple gene traits and societal concerns around genetically modified foods need to be addressed.

Integrating microbiome tools into farming practices requires a thorough understanding of plant-microbiome interactions and the factors influencing phytomicrobiome functions. While the effectiveness of microbial products like biofertilizers varies, they are anticipated to play a vital role in future farming practices.

Conclusion

The implications of phytomicrobiome research for agriculture are significant, as it holds the potential to enhance nutrient cycling, promote plant growth, suppress diseases, and improve tolerance to abiotic stresses. Exploring the intricate connections between plants and their microbial counterparts can guide the advancement of sustainable farming methods, optimizing plant-microbe interactions for enhanced crop yield and environmental preservation, potentially revolutionizing agricultural approaches and enhancing food security amid changing climates.

Acknowledgements

I would like to express my sincere gratitude to the Ex Vice-Chancellor Dr.K.Ramasamy, Professor (Agrl. Microbiology), TNAU, Coimbatore for his valuable guidance to write this paper. I am grateful to all the scientists who provided a qualitative digital environment for academic exploration and knowledge acquisition.

Authors' contributions

RU gathered the relevant material and produced a well-organized diagrammatic paper. JP made a contribution by offering a suggestion for the material compilation. TS provided a summary and revision assistance for the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

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

Ethical issues: None.

AI Declaration

During the preparation of this review article, all the authors listed were used (Grammarly Software Tool) in order to pharaphrase the sentence and figure was drawn using bio render Software. After using this tool, the authors reviewed and edited the content as needed and take the full responsibility for the content of the publication.

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