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MICROBIOME AND PLANT METABOLITES IN ECOSYSTEM RESTORATION

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Abstract

Plant-microbiome interactions play a crucial role in ecosystem restoration, offering a natural and effective means to restore soil health, promote biodiversity, and enhance resilience in degraded landscapes. This article explores the functions and ecological contributions of plant metabolites and soil microbiomes in supporting key restoration processes, such as stress tolerance, nutrient cycling, and pathogen defense. Plant metabolites, including primary and secondary compounds like flavonoids, terpenoids, and phenolics, act as biochemical signals that attract beneficial microbes and deter pathogens, establishing a dynamic exchange that enhances soil fertility and microbial diversity. Soil microbiomes, in turn, support plant growth by transforming nutrients into bioavailable forms, improving root structure, and enabling plants to withstand environmental stressors like drought and salinity. Advanced technologies, including genomics, metabolomics, and synthetic biology, offer new insights into these complex plant-microbe relationships, allowing for targeted restoration strategies that optimize nutrient cycling and ecosystem resilience. However, challenges remain, such as the high costs of omics technologies, the need for interdisciplinary collaboration, and the ecological considerations of using genetically modified organisms in natural environments. By integrating advanced scientific tools with ecological principles, restoration efforts can harness plant-microbiome synergy to create self-sustaining, resilient ecosystems capable of adapting to future environmental changes. This study highlights the potential of plant-microbiome interactions as a foundation for sustainable ecosystem restoration, emphasizing the importance of interdisciplinary approaches to foster innovation and long-term ecological stability.

Key words: Ecosystem restoration; Plant-microbiome interactions; Soil health; Nutrient cycling; Microbial diversity; Resilience; Synthetic biology.

Introduction

Ecosystem degradation has become a pressing issue worldwide, with diverse landscapes affected by human-induced changes such as deforestation, agricultural expansion, pollution, and climate change (Jie *et al*., 2002; Haq *et al*., 2024). These disruptions harm biodiversity, alter soil composition, and destabilize vital ecosystem services, affecting everything from carbon sequestration and water purification to nutrient cycling (Elisha & Felix, 2020). Restoration ecology, therefore, aims to reverse these negative impacts, with approaches that often integrate biological, chemical, and ecological strategies to rehabilitate degraded landscapes and foster resilient ecosystems (Temperton *et al*., 2019). Restoration efforts seek to mimic natural processes, often reintroducing native species and soil organisms to create self-sustaining systems that can adapt to future environmental challenges (Simenstad *et al*., 2006). Given the complex interplay of biotic and abiotic factors in these ecosystems, successful restoration requires an in-depth understanding of ecosystem dynamics, including the interactions between plants, soil, and microbial communities (Eisenhauer *et al*., 2019; Ali *et al*., 2024). Restoration efforts have historically focused on replanting or soil amendment, but recent studies suggest that the integration of plant metabolites and soil microbiomes plays a crucial role in speeding up recovery, enhancing biodiversity, and creating stable, adaptive ecosystems that resist future degradation (Coban *et al*., 2022).

In degraded environments, soil health is often compromised, with the loss of beneficial microbial communities and essential nutrients that plants rely on for growth (Lehman *et al*., 2015; Akram *et al*., 2024). Reintroducing plant metabolites bioactive compounds that plants naturally produce and fostering a healthy soil microbiome can significantly aid restoration efforts by promoting nutrient cycling, stabilizing soil structure, and enhancing plant resilience (Singh Rawat *et al*., 2023). Plant metabolites, such as flavonoids, terpenoids, and phenolics, are known for their multifaceted roles in ecological processes, acting as chemical signals to attract beneficial microbes, deter pathogens, and facilitate nutrient exchange (Shah and Smith, 2020; Saud *et al*., 2023; Younis *et al*., 2024). These metabolites serve as a bridge between plants and microbes, establishing a symbiotic relationship that is vital for nutrient cycling and soil fertility (Mhlongo *et al*., 2018). The interactions between plant metabolites and microbial communities create a dynamic microenvironment around plant roots, or the rhizosphere, which acts as a hub for microbial activity and nutrient transformation (Ho *et al*., 2017). By understanding and harnessing these interactions, scientists and ecologists can design targeted restoration strategies that restore ecological functions, improve soil quality, and ensure long-term ecosystem stability (Miller *et al*., 2017).

Soil microbiomes, the diverse communities of bacteria, fungi, and other microorganisms in the soil, play a central role in ecosystem health and resilience (Dubey *et al*., 2019). In healthy soils, these microbiomes contribute to processes like nitrogen fixation, phosphorus solubilization, and organic matter decomposition, all of which are critical for plant growth and soil structure (Hartmann and Six, 2023). However, in degraded ecosystems, microbial diversity and functionality are often reduced, leading to imbalanced nutrient cycles and poor soil fertility (Lal, 2015). By introducing specific plant species that release metabolites beneficial for microbial growth, restoration projects can effectively 'seed' the soil with a supportive environment for these microbial communities to thrive (de-Bashan *et al*., 2012). Furthermore, soil microbes are instrumental in mitigating abiotic stressors such as drought, salinity, and soil compaction, factors often exacerbated in degraded landscapes (Nizamani *et al*., 2024). When beneficial microbes are reintroduced or stimulated through plant metabolites, they can help create conditions that allow other native species to reestablish, fostering a return to biodiversity and ecosystem stability (Coban *et al*., 2022). This synergy between plant metabolites and soil microbiomes not only accelerates restoration but also creates a self-sustaining system, where plants and microbes support each other, maintaining soil health and ecosystem function over time (Fig. 1) (Pedrinho *et al*., 2024).

The objective of this study is to explore and synthesize the role of plant metabolites and soil microbiomes in ecosystem restoration, particularly their contributions to improving soil health, promoting biodiversity, and fostering resilience in degraded landscapes. This article examined the types of plant metabolites critical to restoration, the structure and functions of soil microbiomes, and the mechanisms by which plant-microbiome interactions aid in nutrient cycling, stress tolerance, and soil stabilization. Additionally, it considered emerging technologies such as genomics and synthetic biology that offer new tools for optimizing these interactions. Through this comprehensive analysis, the study aims to underscore the importance of plant-microbiome relationships as foundational to effective, sustainable restoration strategies.

Plant metabolites and their ecological functions: Plant metabolites are essential to the ecological health and resilience of ecosystems, particularly in the context of ecosystem restoration (Singh *et al*., 2019). These bioactive compounds, produced by plants as part of their metabolic processes, play critical roles in supporting plant growth, facilitating interactions with soil microbiomes, and enhancing plant resilience against environmental stressors (Trivedi *et al*., 2022). In restoration projects, plant metabolites serve as chemical bridges that connect plants with soil microorganisms, enabling nutrient cycling and fostering healthy microbial communities (Afridi *et al*., 2022). They also aid plants in adapting to abiotic stressors, such as drought or salinity, commonly found in degraded ecosystems (Beattie *et al*., 2024). By examining the various types of plant metabolites, their production under different environmental conditions, and their interactions with soil microbiomes, we can better understand how these compounds contribute to the restoration and long-term sustainability of ecosystems.

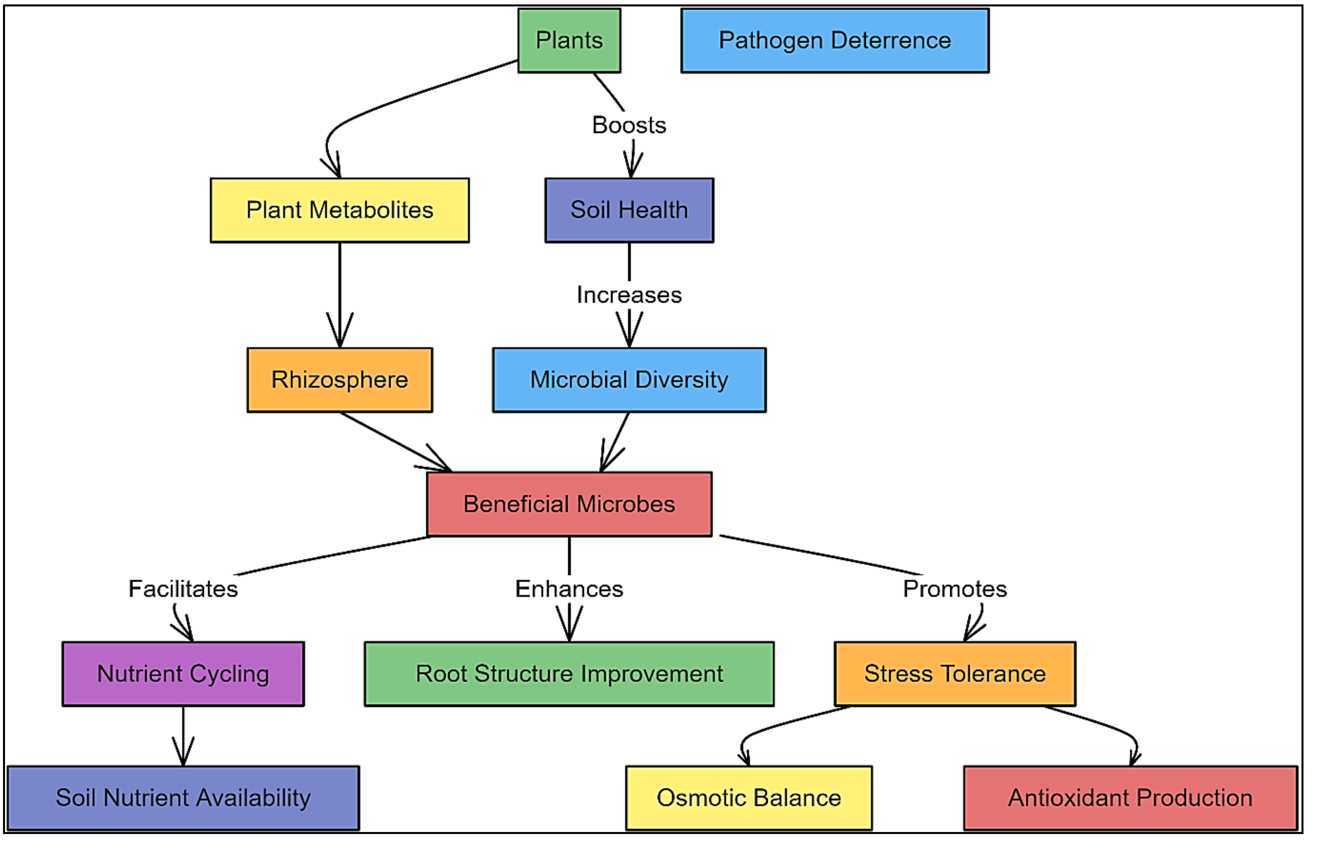

Fig. 1. Flowchart of Plant-Microbiome Interactions in Restoration.

Table 1. Overview of key plant metabolites.

S. No.	Main metabolite	Role	Examples	References
1.	Primary Metabolites	Essential for plant growth and development, including sugars, amino acids, and fatty acids	Integral to biomass production in plants	(Adetunji *et al*., 2021)
2.	Secondary Metabolites	Play roles in defense, pollination, and environmental interactions	alkaloids, tannins, resins, gums, latex	(Stevenson *et al*., 2017)
2.1	Phenolics	Function as antioxidants, UV protectants, and structural components in plant cell walls	Flavonoids, tannins	(Lattanzio *et al*., 2009; Panchawat & Ameta, 2021)
2.2	Terpenes	Defense against herbivores, antibacterial properties, widely used in commercial applications	Limonene in citrus, menthol in mint	(Ninkuu *et al*., 2021)
2.3	Alkaloids	Toxicity against herbivores and pathogens; widely used in pharmacology for physiological effects	Nicotine in tobacco, morphine in poppies	(Matsuura & Fett-Neto, 2015)
2.4	Flavonoids	Antioxidant, anti-inflammatory, and protective roles in plants and human health	Found in fruits and vegetables	(Maleki *et al*., 2019)
2.5	Lignans and Neolignans	Exhibit anti-inflammatory and anticancer properties; important for dietary contributions	Enterolactone, schibitubin B	(Zálešák *et al*., 2019)
2.6	Shikimate-Phenylpropanoid Pathway Metabolites	Defense against pathogens and pests, provide structural support in plants	Lignin, stilbenes in wood and bark	(Li *et al*., 2024)

Types of plant metabolites: Plant metabolites are generally divided into two categories: primary metabolites and secondary metabolites, each with unique ecological roles (Table 1). Primary metabolites, such as carbohydrates, amino acids, and nucleotides, are essential for the plant's basic physiological functions, including growth, development, and reproduction (Sanchez & Demain, 2008). These compounds are universal to nearly all plant species and serve as foundational molecules in the formation of more complex secondary metabolites (Salam *et al*., 2023). While primary metabolites are crucial for the plant's internal metabolism, their ecological impact extends to providing an initial energy source for soil microbes, which, in turn, contribute to nutrient cycling within the ecosystem (Philippot *et al*., 2013). This metabolic foundation is especially relevant in restoration settings, where nutrient availability may be limited, and primary metabolites can serve as initial “fuel” to help rebuild soil microbial communities and encourage plant establishment (Jacoby *et al*., 2017).

Secondary metabolites, on the other hand, are diverse compounds synthesized from primary metabolites and are not essential for the plant’s survival but provide ecological advantages (Karlovsky, 2008). These include classes such as flavonoids, terpenoids, alkaloids, and phenolic compounds, each with distinct biological functions that extend to ecosystem-level impacts (Horner *et al*., 1988). Flavonoids, for example, act as antioxidants and protect plants from UV damage, while also serving as signaling molecules that attract beneficial microbes (Shah & Smith, 2020). Terpenoids are known for their aromatic properties, which play roles in deterring herbivores and attracting pollinators, contributing to both plant defense and reproduction (Boncan *et al*., 2020). Alkaloids and phenolics have antimicrobial properties, protecting plants from pathogenic bacteria and fungi (Tiku, 2018). By understanding the specific roles of these secondary metabolites in ecosystem interactions, restoration projects can leverage particular plant species to introduce these beneficial compounds into degraded soils, fostering a favorable microenvironment that supports both plant and microbial community recovery (Barea, 2015).

The ecological roles of primary and secondary metabolites reveal how plants interact with their environment beyond their own survival needs (Karlovsky, 2008). In restoration, selecting plant species with rich profiles of specific secondary metabolites can aid in re-establishing soil health, providing plants with natural defenses, and enabling mutualistic relationships with soil microbes (Su *et al*., 2023). These interactions create a feedback loop where plant growth and soil health reinforce each other, contributing to a stable, resilient ecosystem (Zhao & Riaz, 2024). Secondary metabolites, in particular, have gained attention in ecological restoration because of their multifunctional roles in plant-microbe interactions, abiotic stress tolerance, and even enhancing soil structure (Iqbal *et al*., 2023). Consequently, both primary and secondary metabolites are integral components in designing restoration strategies that aim to rehabilitate degraded ecosystems holistically (Butu *et al*., 2021).

Environmental influence on metabolite production: The production and composition of plant metabolites are not static; they are highly influenced by environmental factors such as soil type, temperature, moisture, and light availability (Ncube *et al*., 2012). Variability in these factors leads to significant differences in metabolite profiles, which, in turn, affects plant-microbe interactions and overall ecosystem function (Akula & Ravishankar, 2011). Soil type, for example, determines the availability of essential nutrients and minerals, directly impacting the metabolic pathways that plants utilize (Jacoby *et al*., 2017). In nutrient-poor soils, plants may prioritize the production of primary metabolites to support basic growth needs (Kleinert *et al*., 2018). Conversely, in nutrient-rich soils, plants have the resources to produce a wider range of secondary metabolites, which can enhance their interactions with the surrounding microbial community (Chomel *et al*., 2016). This adaptability is particularly relevant in restoration settings, where soil conditions are often suboptimal, and selecting plants that can thrive in specific soil types and produce beneficial metabolites can accelerate the restoration process (Ehlers *et al*., 2020).

Temperature and moisture levels are also crucial determinants of metabolite production, particularly secondary metabolites (Yang *et al*., 2018). High temperatures often induce the synthesis of stress-related metabolites, such as terpenoids and phenolic compounds, which help plants cope with heat and drought conditions (Yeshi *et al*., 2022). Similarly, fluctuating moisture levels impact the production of certain metabolites that protect plants from dehydration or root pathogens, which can be common in degraded soils (Bogati & Walczak, 2022). Under drought stress, for instance, plants may increase the synthesis of osmo-protectants and antioxidants to prevent cellular damage (Nawaz *et al*., 2022). These compounds not only aid the plants in surviving stressful conditions but also influence microbial communities in the rhizosphere, as certain stress-related metabolites attract beneficial microbes that can help plants cope with adverse conditions (Rasheed *et al*., 2024). Understanding these environmental influences is vital for selecting plant species that can maintain their metabolite production even under the challenging conditions typical of degraded ecosystems.

Additionally, light availability plays a role in shaping metabolite production, especially for compounds like flavonoids, which protect plants from UV radiation (Idris *et al*., 2018). In shaded or low-light conditions, plants may reduce flavonoid production, which could impact their ability to interact effectively with specific microbial communities (Xu *et al*., 2024). This relationship between environmental conditions and metabolite production has significant implications for restoration projects (Ehrenfeld & Toth, 1997). By selecting plant species that can adapt their metabolite profiles according to environmental cues, restoration practitioners can encourage the establishment of resilient plant and microbial communities (Ortíz-Castro *et al*., 2009). In environments with extreme conditions, such as those with high temperatures or drought-prone areas, plants that can produce stress-resistant metabolites are invaluable in promoting ecosystem stability and long-term restoration success (Majhi *et al*., 2022).

Interactions between plant metabolites and soil microbiomes: Plant metabolites play a central role in shaping soil microbiomes by attracting beneficial microbes, deterring pathogens, and modulating the overall microbial community structure (Jacoby *et al*., 2021). The root exudates released by plants, which are rich in metabolites, create a microenvironment in the rhizosphere that acts as a “recruitment zone” for soil microorganisms (Yeates, 2018). Beneficial microbes, such as nitrogen-fixing bacteria and mycorrhizal fungi, are drawn to specific metabolites, which signal the presence of a compatible host plant (Chagas *et al*., 2018). For instance, flavonoids act as chemical signals that stimulate nodulation in legume-rhizobia interactions, facilitating nitrogen fixation and enhancing soil fertility (Bag *et al*., 2022). These interactions are crucial for restoration because they help to re-establish nutrient cycling processes that may have been disrupted by soil degradation (Vithanage, 2023). By understanding the types of metabolites that attract beneficial microbes, restoration strategies can be designed to introduce plants that will enhance the establishment of these supportive microbial communities (Musilova *et al*., 2016).

In addition to attracting beneficial microbes, certain metabolites also play a role in pathogen defense, helping to prevent the establishment of harmful microbes that can hinder plant growth (Ab-Rahman *et al*., 2018). Phenolic compounds, for example, have antimicrobial properties that inhibit the growth of pathogenic bacteria and fungi in the soil (Siqueira *et al*., 1991). This natural defense mechanism is particularly valuable in restoration contexts where degraded soils may harbor opportunistic pathogens (Puupponen-Pimiä *et al*., 2001). By selecting plants that produce antimicrobial metabolites, restoration practitioners can create a more balanced microbial environment, reducing the risk of disease and supporting the establishment of healthy plant communities (Iqbal *et al*., 2023). This balance between attracting beneficial microbes and deterring pathogens is essential for promoting soil health and stability in restored ecosystems (Radulovic *et al*., 2013).

The impact of plant metabolites on soil health extends beyond individual microbial interactions; these compounds contribute to the overall microbial diversity and functional capacity of the soil (Nizamani *et al*., 2024). Diverse microbial communities are more resilient and better able to adapt to environmental changes, which is vital for the long-term success of restoration projects (Shade *et al*., 2012). The interactions between plant metabolites and soil microbiomes create a feedback loop where plants and microbes mutually benefit from each other, resulting in improved soil fertility, structure, and resilience (Moreno-Mateos *et al*., 2020). In restoration, introducing plant species with specific metabolite profiles can be a targeted approach to cultivate a soil microbiome that supports both plant growth and ecosystem recovery (Robinson *et al*., 2023). This synergistic relationship between plants and microbes offers a natural, sustainable strategy for restoring degraded lands, with plant metabolites serving as the cornerstone for re-establishing ecological balance and resilience in the soil (Islam *et al*., 2024).

Microbiome in soil health and restoration: Soil microbiomes are fundamental to the health and resilience of ecosystems, especially in restoration contexts where soil and plant communities need to re-establish balance and function (Sekhohola-Dlamini *et al*., 2022). These complex communities of bacteria, fungi, archaea, and other microorganisms interact with plants to facilitate essential ecological processes, from nutrient cycling and organic matter decomposition to soil structure stabilization and pathogen defense (Bernreiter & Teijeiro, 2022). In degraded soils, where microbial diversity and functionality are often severely compromised, restoring a healthy microbiome can be a cornerstone of ecosystem recovery (Jagadesh *et al*., 2024). The role of soil microbiomes extends beyond merely supporting plant growth; they create a foundation for ecosystem stability by improving soil fertility, increasing resilience to abiotic stress, and promoting biodiversity (Suman *et al*., 2022). Understanding the structure of soil microbiomes, their impact on plant health and stress resilience, and the strategies to restore microbial diversity in degraded soils are essential steps in developing effective and sustainable restoration approaches (Lehman *et al*., 2015).

Structure and roles of soil microbiomes: The structure of soil microbiomes is highly diverse and includes a vast array of organisms, such as bacteria, fungi, archaea, and protozoa, each contributing unique functions to soil health (Fig. 2) (Geisen *et al*., 2018). Bacteria are among the most abundant and diverse groups in soil microbiomes and play critical roles in nutrient cycling, including nitrogen fixation, which converts atmospheric nitrogen into forms that plants can use (Hirsch & Mauchline, 2015). Certain bacteria, such as *Rhizobium* species, form symbiotic relationships with leguminous plants to fix nitrogen, enriching soil fertility and supporting plant growth (Huang, 2024). Other bacterial species contribute to phosphorus solubilization, making this essential nutrient more accessible to plants (Billah *et al*., 2019). Archaea, while less abundant than bacteria, also contribute to nutrient cycling, especially under extreme conditions where they play a role in methane production and decomposition of organic matter in anaerobic environments (Offre *et al*., 2013). Fungi, particularly mycorrhizal fungi, are another critical component of soil microbiomes, forming symbiotic associations with plant roots that enhance water and nutrient absorption (Wahab *et al*., 2023). Ectomycorrhizal fungi, which form a sheath around plant roots, and arbuscular mycorrhizal fungi, which penetrate root cells, significantly improve the plant's access to phosphorus and other immobile nutrients (Becquer *et al*., 2014; Etesami *et al*., 2021). These fungal associations are vital for plant establishment in nutrient-poor soils, such as those found in degraded ecosystems (Koshila Ravi *et al*., 2019).

The roles of these microbial communities extend to decomposing organic matter, which recycles nutrients back into the soil, stabilizes soil structure, and enhances soil porosity (Bhattacharyya *et al*., 2022). Microbial activity breaks down dead plant and animal material, releasing nutrients and organic compounds that enrich the soil (Condron *et al*., 2010). Additionally, microbes produce extracellular polysaccharides that help bind soil particles, increasing soil aggregate stability and improving its capacity to retain water (Costa *et al*., 2018). These structural benefits are crucial for preventing soil erosion and improving root growth, particularly in restoration contexts where soil integrity may be compromised (Ali *et al*., 2024). The interplay between different microbial groups creates a dynamic soil environment where nutrient availability, water retention, and disease suppression are enhanced, providing a stable foundation for plant communities to flourish (Nizamani *et al*., 2024). In this way, the diversity and interactions of soil microbes are essential for a healthy, functioning ecosystem, and their presence in restored soils helps establish a self-sustaining environment that can resist future degradation (Maiti & Ghosh, 2020).

Soil microbiome's impact on plant growth and stress resilience: The soil microbiome plays a significant role in enhancing plant growth and resilience to environmental stresses, making it a key focus in ecosystem restoration (Arif *et al*., 2020). Beneficial soil microbes improve nutrient uptake by transforming nutrients into bioavailable forms and facilitating their transport to plant roots (Kumar *et al*., 2016). Mycorrhizal fungi, for example, extend the root surface area through hyphal networks, allowing plants to access nutrients and water from a larger soil volume. This symbiosis is particularly valuable in nutrient-deficient soils, as it enables plants to thrive in environments where resources are limited (Smith *et al*., 2015). Additionally, nitrogen-fixing bacteria convert atmospheric nitrogen into ammonium, which plants can assimilate, supporting growth even in nitrogen-poor soils (Chellem *et al*., 2024). Phosphate-solubilizing bacteria also enhance phosphorus availability, an essential nutrient that is often limited in degraded soils (Billah *et al*., 2019). Through these processes, the soil microbiome not only provides plants with essential nutrients but also reduces the need for synthetic fertilizers, promoting a more natural and sustainable approach to soil fertility in restoration projects (Ray *et al*., 2020).

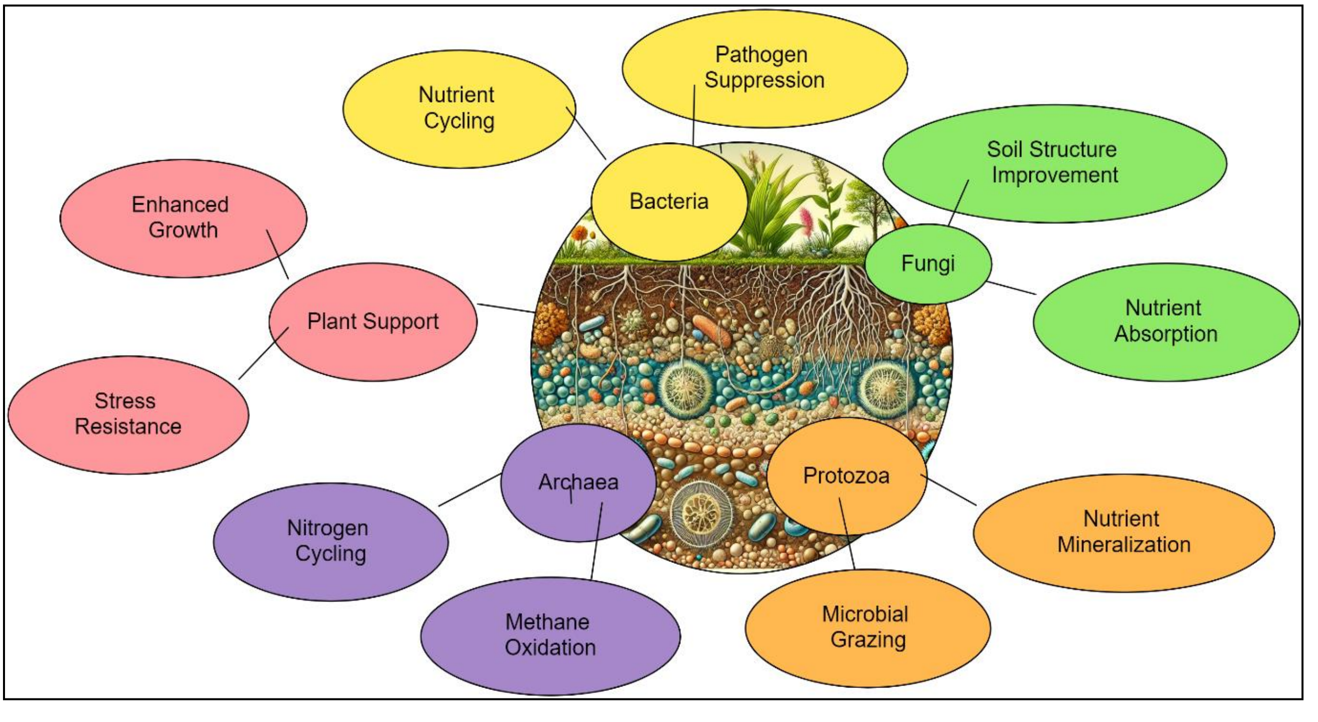

Fig. 2. Mindmap of Soil microbiome functions in ecosystem restoration.

Beyond nutrient uptake, soil microbes contribute to plant health by enhancing root growth and structure, making plants more resilient to physical stresses such as drought and salinity (Muhammad *et al*., 2023). Certain bacteria, known as plant growth-promoting rhizobacteria (PGPR), produce hormones like auxins and cytokinins that stimulate root elongation and branching, increasing the plant's capacity to absorb water and nutrients (Spaepen *et al*., 2009). This root development is crucial for establishing plants in degraded landscapes, where soil conditions may limit root penetration and water retention (Etesami & Maheshwari, 2018). Additionally, beneficial microbes enhance plants' resistance to abiotic stresses by producing osmoprotectants and antioxidants that help plants cope with drought, salinity, and extreme temperatures (Enebe & Babalola, 2018). By supporting both root architecture and physiological adaptations, soil microbiomes enable plants to withstand challenging conditions, making them a powerful ally in restoration efforts focused on degraded or marginal lands (Fahad *et al*., 2022).

The role of soil microbiomes in stress resilience also includes protection against pathogens, as beneficial microbes outcompete or inhibit harmful organisms in the rhizosphere (Arif *et al*., 2020). Certain bacteria produce antimicrobial compounds that suppress soil-borne pathogens, while others occupy root niches that might otherwise be invaded by harmful microbes (Garrett, 1965). This protective effect is particularly valuable in degraded soils, where pathogen populations can increase due to a lack of microbial diversity and competition (Tarkka *et al*., 2008). By reintroducing a diverse microbial community, restoration projects can establish a balanced soil environment where beneficial microbes dominate, reducing the prevalence of disease and promoting healthy plant growth (Singh *et al*., 2019). The combined effects of enhanced nutrient uptake, improved root structure, and pathogen suppression underscore the importance of soil microbiomes in restoration, as they help plants establish and thrive in otherwise challenging environments (Fabiyi *et al*., 2024).

Restoration of microbial diversity in degraded soils: Restoring microbial diversity in degraded soils is critical for creating resilient ecosystems capable of self-sustenance and adaptation (Ray *et al*., 2024). In degraded soils, microbial communities are often disrupted or reduced in diversity due to factors like contamination, erosion, or compaction (Lal, 2015). This reduction in diversity weakens the soil's capacity for nutrient cycling, disease suppression, and structural stability, making it harder for plants to establish and thrive (Osman, 2014). Reintroducing microbial diversity through restoration strategies can address these challenges by fostering a balanced and functional soil ecosystem (Timmis & Ramos, 2021). One effective approach to restoring microbial diversity is the application of microbial inoculants, which include beneficial bacteria and fungi selected for their roles in nutrient cycling, pathogen suppression, and plant growth promotion (Ambrosini *et al*., 2016). These inoculants can be applied to the soil or directly to seeds and plant roots, allowing beneficial microbes to colonize the rhizosphere and establish symbiotic relationships with plants (Singh *et al*., 2019). For example, inoculating degraded soils with mycorrhizal fungi can improve phosphorus availability, while nitrogen-fixing bacteria can enhance nitrogen levels, creating a supportive environment for plant growth (Rashid *et al*., 2016; Amirnia *et al*., 2019).

Another strategy to reintroduce microbial diversity involves the use of organic amendments, such as compost, biochar, or manure, which provide a source of nutrients and organic matter that stimulate microbial growth and diversity (Bhattacharyya *et al*., 2022). These amendments enrich the soil with carbon sources that support a range of microbial metabolic processes, promoting the growth of both bacteria and fungi that are essential for nutrient cycling and soil structure (Usharani *et al*., 2019). Organic amendments also improve soil texture and water-holding capacity, creating favorable conditions for microbial colonization and activity (Chaudhari *et al*., 2021). By increasing organic matter in degraded soils, these amendments support the development of a complex microbial community that enhances soil health and promotes plant establishment (Bonilla *et al*., 2012). In restoration contexts, organic amendments offer a practical and sustainable means of boosting microbial diversity while simultaneously addressing soil fertility and structure (Singh *et al*., 2024).

Long-term strategies for microbial restoration may also involve managing the plant community to create a stable environment for microbial diversity (Smith *et al*., 2003). Different plant species produce distinct root exudates that attract specific microbial communities, creating a diverse rhizosphere microbiome that varies with plant diversity (Vives-Peris *et al*., 2020). By planting a mix of species with complementary metabolite profiles, restoration projects can promote a more diverse and resilient microbial community (Robinson *et al*., 2023). This approach, known as phytoremediation or phyto management, leverages natural plant-microbe interactions to restore soil health, enhance nutrient cycling, and reduce the need for additional inputs over time (Iqbal *et al*., 2023). Through these combined strategies of microbial inoculation, organic amendment, and plant diversity, restoration practitioners can effectively rebuild microbial communities, creating soils that support a resilient and self-sustaining ecosystem (Larson *et al*., 2022).

Plant-microbiome synergy mechanisms in restoration: The synergy between plants and soil microbiomes is fundamental to restoring ecosystem health, as their interactions directly impact soil fertility, nutrient cycling, and plant resilience (Dubey *et al*., 2019). This partnership not only supports the growth of plants in degraded soils but also re-establishes critical ecosystem functions that enhance biodiversity and ecological stability (Chauhan *et al*., 2023). By leveraging the natural biochemical pathways and signaling mechanisms that plants and microbes use to communicate and support each other, restoration practices can promote a self-sustaining ecosystem capable of enduring environmental challenges (Majumdar *et al*., 2025). These mechanisms allow for efficient nutrient cycling, soil fertility enhancement, and increased tolerance to environmental stressors, all of which are vital for the long-term success of restoration projects (Murugan *et al*., 2021).

Nutrient cycling and soil fertility enhancement: One of the primary benefits of plant-microbiome interactions in restoration is their role in nutrient cycling, a process crucial for soil fertility and ecosystem productivity (Chauhan *et al*., 2023). Microbial communities, including bacteria, fungi, and archaea, play a central role in converting organic matter and plant metabolites into bioavailable nutrients that plants can absorb (Condron *et al*., 2010). For instance, nitrogen-fixing bacteria such as *Rhizobium* and *Azospirillum* form symbiotic relationships with leguminous plants, where they convert atmospheric nitrogen into ammonium, an accessible form of nitrogen essential for plant growth (Raza *et al*., 2020). This symbiosis enriches the nitrogen content of the soil, supporting the growth of not only the host plant but also neighboring vegetation, thereby fostering a healthier and more diverse ecosystem (Jehani *et al*., 2023). This process is particularly beneficial in degraded landscapes, where nitrogen levels are often depleted, and introducing nitrogen-fixing plants and their microbial partners can significantly enhance soil fertility (Abd-Alla *et al*., 2023).

Phosphorus, another essential nutrient often limited in degraded soils, becomes more accessible to plants through interactions with phosphate-solubilizing bacteria and mycorrhizal fungi (Sharma *et al*., 2013). Certain bacteria produce organic acids and enzymes that dissolve bound phosphate in the soil, releasing it in a form that plants can readily uptake (Hocking, 2001). Mycorrhizal fungi, especially arbuscular mycorrhizal fungi (AMF), extend their hyphal networks into the soil, reaching distant phosphate sources and transporting them back to the plant roots (Wang *et al*., 2022). This nutrient-sharing network not only enhances phosphorus availability but also improves soil structure by stabilizing soil aggregates, which increases water retention and root penetration (Bhantana *et al*., 2021). The collaboration between plants and soil microbes in phosphorus cycling is crucial in nutrient-poor soils, as it allows plants to access essential nutrients without the need for synthetic fertilizers, promoting a natural and sustainable approach to soil fertility (Das *et al*., 2022).

Moreover, microbial decomposition processes contribute significantly to carbon and sulfur cycling, further enhancing soil fertility (Basu *et al*., 2021). Microbes break down organic matter, such as dead plant material and animal remains, releasing essential nutrients like carbon, sulfur, and trace minerals into the soil. This decomposition process also produces humus, an organic component that improves soil texture, increases water-holding capacity, and supports microbial habitats (Condron *et al*., 2010; Frank *et al*., 2023). The presence of a diverse microbial community accelerates these nutrient cycling processes, creating a more dynamic and fertile soil environment (Table 2) (Dai *et al*., 2021). In restoration projects, these nutrient cycling mechanisms provided by plant-microbiome interactions are fundamental for building a robust soil foundation that can support diverse plant communities and foster ecosystem resilience (Peddle *et al*., 2024).

Improving stress tolerance in restored ecosystems: Soil microbiomes play a vital role in enhancing the stress tolerance of plants, making them more resilient to harsh environmental conditions commonly found in degraded landscapes (Coban *et al*., 2022). Drought and salinity are two of the most significant abiotic stressors that impact plant survival and growth, particularly in arid and semi-arid regions undergoing restoration (Hussain *et al*., 2019). Beneficial microbes, including plant growth-promoting rhizobacteria (PGPR) and mycorrhizal fungi, help plants mitigate these stresses through various physiological and biochemical mechanisms (Nadeem *et al*., 2014). For instance, certain PGPR produce osmolytes, compounds that maintain cellular osmotic balance and prevent water loss, which is crucial for plant survival during drought conditions (Khan *et al*., 2020). Additionally, these microbes produce stress-responsive hormones such as abscisic acid (ABA) and cytokinin, which regulate stomatal closure and water uptake, enabling plants to conserve water and maintain their metabolic functions during dry periods (Kaya, 2024).

Table 2. Nutrient cycling contributions of plant-microbiome systems.

Key nutrient	Nutrient Cycling Contribution	Examples	References
Nitrogen (N)	Nitrogen-fixing bacteria like *Rhizobium* establish symbiotic relationships with plant roots to fix atmospheric nitrogen, essential for plant growth	Legumes like chickpea and soybean	(Zahran, 1999; Rashid *et al*., 2015)
Phosphorus (P)	Mycorrhizal fungi enhance phosphorus uptake by extending root absorption area, critical in phosphorus-limited soils	Mycorrhizal fungi association in crops	(Schroeder and Janos, 2005; Dixon *et al*., 2020)
Carbon (C)	Rhizodeposition from plant roots stimulates microbial activity in soil, contributing to carbon cycling and soil organic matter formation	Root exudates in low-input agriculture	(Paterson, 2003; Zhou *et al*., 2020)
Potassium (K)	Plant-growth-promoting rhizobacteria (PGPR) assist in potassium solubilization, making it more available to plants, which is important for plant metabolism and stress resistance	Citrus with PGPR like *STILO® µ KUALITY*	(Ashfaq *et al*., 2020; Etesami & Adl, 2020)
Mineral nutrients	Microbial communities around roots, including bacteria and fungi, contribute to the cycling of mineral nutrients like calcium and magnesium, maintaining homeostasis in plant systems	Root-associated microbiota in mineral uptake	(Bhatla *et al*., 2018)
Overall nutrient pool	Microbial decomposers play a critical role in litter decomposition, enhancing the nutrient pool by converting organic matter into plant-available forms	Diverse decomposer communities in plant-soil systems	(Condron *et al*., 2010; Raza *et al*., 2023)

In saline soils, where high salt concentrations can disrupt plant cell functions and reduce nutrient availability, microbes help alleviate salt stress by enhancing ion homeostasis and nutrient uptake (Ondrasek *et al*., 2022). Halotolerant bacteria, which can thrive in saline environments, assist plants by balancing ion concentrations in their tissues, preventing toxic levels of sodium and chloride ions (Etesami & Glick, 2020). Mycorrhizal fungi also play a crucial role in salinity tolerance by improving the root architecture and increasing the plant's ability to absorb water and nutrients despite high salt levels (Evelin *et al*., 2019). Through these symbiotic relationships, plants gain access to a network of microbial support that buffers them against adverse conditions, allowing them to establish and thrive in degraded or challenging environments (Selosse *et al*., 2004). By fostering these plant-microbe partnerships, restoration efforts can improve plant survival rates, accelerate vegetation establishment, and enhance overall ecosystem resilience (Birnbaum & Trevathan-Tackett, 2023).

Microbial contributions to plant stress tolerance extend to managing oxidative stress, a common challenge in degraded environments (Guan *et al*., 2017). Many beneficial microbes produce antioxidant enzymes, such as catalase and superoxide dismutase, which help plants neutralize reactive oxygen species (ROS) generated under stress conditions (Zandi & Schnug, 2022). ROS can cause cellular damage, impacting plant health and survival; however, the presence of antioxidant-producing microbes mitigates these effects, enabling plants to adapt more effectively to stressful environments (Pandey *et al*., 2023). This collaborative defense against oxidative stress highlights the importance of introducing or stimulating beneficial microbial communities in restoration projects, as they provide plants with a biochemical toolkit to withstand and recover from environmental challenges (Csorba *et al*., 2024). Enhancing stress tolerance through plant-microbiome interactions is thus a key strategy in restoring degraded ecosystems, as it enables plants to establish more quickly and persist in ecosystems prone to fluctuations in moisture, temperature, and salinity (Rahman *et al*., 2021).

Biochemical pathways in plant-microbe interactions: The biochemical pathways and signaling mechanisms underpinning plant-microbiome interactions are central to the success of these partnerships and have significant implications for ecosystem restoration (Jain *et al*., 2024). Plants and microbes communicate through a complex network of signaling molecules, including flavonoids, strigolactones, and various secondary metabolites, which allow them to establish and regulate symbiotic relationships (Phour *et al*., 2020). Flavonoids, for example, are produced by plants as root exudates and act as signaling molecules that attract specific rhizobial bacteria to the root zone (Singla & Garg, 2017). These bacteria recognize flavonoid signals and respond by producing Nod factors, which trigger root nodule formation in legumes, allowing the bacteria to fix nitrogen and supply it to the plant (Cooper, 2004). This exchange of signals ensures that the symbiotic relationship is both efficient and beneficial, as the plant gains access to nitrogen while providing the bacteria with carbohydrates derived from photosynthesis (Hassan & Mathesius, 2012). Understanding these signaling pathways is crucial in restoration, as it can inform the selection of plant species that produce specific exudates to attract beneficial microbes in degraded soils (Vithanage, 2023).

Strigolactones are another group of signaling molecules that facilitate plant-microbe interactions, particularly in the formation of mycorrhizal associations (Rochange *et al*., 2019). These compounds are secreted by plant roots to attract mycorrhizal fungi, which respond by growing towards the plant and establishing a symbiotic relationship that enhances nutrient exchange (Boyno *et al*., 2023). In nutrient-poor soils, the production of strigolactones is upregulated, ensuring that plants attract the fungi needed to access phosphorus and other scarce resources (Miyata & Umehara, 2024). This adaptation is particularly advantageous in degraded ecosystems, where nutrient availability is limited, and plants rely heavily on microbial partners to meet their nutritional needs (Francis *et al*., 2023). The strigolactone-mycorrhizal signaling pathway exemplifies how plants can actively recruit beneficial microbes in response to environmental conditions, highlighting the adaptive nature of plant-microbiome interactions in restoring soil fertility and supporting plant establishment (Boyno *et al*., 2023; Wahab *et al*., 2023).

Additional biochemical pathways involve the production of antimicrobial compounds by both plants and microbes, which help maintain a healthy microbial community by deterring pathogenic organisms (Saraf *et al*., 2014). Plants produce phenolic compounds and phytoalexins that inhibit the growth of harmful bacteria and fungi, while certain soil microbes secrete antibiotics and siderophores that suppress pathogens and enhance plant health (Hussain *et al*., 2020). This biochemical defense system is critical in restoration projects, as degraded soils often harbor opportunistic pathogens that can hinder plant growth and disrupt the re-establishment of plant communities (Saraf *et al*., 2014). By understanding and harnessing these biochemical pathways, restoration ecologists can design strategies to encourage beneficial plant-microbe interactions while minimizing the impact of harmful microbes, creating a balanced and resilient soil environment (Singh *et al*., 2019).

In short, the biochemical pathways and signaling mechanisms involved in plant-microbe interactions are essential for facilitating nutrient exchange, enhancing stress tolerance, and promoting pathogen defense in restored ecosystems (Iqbal *et al*., 2023). By studying these pathways, restoration practitioners can optimize plant-microbe relationships to accelerate ecosystem recovery, improve soil health, and build resilience in the face of environmental stressors (Vishwakarma *et al*., 2020). These mechanisms highlight the intricate web of interactions that sustain ecosystem stability, offering a natural and adaptive framework for restoration strategies that go beyond traditional methods and embrace the complexity of ecological relationships (Rosier *et al*., 2018).

Future directions and challenges: The integration of advanced technologies and novel approaches holds great promise for advancing ecosystem restoration, particularly through plant-microbiome interactions (Jagadesh *et al*., 2024). While conventional restoration methods focus on replanting native species or improving soil quality, cutting-edge tools in genomics, metabolomics, bioinformatics, and synthetic biology provide an unprecedented opportunity to deepen our understanding of plant-microbiome dynamics and to apply these insights for more efficient and sustainable restoration (Stanturf *et al*., 2014). These tools allow researchers to map complex microbial networks, uncover biochemical pathways, and even engineer plants or microbes to improve their resilience in degraded environments. However, the use of these technologies is not without challenges, as they come with high costs, require specialized expertise, and necessitate collaboration across scientific disciplines. Additionally, efforts to maintain and enhance microbial diversity in restored soils face environmental and biological constraints, and the application of synthetic biology in natural ecosystems raises ethical and regulatory questions. Addressing these challenges and harnessing the potential of these technologies could transform restoration ecology, creating ecosystems that are not only restored but also equipped to adapt to future environmental changes.

Integrating advanced technologies for deeper insights: One of the most exciting areas for future research in ecosystem restoration is the use of "omics" technologies, including genomics, metabolomics, and bioinformatics, to gain a deeper understanding of plant-microbiome interactions (Fig. 3) (Jain *et al*., 2024). Genomics, which involves mapping the complete genetic material of organisms, can reveal the genetic diversity and functional capabilities of soil microbial communities. This is particularly useful in restoration, as understanding the genetic makeup of these communities can inform the selection of specific microbes that promote nutrient cycling, enhance stress tolerance, or support plant growth (Allen & Banfield, 2005). Similarly, metabolomics, the study of the unique chemical fingerprints left by metabolic processes, allows researchers to identify key metabolites involved in plant-microbe signaling and nutrient exchange (Mhlongo *et al*., 2018). By analyzing metabolomic profiles, scientists can better understand how certain plants and microbes communicate and support each other, providing insights into which species combinations are most beneficial for restoration (Kimotho & Maina, 2024). Bioinformatics, the computational analysis of biological data, plays a crucial role in integrating and interpreting omics data, allowing researchers to model complex ecological interactions and predict the outcomes of different restoration strategies (Mukherjee *et al*., 2024).

Despite their potential, these technologies come with significant challenges that must be addressed to make them more accessible and effective for restoration. The cost of sequencing and metabolomic analysis remains high, which can be prohibitive for large-scale restoration projects (Kumar *et al*., 2021). Moreover, the complexity of omics data requires specialized expertise in data analysis and interpretation, as well as advanced computational resources. Restoration projects often involve multiple disciplines, including ecology, microbiology, chemistry, and data science, making interdisciplinary collaboration essential but challenging to coordinate. The integration of these various fields demands time, effort, and effective communication among scientists from diverse backgrounds, each with their own specialized knowledge and methodologies (Akob *et al*., 2024). Addressing these challenges will require investments in training, infrastructure, and interdisciplinary research programs to make omics technologies more accessible and applicable to real-world restoration efforts. As these technologies become more refined and cost-effective, they hold the potential to revolutionize our understanding of plant-microbiome interactions and create new pathways for restoring and maintaining resilient ecosystems.

Maintaining and enhancing microbial diversity in restored soils: A key challenge in restoration ecology is the maintenance and enhancement of microbial diversity in restored soils, which is crucial for creating a stable and resilient ecosystem. Degraded soils often suffer from reduced microbial diversity due to factors such as soil pollution, erosion, or loss of organic matter, which limit the range of microbial species capable of thriving (Singh *et al*., 2019). This loss of diversity weakens the soil's ability to support nutrient cycling, pathogen suppression, and other essential functions, making it difficult for plants to establish and grow. Soil pollution, for instance, can create toxic environments where only a few resilient microbial species survive, limiting the overall functionality of the soil microbiome (Timmis & Ramos, 2021). Similarly, microbial competition and ecological niches in restored soils can restrict the establishment of beneficial microbes, leading to imbalanced communities dominated by a few species rather than a diverse and balanced microbiome (Coban *et al*., 2022).

One approach to overcoming these challenges is the use of microbial inoculants, which are formulations containing specific beneficial microbes that can be introduced to the soil to kickstart microbial diversity and enhance ecological functions. These inoculants often include nitrogen-fixing bacteria, phosphate-solubilizing bacteria, and mycorrhizal fungi, all of which play critical roles in supporting plant growth and soil health (Alori *et al*., 2017). When applied to degraded soils, microbial inoculants can establish beneficial microbial communities that promote nutrient availability, improve soil structure, and enhance plant-microbe interactions (Sujata & Nibha, 2011). However, the success of these inoculants depends on the compatibility of the introduced microbes with the existing soil conditions and plant species, as well as their ability to compete with native or established microbial populations. To maximize the effectiveness of microbial inoculants, restoration practitioners may need to adjust soil conditions, such as pH and organic matter content, to create a more hospitable environment for these introduced microbes (Singh Rawat *et al*., 2023).

Another promising solution is the use of organic amendments, such as compost or biochar, which provide a rich source of organic matter that supports microbial growth and diversity (Sun *et al*., 2021). Organic amendments improve soil texture, water retention, and nutrient content, creating favorable conditions for a diverse microbial community to thrive (Farooqi *et al*., 2023). Biochar, in particular, has gained attention for its ability to create stable microhabitats for microbes due to its porous structure, which provides shelter and supports long-term microbial colonization (Mukherjee *et al*., 2022). By combining microbial inoculants with organic amendments, restoration projects can create a synergistic effect that enhances microbial diversity and functionality, promoting a resilient soil ecosystem capable of supporting plant growth and resisting future degradation (Ahmed *et al*., 2023).

Synthetic biology for optimized plant-microbiome interactions: Synthetic biology represents an innovative and potentially transformative approach to optimizing plant-microbiome interactions in ecosystem restoration. Through genetic engineering, synthetic biology allows scientists to modify the genomes of plants or microbes to enhance traits such as nutrient uptake, stress tolerance, or pathogen resistance (Singla, 2020). For instance, genetic modifications can enable plants to produce specific metabolites that attract beneficial microbes or repel pathogens, creating a more supportive rhizosphere environment (Mhlongo *et al*., 2018). Similarly, microbes can be engineered to increase their efficiency in nutrient cycling processes, such as nitrogen fixation or phosphate solubilization, making essential nutrients more readily available to plants in nutrient-poor soils. These engineered organisms could be applied to restoration projects to accelerate ecosystem recovery, particularly in challenging environments where native species may struggle to survive without additional support (Bargaz *et al*., 2018; Koshila Ravi *et al*., 2019). However, the application of synthetic biology in natural ecosystems is accompanied by significant ethical, ecological, and regulatory considerations. One major concern is the potential impact of genetically modified organisms (GMOs) on biodiversity, as engineered plants or microbes could outcompete native species, leading to a loss of natural genetic diversity (Crawley, 1995). There are also ecological risks, such as unintended interactions with non-target organisms or the potential for engineered genes to transfer to other species through horizontal gene transfer. These concerns have led to stringent regulatory frameworks for the use of GMOs in natural settings, which can limit the deployment of synthetic biology solutions in restoration projects (Keese, 2008). Additionally, there are ethical questions about the human role in engineering natural systems and the potential consequences of altering ecological relationships that have evolved over millennia.

To address these challenges, researchers are exploring more targeted and reversible genetic modifications, as well as containment strategies that limit the spread of engineered organisms in natural ecosystems. Advances in gene editing technologies, such as CRISPR-Cas9, allow for precise modifications that can minimize off-target effects, while biosafety mechanisms, like kill-switches, can be built into engineered organisms to ensure they do not persist beyond their intended use (Bohua *et al*., 2023). Nevertheless, the use of synthetic biology in restoration remains a complex and debated field, requiring careful consideration of ecological impacts, regulatory compliance, and long-term monitoring. As synthetic biology advances, it may provide valuable tools for restoration, offering new possibilities for supporting plant-microbiome interactions in ways that are both effective and mindful of ecological integrity (Iqbal *et al*., 2023).

In short, the future of plant-microbiome interactions in restoration will likely be shaped by a combination of advanced technologies, microbial diversity management, and ethical innovations in synthetic biology. By addressing the associated challenges and harnessing the potential of these tools, restoration ecology can move towards a more science-driven approach that not only restores degraded ecosystems but also equips them for resilience in an increasingly unpredictable environmental landscape.

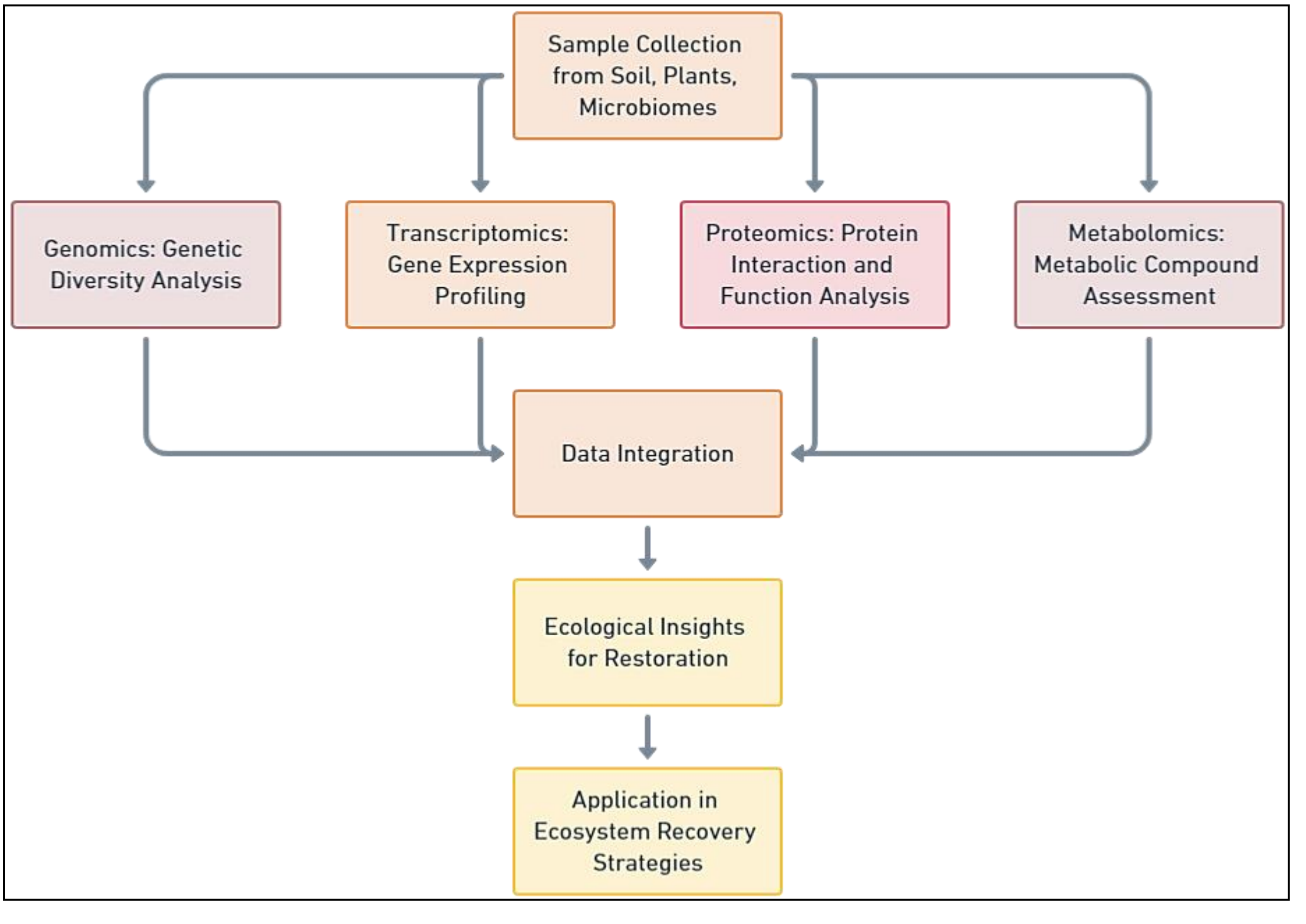

Fig. 3. Pathway of omics integration in ecosystem recovery.

Conclusion

The contributions of plant-microbiome interactions to ecosystem restoration highlight the essential role of these partnerships in building resilient, self-sustaining environments. As this article has demonstrated, plant metabolites and soil microbiomes work synergistically to support nutrient cycling, improve soil structure, enhance stress tolerance, and protect against pathogens. These functions are particularly valuable in degraded ecosystems, where nutrient availability, microbial diversity, and soil health are often compromised. Through the release of specific metabolites, plants actively shape the microbial communities in their rhizosphere, attracting beneficial microbes while deterring harmful ones. This dynamic exchange enables plants to establish and thrive, even in challenging conditions, as microbes support them with vital resources, improved root structure, and protective mechanisms against abiotic stresses. These plant-microbiome interactions foster a balanced, nutrient-rich soil environment, creating a foundation upon which diverse plant communities can grow and ecosystem functions can recover. The restoration of degraded soils thus relies heavily on the re-establishment of these natural processes, allowing plants and microbes to work together in ways that mimic, and ultimately restore, natural ecosystem dynamics.

In addition to promoting specific ecological functions, plant-microbiome partnerships contribute to broader ecosystem stability and resilience. As plants and microbes interact, they create feedback loops that reinforce soil health, nutrient availability, and microbial diversity. This interconnectedness not only supports individual plant survival but also strengthens the ecosystem's capacity to withstand environmental fluctuations, such as changes in climate, soil composition, or water availability. Restoration strategies that harness the power of these interactions are therefore more likely to achieve sustainable outcomes, as they work with, rather than against, natural processes. In environments prone to stressors like drought or soil erosion, plant-microbiome partnerships can provide the adaptive advantages needed to resist further degradation, promote biodiversity, and maintain ecosystem functions over time. The success of these strategies depends on a comprehensive understanding of the complex biochemical pathways and signaling mechanisms involved in plant-microbe interactions, underscoring the need for continued research into how these processes operate in diverse environmental conditions.

Achieving sustainable ecosystem restoration, however, requires interdisciplinary collaboration that bridges the gaps between fields such as microbiology, botany, ecology, soil science, bioinformatics, and environmental engineering. Restoration is inherently a complex process, involving various biological, chemical, and physical elements that interact across scales from microscopic microbes to large-scale landscape processes. Effective restoration solutions thus require input from diverse scientific disciplines to understand and manage these interactions fully. For example, genomics and metabolomics provide insights into the functional capacities of soil microbiomes, but interpreting this data in the context of ecosystem dynamics requires expertise in bioinformatics and ecological modeling. Soil scientists and ecologists contribute knowledge on how environmental factors shape plant and microbial communities, while bioengineers may develop technologies, such as synthetic biology tools, to enhance specific plant-microbiome functions. This convergence of knowledge and expertise fosters a holistic approach to restoration, where strategies are informed by the latest scientific advancements while remaining grounded in ecological principles that prioritize natural resilience and sustainability.

Interdisciplinary collaboration not only enhances scientific understanding but also encourages innovative approaches to restoration that can adapt to the unique challenges of different ecosystems. By combining methodologies and perspectives from various fields, restoration practitioners can tailor strategies to address specific issues, such as nutrient deficiencies, microbial diversity loss, or abiotic stress factors, in ways that maximize ecological recovery. This collaborative approach also facilitates the sharing of resources, ideas, and technologies, ensuring that restoration projects benefit from a broad knowledge base and cutting-edge solutions. As environmental challenges continue to evolve, particularly with the impacts of climate change, the need for interdisciplinary collaboration in restoration will only grow. A unified, science-driven approach is essential for developing adaptive, scalable solutions that can restore ecosystem functions and resilience in a sustainable, long-lasting manner. In this way, the future of ecosystem restoration lies in the collaborative efforts of scientists, practitioners, and policymakers, working together to restore not only the land but also the intricate web of life that sustains it.

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References

Ab-Rahman, S.F.S., E. Singh, C.M. Pieterse and P.M. Schenk. 2018. Emerging microbial biocontrol strategies for plant pathogens. *Plant Sci.*, 267: 102-111.

Abd-Alla, M.H., S.M. Al-Amri and A.W.E. El-Enany. 2023. Enhancing rhizobium–legume symbiosis and reducing nitrogen fertilizer use are potential options for mitigating climate change. *Agriculture*, 13(11): 2092.

Adetunji, C.O., S. Palai, C.P. Ekwuabu, C. Egbuna, J.B. Adetunji, C.B. Ehis-Eriakha, S.S. Kesh and A.G. Mtewa. 2021. General principle of primary and secondary plant metabolites: Biogenesis, metabolism, and extraction. In: Preparation of phytopharmaceuticals for the management of disorders. *Elsevier*: pp: 3-23.

Afridi, M.S., S. Ali, A. Salam, W. César Terra, A. Hafeez, Sumaira, B. Ali, M.S. AlTami, F. Ameen and S. Ercisli. 2022. Plant microbiome engineering: Hopes or hypes. *Biology*, 11(12): 1782.

Ahmed, T., M. Noman, Y. Qi, M. Shahid, S. Hussain, H.A. Masood, L. Xu, H.M. Ali, S. Negm and A.F. El-Kott. 2023. Fertilization of microbial composts: A technology for improving stress resilience in plants. *Plants*, 12(20): 3550.

Akob, D.M., A.E. Oates, P.R. Girguis, B.D. Badgley, V.S. Cooper, R.S. Poretsky, B.T. Tierney, E. Litchman, R.J. Whitaker and K.L. Whiteson, 2024. Perspectives on the future of ecology, evolution, and biodiversity from the council on microbial sciences of the american society for microbiology. *mSphere*: e00307-00324.

Akram, M., S. Ullah, K. Ikram, M.S. Zaheer, M.Z. Mansha, H.H. Ali, Y. Niaz, M.F. Seleiman and N. Khan, 2024. Effect of cadmium toxicity on zn, mn, cd, fe concentration and translocation, bioaccumulation, uptake of cd in root and shoot of different rice varieties. *Pak. J. Bot.*, 56(1): 55-63.

Akula, R. and G.A. Ravishankar. 2011. Influence of abiotic stress signals on secondary metabolites in plants. *Plant Sign. Behav.*, 6(11): 1720-1731.

Ali, M.U., N.A. Rajput, M. Atiq, R.M. Atif and S.G. Crandall. 2024. Population dynamics and aggressiveness of fungal pathogens associated with chilli root rot. *Pak. J. Bot.*, 56(1): 377-387.

Ali, N., S.A.A.A. Abbas, L. Sharif, M. Shafiq, Z. Kamran, M. Haseeb and M.A. Shahid. 2024. Microbial extracellular polymeric substance and impacts on soil aggregation. In: Bacterial secondary metabolites. *Elsevier*: pp: 221-237.

Allen, E.E. and J.F. Banfield. 2005. Community genomics in microbial ecology and evolution. *Nat. Rev. Microbiol.*, 3(6): 489-498.

Alori, E.T., M.O. Dare and O.O. Babalola. 2017. Microbial inoculants for soil quality and plant health. *Sustain. Agri. Rev.*, 281-307.

Ambrosini, A., R. de Souza and L.M. Passaglia. 2016. Ecological role of bacterial inoculants and their potential impact on soil microbial diversity. *Plant Soil*, 400(1-2): 193-207.

Amirnia, R., M. Ghiyasi, S. Siavash Moghaddam, A. Rahimi, C.A. Damalas and S. Heydarzadeh. 2019. Nitrogen-fixing soil bacteria plus mycorrhizal fungi improve seed yield and quality traits of lentil (*Lens culinaris* Medik). *J. Soil Sci. Plant Nut.*, 19(3): 592-602.

Arif, I., M. Batool and P.M. Schenk. 2020. Plant microbiome engineering: Expected benefits for improved crop growth and resilience. *Trends Biotechnol.*, 38(12): 1385-1396.

Ashfaq, M., H.M. Hassan, A.H.A. Ghazali and M. Ahmad. 2020. Halotolerant potassium solubilizing plant growth promoting rhizobacteria may improve potassium availability under saline conditions. *Environ. Monitor. Assess.*, 192(11): 1-20.

Bag, S., A. Mondal, A. Majumder, S.K. Mondal and A. Banik. 2022. Flavonoid mediated selective cross-talk between plants and beneficial soil microbiome. *Phytochem. Rev.*, 21(5): 1739-1760.

Barea, J. 2015. Future challenges and perspectives for applying microbial biotechnology in sustainable agriculture based on a better understanding of plant-microbiome interactions. *J. Soil Sci. Plant Nut.*, 15(2): 261-282.

Bargaz, A., K. Lyamlouli, M. Chtouki, Y. Zeroual and D. Dhiba. 2018. Soil microbial resources for improving fertilizers efficiency in an integrated plant nutrient management system. *Front. Microbiol.*, 9: 1606.

Basu, S., G. Kumar, S. Chhabra and R. Prasad. 2021. Role of soil microbes in biogeochemical cycle for enhancing soil fertility. In: New and future developments in microbial biotechnology and bioengineering. *Elsevier*: pp: 149-157.

Beattie, G.A., K.L. Bayliss, D.A. Jacobson, R. Broglie, M. Burkett-Cadena, A. Sessitsch, P. Kankanala, J. Stein, K. Eversole and A. Lichens-Park. 2024. From microbes to microbiomes: Applications for plant health and sustainable agriculture. *Phytopathology*, 114(8): 1742-1752.

Becquer, A., J. Trap, U. Irshad, M.A. Ali and P. Claude. 2014. From soil to plant, the journey of p through trophic relationships and ectomycorrhizal association. *Front. Plant Sci.*, 5: 548.

Bernreiter, A. and R.G. Teijeiro. 2022. Fungal biodiversity and forest soil health ecosystems. IUSS Vienna, Austria: pp: 54-58.

Bhantana, P., M.S. Rana, X.C. Sun, M.G. Moussa, M.H. Saleem, M. Syaifudin, A. Shah, A. Poudel, A.B. Pun and M.A. Bhat. 2021. Arbuscular mycorrhizal fungi and its major role in plant growth, zinc nutrition, phosphorous regulation and phytoremediation. *Symbiosis*, 84(1): 19-37.

Bhatla, S.C., M.A. Lal, R. Kathpalia and S.C. Bhatla. 2018. Plant mineral nutrition. *Plant Physiol. Devel. Metabol*., 37-81.

Bhattacharyya, S.S., G.H. Ros, K. Furtak, H.M. Iqbal and R. Parra-Saldívar. 2022. Soil carbon sequestration–an interplay between soil microbial community and soil organic matter dynamics. *Sci. Total Environ.*, 815: 152928.

Billah, M., M. Khan, A. Bano, T.U. Hassan, A. Munir and A.R. Gurmani. 2019. Phosphorus and phosphate solubilizing bacteria: Keys for sustainable agriculture. *Geomicrob. J.*, 36(10): 904-916.

Birnbaum, C. and S.M. Trevathan-Tackett. 2023. Aiding coastal wetland restoration via the belowground soil microbiome: An overview. *Restor. Ecol.*, 31(7): e13824.

Bogati, K. and M. Walczak. 2022. The impact of drought stress on soil microbial community, enzyme activities and plants. *Agron. Basel*, 12(1): 189.

Bohua, L., W. Yuexin, O. Yakun, Z. Kunlan, L. Huan and L. Ruipeng. 2023. Ethical framework on risk governance of synthetic biology. *J. Biosaf. Biosec.*, 5(2): 45-56.

Boncan, D.A.T., S.S. Tsang, C. Li, I.H. Lee, H.M. Lam, T.F. Chan and J.H. Hui. 2020. Terpenes and terpenoids in plants: Interactions with environment and insects. *Int. J. Mol. Sci.*, 21(19): 7382.

Bonilla, N., J.A. Gutiérrez-Barranquero, A. de Vicente and F.M. Cazorla. 2012. Enhancing soil quality and plant health through suppressive organic amendments. *Diversity*, 4(4): 475-491.

Boyno, G., Y. Rezaee Danesh, S. Demir, N. Teniz, J.M. Mulet and R. Porcel. 2023. The complex interplay between arbuscular mycorrhizal fungi and strigolactone: Mechanisms, sinergies, applications and future directions. *Int. J. Mol. Sci.*, 24(23): 16774.

Butu, M., I. Sarac, M. Corneanu and M. Butnariu. 2021. Advanced technologies for ecological reconstruction and bioremediation of degraded land. *Environ. Pollut. Remed.*, 81-130.

Chagas, F.O., R. de Cassia Pessotti, A.M. Caraballo-Rodríguez and M.T. Pupo. 2018. Chemical signaling involved in plant-microbe interactions. *Chem. Soci. Rev.*, 47(5): 1652-1704.

Chaudhari, S., A. Upadhyay and S. Kulshreshtha. 2021. Influence of organic amendments on soil properties, microflora and plant growth. *Sustain. Agri. Rev*., 52: 147-191.

Chauhan, P., N. Sharma, A. Tapwal, A. Kumar, G.S. Verma, M. Meena, C.S. Seth and P. Swapnil. 2023. Soil microbiome: Diversity, benefits and interactions with plants. *Sustainability*, 15(19): 14643.

Chellem, S.R., C.V.L. Kishore, G.S.V. Reddy, D. Akshay, K. Kalpana, P. Lavanya and K.H. Choragudi. 2024. Symbiotic relationships between nitrogen-fixing bacteria and leguminous plants ecological and evolutionary perspectives: A review. *U.P. J. Zool.*, 45(13): 145-160.

Chomel, M., M. Guittonny-Larchevêque, C. Fernandez, C. Gallet, A. DesRochers, D. Paré, B.G. Jackson and V. Baldy. 2016. Plant secondary metabolites: A key driver of litter decomposition and soil nutrient cycling. *J. Ecol.*, 104(6): 1527-1541.

Coban, O., G.B. De Deyn and M. van der Ploeg. 2022. Soil microbiota as game-changers in restoration of degraded lands. *Science*, 375(6584): abe0725.

Condron, L., C. Stark, M. O'Callaghan, P. Clinton and Z. Huang. 2010. The role of microbial communities in the formation and decomposition of soil organic matter. *Soil Microb. Sustain. Crop Prod*., 81-118.

Cooper, J.E. 2004. Multiple responses of rhizobia to flavonoids during legume root infection. In: Advances in botanical research. *Elsevier*: pp: 1-62.

Costa, O.Y., J.M. Raaijmakers and E.E. Kuramae. 2018. Microbial extracellular polymeric substances: Ecological function and impact on soil aggregation. *Front. Microbiol.*, 9: 1636.

Crawley, M. 1995. Long term ecological ecological impacts of the release of genetically modified organisms. In: Pan-European Conference on the Potential Long-Term Ecological Impact of Genetically Modified Organisms: Proceedings, Strasbourg, 24-26 November 1993. Council of Europe.

Csorba, C., E. Hackl, T. Reichenauer, W. van der Putten and A. Sessitsch. 2024. Sustainable use and conservation of soil microorganisms and invertebrates contributing to bioremediation and nutrient cycling. Food & Agriculture Org: pp: 1-114

Dai, Z., X. Xiong, H. Zhu, H. Xu, P. Leng, J. Li, C. Tang and J. Xu. 2021. Association of biochar properties with changes in soil bacterial, fungal and fauna communities and nutrient cycling processes. *Biochar*, 3(3): 239-254.

Das, P.P., K.R. Singh, G. Nagpure, A. Mansoori, R.P. Singh, I.A. Ghazi, A. Kumar and J. Singh, 2022. Plant-soil-microbes: A tripartite interaction for nutrient acquisition and better plant growth for sustainable agricultural practices. *Environ. Res.*, 214(Pt 1): 113821.

de-Bashan, L.E., J.P. Hernandez and Y. Bashan. 2012. The potential contribution of plant growth-promoting bacteria to reduce environmental degradation–a comprehensive evaluation. *Appl. Soil Ecol.*, 61: 171-189.

Dixon, M., E. Simonne, T. Obreza and G. Liu. 2020. Crop response to low phosphorus bioavailability with a focus on tomato. *Agronomy*, 10(5): 617.

Dubey, A., M.A. Malla, F. Khan, K. Chowdhary, S. Yadav, A. Kumar, S. Sharma, P.K. Khare and M.L. Khan. 2019. Soil microbiome: A key player for conservation of soil health under changing climate. *Biodiv. Conser.*, 28(8-9): 2405-2429.

Ehlers, B.K., M.P. Berg, M. Staudt, M. Holmstrup, M. Glasius, J. Ellers, S. Tomiolo, R.B. Madsen, S. Slotsbo and J. Penuelas, 2020. Plant secondary compounds in soil and their role in belowground species interactions. *Trends Ecol. Evol.*, 35(8): 716-730.

Ehrenfeld, J.G. and L.A. Toth. 1997. Restoration ecology and the ecosystem perspective. *Restor. Ecol.*, 5(4): 307-317.

Eisenhauer, N., M. Bonkowski, U. Brose, F. Buscot, W. Durka, A. Ebeling, M. Fischer, G. Gleixner, A. Heintz-Buschart and J. Hines, 2019. Biotic interactions, community assembly, and eco-evolutionary dynamics as drivers of long-term biodiversity–ecosystem functioning relationships. *Res. Ideas Outcomes,* 5: e47042.

Elisha, O.D. and M.J. Felix. 2020. The loss of biodiversity and ecosystems: A threat to the functioning of our planet, economy and human society. *Int. J. Econ. Environ. Develop. Soc.*, 1(1): 30-44.

Enebe, M.C. and O.O. Babalola. 2018. The influence of plant growth-promoting rhizobacteria in plant tolerance to abiotic stress: A survival strategy. *Appl. Microb. Biotechnol.*, 102(18): 7821-7835.

Etesami, H. and S.M. Adl. 2020. Plant growth-promoting rhizobacteria (pgpr) and their action mechanisms in availability of nutrients to plants. *Phyto-Microb. Stress Regul*., 147-203.

Etesami, H. and B.R. Glick. 2020. Halotolerant plant growth–promoting bacteria: Prospects for alleviating salinity stress in plants. *Environ. Exp. Bot.*, 178: 104124.

Etesami, H., B.R. Jeong and B.R. Glick. 2021. Contribution of arbuscular mycorrhizal fungi, phosphate–solubilizing bacteria, and silicon to p uptake by plant. *Front. Plant Sci.*, 12: 699618.

Etesami, H. and D.K. Maheshwari. 2018. Use of plant growth promoting rhizobacteria (pgprs) with multiple plant growth promoting traits in stress agriculture: Action mechanisms and future prospects. *Ecotoxicol. Environ. Safety*, 156: 225-246.

Evelin, H., T.S. Devi, S. Gupta and R. Kapoor. 2019. Mitigation of salinity stress in plants by arbuscular mycorrhizal symbiosis: Current understanding and new challenges. *Front. Plant Sci.*, 10: 470.

Fabiyi, O.A., R.A. Ansari, R. Rizvi, A. Sumbul and I. Mahmood. 2024. Influence of arbuscular mycorrhizal fungi on soil health amelioration and plant fitness under hostile environment. In: Mycorrhizal symbiosis and agroecosystem restoration. Springer: pp: 227-248.

Fahad, S., S.B. Chavan, A.R. Chichaghare, A.R. Uthappa, M. Kumar, V. Kakade, A. Pradhan, D. Jinger, G. Rawale and D.K. Yadav. 2022. Agroforestry systems for soil health improvement and maintenance. *Sustainability*, 14(22): 14877.

Farooqi, Z.U.R., A.A. Qadir, H. Alserae, A. Raza and W. Mohy-ud-Din. 2023. Organic amendment–mediated reclamation and build-up of soil microbial diversity in salt-affected soils: Fostering soil biota for shaping rhizosphere to enhance soil health and crop productivity. *Environ. Sci. Pollut. Res.*, 30(51): 109889-109920.

Francis, B., C. Aravindakumar, P.B. Brewer and S. Simon. 2023. Plant nutrient stress adaptation: A prospect for fertilizer limited agriculture. *Environ. Exp. Bot.*, 213: 105431.

Frank, T., H.J. Brauckmann and G. Broll, 2023. Humus forms of moist and wet forest stands. A review. *Int. J. Plant Biol.*, 14(3): 780-796.

Garrett, S.D., 1965. Toward biological control of soil-borne plant pathogens. *Ecol. Soil-borne Plant Pathog.,* 4-17.

Geisen, S., E.A. Mitchell, S. Adl, M. Bonkowski, M. Dunthorn, F. Ekelund, L.D. Fernández, A. Jousset, V. Krashevska and D. Singer, 2018. Soil protists: A fertile frontier in soil biology research. *FEMS Microbiol. Rev.*, 42(3): 293-323.

Guan, N., J. Li, H.-d. Shin, G. Du, J. Chen and L. Liu, 2017. Microbial response to environmental stresses: From fundamental mechanisms to practical applications. *Appl. Microbiol. Biotechnol.*, 101(10): 3991-4008.

Haq, S.M., F.A. Lone, M. Waheed, M.H. Siddiqui, F. Arshad and R.W. Bussmann, 2024. Analyzing anthropogenic determinants of vegetation distributions pattern in high-elevation forests of the himalayas. *Pak. J. Bot.*, 56(4): 1441-1450.

Hartmann, M. and J. Six. 2023. Soil structure and microbiome functions in agroecosystems. *Nature Rev. Earth Environ.*, 4(1): 4-18.

Hassan, S. and U. Mathesius. 2012. The role of flavonoids in root–rhizosphere signalling: Opportunities and challenges for improving plant–microbe interactions. *J. Exp. Bot.*, 63(9): 3429-3444.

Hirsch, P.R. and T.H. Mauchline. 2015. The importance of the microbial n cycle in soil for crop plant nutrition. *Adv. Appl. Microbiol.*, 93: 45-71.

Ho, Y.N., D.C. Mathew and C.C. Huang. 2017. Plant-microbe ecology: Interactions of plants and symbiotic microbial communities. *Plant Ecology-Traditional Approaches to recent trends*, 93: 119.

Hocking, P.J. 2001. Organic acids exuded from roots in phosphorus uptake and aluminum tolerance of plants in acid soils. *Adv. Agron.*, 74: 63-97.

Horner, J.D., J.R. Gosz and R.G. Cates. 1988. The role of carbon-based plant secondary metabolites in decomposition in terrestrial ecosystems. *The Amer. Naturalist*, 132(6): 869-883.

Huang, Q. 2024. Enhancing soil health and biodiversity through nitrogen fixation symbiosis in leguminous plants. *Mol. Microbiol. Res.,* 14.

Hussain, S., M. Shaukat, M. Ashraf, C. Zhu, Q. Jin and J. Zhang. 2019. Salinity stress in arid and semi-arid climates: Effects and management in field crops. *Clim. Change Agri.*, 13: 201-226.

Hussain, T., S. Singh, M. Danish, R. Pervez, K. Hussain and R. Husain. 2020. Natural metabolites: An eco-friendly approach to manage plant diseases and for better agriculture farming. *Nat. Bioac. Prod. Sustain. Agri.,* 1-13.

Idris, A., A.C. Linatoc, M.F.A. Bakar, Z.T. Ibrahim and Y. Audu. 2018. Effect of light quality and quantity on the accumulation of flavonoid in plant species. *J. Sci. Technol.*, 10(3): 32-45

Iqbal, B., G. Li, K.F. Alabbosh, H. Hussain, I. Khan, M. Tariq, Q. Javed, M. Naeem and N. Ahmad. 2023. Advancing environmental sustainability through microbial reprogramming in growth improvement, stress alleviation, and phytoremediation. *Plant Stress*, 10: 100283.

Islam, W., F. Zeng, M.O. Alotaibi and K.A. Khan. 2024. Unlocking the potential of soil microbes for sustainable desertification management. *Earth-Sci. Rev.,* 252: 104738.

Jacoby, R., M. Peukert, A. Succurro, A. Koprivova and S. Kopriva. 2017. The role of soil microorganisms in plant mineral nutrition—current knowledge and future directions. *Front. Plant Sci.*, 8: 1617.

Jacoby, R.P., A. Koprivova and S. Kopriva. 2021. Pinpointing secondary metabolites that shape the composition and function of the plant microbiome. *J. Exp. Bot.*, 72(1): 57-69.

Jagadesh, M., M. Dash, A. Kumari, S.K. Singh, K.K. Verma, P. Kumar, R. Bhatt and S.K. Sharma. 2024. Revealing the hidden world of soil microbes: Metagenomic insights into plant, bacteria, and fungi interactions for sustainable agriculture and ecosystem restoration. *Microbiol. Res.*, 285: 127764.

Jain, A., S. Sarsaiya, R. Singh, Q. Gong, Q. Wu and J. Shi. 2024. Omics approaches in understanding the benefits of plant-microbe interactions. *Front. Microbiol.*, 15: 1391059.

Jehani, M., S. Singh, T. Archana, D. Kumar and G. Kumar. 2023. Azospirillum a free-living nitrogen-fixing bacterium. In: Rhizobiome. *Elsevier*: pp: 285-308.

Jie, C., C. Jing-zhang, T. Man-zhi and G. Zi-tong. 2002. Soil degradation: A global problem endangering sustainable development. *J. Geograph. Sci.*, 12(2): 243-252.

Karlovsky, P. 2008. Secondary metabolites in soil ecology. In: Secondary metabolites in soil ecology. *Springer*: pp: 1-19.

Kaya, C. 2024. Microbial modulation of hormone signaling, proteomic dynamics, and metabolomics in plant drought adaptation. *Food Energy Secu.*, 13(1): e513.

Keese, P. 2008. Risks from gmos due to horizontal gene transfer. *Environ. Biosaf. Res.*, 7(3): 123-149.

Khan, N., S. Ali, H. Tariq, S. Latif, H. Yasmin, A. Mehmood and M.A. Shahid. 2020. Water conservation and plant survival strategies of rhizobacteria under drought stress. *Agron. Basel*., 10(11): 1683.

Kimotho, R.N. and S. Maina. 2024. Unraveling plant–microbe interactions: Can integrated omics approaches offer concrete answers? *J. Exp. Bot.*, 75(5): 1289-1313.

Kleinert, A., V. Benedito, R. Morcillo, J. Dames, P. Cornejo-Rivas, A. Zuniga-Feest, M. Delgado and G. Muñoz. 2018. Morphological and symbiotic root modifications for mineral acquisition from nutrient-poor soils. *Root Biol.,* 85-142.

Koshila Ravi, R., S. Anusuya, M. Balachandar and T. Muthukumar. 2019. Microbial interactions in soil formation and nutrient cycling. *Mycorrhizosphere and Pedogenesis*, 363-382.

Kumar, V., M. Kumar, N. Shrivastava, S. Bisht, S. Sharma and A. Varma. 2016. Interaction among rhizospheric microbes, soil, and plant roots: Influence on micronutrient uptake and bioavailability. *Plant, Soil Microb., Mech. Mol. Interact.,* 2: 169-185.

Kumar, V., K. Singh, M.P. Shah, A.K. Singh, A. Kumar and Y. Kumar. 2021. Application of omics technologies for microbial community structure and function analysis in contaminated environment. In: Wastewater treatment. *Elsevier*: pp: 1-40.

Lal, R. 2015. Restoring soil quality to mitigate soil degradation. *Sustain.-Basel*., 7(5): 5875-5895.

Larson, J.L., R.C. Venette and D.L. Larson. 2022. Restoration for resilience: The role of plant–microbial interactions and seed provenance in ecological restoration. *Nat. Area J.*, 42(2): 152-159.

Lattanzio, V., P.A. Kroon, S. Quideau and D. Treutter. 2009. Plant phenolics-secondary metabolites with diverse functions. *Recent Adv. Polyphenol Res.,* 1: 1-35.

Lehman, R.M., C.A. Cambardella, D.E. Stott, V. Acosta-Martinez, D.K. Manter, J.S. Buyer, J.E. Maul, J.L. Smith, H.P. Collins and J.J. Halvorson. 2015. Understanding and enhancing soil biological health: The solution for reversing soil degradation. *Sustain.-Basel*, 7(1): 988-1027.

Li, J., C. Chen, S. Wen, L. Yang, W. Sun, G. He and D. Zhang. 2024. The cross talk of sesquiterpenes and phenylpropanes mediated by the shikimic acid pathway affects essential oil content in phoebe sheareri leaves. *Ind. Crop Prod.*, 216: 118791.

Maiti, S.K. and D. Ghosh. 2020. Plant–soil interactions as a restoration tool. In: Climate change and soil interactions. *Elsevie*r: pp: 689-730.

Majhi, P.K., B. Raza, P.P. Behera, S.K. Singh, A. Shiv, S.C. Mogali, T.K. Bhoi, B. Patra and B. Behera. 2022. Future-proofing plants against climate change: A path to ensure sustainable food systems. In: Biodiversity, functional ecosystems and sustainable food production. *Springer*: pp: 73-116.

Majumdar, J., J.K. Biswas, A. Majumdar, T. Roychowdhury, S.C. Santra, A. Hossain and D. Moulick. 2025. Rhizomicrobiome: Role in management of heavy metal stress in plants. In: Rhizomicrobiome in sustainable agriculture and environment. *Elsevier*: pp: 315-332.

Maleki, S.J., J.F. Crespo and B. Cabanillas. 2019. Anti-inflammatory effects of flavonoids. *Food Chem.*, 299: 125124.

Matsuura, H.N. and A.G. Fett-Neto. 2015. Plant alkaloids: Main features, toxicity, and mechanisms of action. *Plant Tox.*, 2(7): 1-15.

Mhlongo, M.I., L.A. Piater, N.E. Madala, N. Labuschagne and I.A. Dubery. 2018. 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.*, 9: 112.

Miller, B.P., E.A. Sinclair, M.H. Menz, C.P. Elliott, E. Bunn, L.E. Commander, E. Dalziell, E. David, B. Davis and T.E. Erickson. 2017. A framework for the practical science necessary to restore sustainable, resilient, and biodiverse ecosystems. *Restor. Ecol.*, 25(4): 605-617.

Miyata, K. and M. Umehara. 2024. Roles of arbuscular mycorrhizal fungi for essential nutrient acquisition under nutrient deficiency in plants. In: Arbuscular mycorrhizal fungi and higher plants: Fundamentals and applications. Springer: pp: 123-148.

Moreno-Mateos, D., A. Alberdi, E. Morriën, W.H. van der Putten, A. Rodríguez-Uña and D. Montoya. 2020. The long-term restoration of ecosystem complexity. *Nat. Ecol. Evol.*, 4(5): 676-685.

Muhammad, M., A. Waheed, A. Wahab, M. Majeed, M. Nazim, Y.H. Liu, L. Li and W.J. Li. 2023. Soil salinity and drought tolerance: An evaluation of plant growth, productivity, microbial diversity, and amelioration strategies. *Plant Stress*, 11: 100319.

Mukherjee, A., S. Abraham, A. Singh, S. Balaji and K. Mukunthan. 2024. From data to cure: A comprehensive exploration of multi-omics data analysis for targeted therapies. *Mol. Biotechnol.*: 1-21.

Mukherjee, S., B. Sarkar, V.K. Aralappanavar, R. Mukhopadhyay, B.B. Basak, P. Srivastava, O. Marchut-Mikołajczyk, A. Bhatnagar, K.T. Semple and N. Bolan. 2022. Biochar-microorganism interactions for organic pollutant remediation: Challenges and perspectives. *Environ. Pollut.*, 308: 119609.

Murugan, A., K. Husain, M.J. Rust, C. Hepler, J. Bass, J.M. Pietsch, P.S. Swain, S.G. Jena, J.E. Toettcher and A.K. Chakraborty. 2021. Roadmap on biology in time varying environments. *Phys. Biol.*, 18(4): 041502.

Musilova, L., J. Ridl, M. Polivkova, T. Macek and O. Uhlik. 2016. Effects of secondary plant metabolites on microbial populations: Changes in community structure and metabolic activity in contaminated environments. *Int. J. Mol. Scien.*, 17(8): 1205.

Nadeem, S.M., M. Ahmad, Z.A. Zahir, A. Javaid and M. Ashraf. 2014. The role of mycorrhizae and plant growth promoting rhizobacteria (pgpr) in improving crop productivity under stressful environments. *Biotech. Adv.*, 32(2): 429-448.

Nawaz, M., M.U. Hassan, M.U. Chattha, A. Mahmood, A.N. Shah, M. Hashem, S. Alamri, M. Batool, A. Rasheed and M.A. Thabi., 2022. Trehalose: A promising osmo-protectant against salinity stress-physiological and molecular mechanisms and future prospective. *Mol. Biol. Rep.*, 49(12): 11255-11271.

Ncube, B., J. Finnie and J. Van Staden. 2012. Quality from the field: The impact of environmental factors as quality determinants in medicinal plants. *S. Afr. J. Bot.*, 82: 11-20.

Ninkuu, V., L. Zhang, J. Yan, Z. Fu, T. Yang and H. Zeng. 2021. Biochemistry of terpenes and recent advances in plant protection. *Int. J. Mol. Sci.,* 22(11): 5710.

Nizamani, M.M., A.C. Hughes, S. Qureshi, Q. Zhang, E. Tarafder, D. Das, K. Acharya, Y. Wang and Z.G. Zhang. 2024. Microbial biodiversity and plant functional trait interactions in multifunctional ecosystems. *Appl. Soil Ecol.*, 201: 105515.

Offre, P., A. Spang and C. Schleper. 2013. Archaea in biogeochemical cycles. *Ann. Rev. Microbiol.*, 67(1): 437-457.

Ondrasek, G., S. Rathod, K.K. Manohara, C. Gireesh, M.S. Anantha, A.S. Sakhare, B. Parmar, B.K. Yadav, N. Bandumula and F. Raihan. 2022. Salt stress in plants and mitigation approaches. *Plants*, 11(6): 717.

Ortíz-Castro, R., H.A. Contreras-Cornejo, L. Macías-Rodríguez and J. López-Bucio. 2009. The role of microbial signals in plant growth and development. *Plant Sign. Behav.*, 4(8): 701-712.

Osman, K.T. 2014. Soil degradation, conservation and remediation. *Springer*.

Panchawat, S. and C. Ameta. 2021. Medicinal importance of plant metabolites. In: Chemistry of biologically potent natural products and synthetic compounds. pp: 1-19.

Pandey, P., A. Tripathi, S. Dwivedi, K. Lal and T. Jhang. 2023. Deciphering the mechanisms, hormonal signaling, and potential applications of endophytic microbes to mediate stress tolerance in medicinal plants. *Front. Plant Sci.*, 14: 1250020.

Paterson, E., 2003. Importance of rhizodeposition in the coupling of plant and microbial productivity. *Eur. J. Soil Sci.*, 54(4): 741-750.

Peddle, S.D., R.J. Hodgson, R.J. Borrett, S. Brachmann, T.C. Davies, T.E. Erickson, C. Liddicoat, M. Muñoz-Rojas, J.M. Robinson and C.D. Watson. 2024. Practical applications of soil microbiota to improve ecosystem restoration: Current knowledge and future directions. *Biol. Rev.,* 2024: 1-18

Pedrinho, A., L.W. Mendes, A.P. de Araujo Pereira, A.S.F. Araujo, A. Vaishnav, D.G. Karpouzas and B.K. Singh. 2024. Soil microbial diversity plays an important role in resisting and restoring degraded ecosystems. *Plant Soil.*, 500(1-2): 1-25.

Philippot, L., J.M. Raaijmakers, P. Lemanceau and W.H. Van Der Putten. 2013. Going back to the roots: The microbial ecology of the rhizosphere. *Nat. Rev. Microbiol.*, 11(11): 789-799.

Phour, M., A. Sehrawat, S.S. Sindhu and B.R. Glick. 2020. Interkingdom signaling in plant-rhizomicrobiome interactions for sustainable agriculture. *Microbiol. Res.*, 241: 126589.

Puupponen-Pimiä, R., L. Nohynek, C. Meier, M. Kähkönen, M. Heinonen, A. Hopia and K.M. Oksman-Caldentey. 2001. Antimicrobial properties of phenolic compounds from berries. *J. Appl. Microbiol.*, 90(4): 494-507.

Radulovic, N., P. Blagojevic, Z. Stojanovic-Radic and N. Stojanovic. 2013. Antimicrobial plant metabolites: Structural diversity and mechanism of action. *Curr. Med. Chem.*, 20(7): 932-952.

Rahman, A.N.S.N., N.W. Abdul Hamid and K. Nadarajah. 2021. Effects of abiotic stress on soil microbiome. *Int. J. Mol. Sci.*, 22(16): 9036.

Rasheed, Y., F. Khalid, H. Ashraf, K. Asif, M.F. Maqsood, N. Naz, M. Shahbaz, U. Zulfiqar, Q. Ali and S. Rana. 2024. Enhancing plant stress resilience with osmolytes and nanoparticles. *J. Soil Sci. Plant Nut.*, 24(2): 1-36.

Rashid, M.H.O., M. Krehenbrink and M.S. Akhtar. 2015. Nitrogen-fixing plant-microbe symbioses. *Sustain. Agri. Rev.,* 15: 193-234.

Rashid, M.I., L.H. Mujawar, T. Shahzad, T. Almeelbi, I.M. Ismail and M. Oves. 2016. Bacteria and fungi can contribute to nutrients bioavailability and aggregate formation in degraded soils. *Microbiol. Res.*, 183: 26-41.

Ray, K., S.K. Basak, C.K. Giri, H.N. Kotal, A. Mandal, K. Chatterjee, S. Saha, B. Biswas, S. Mondal and I. Das. 2024. Ecological restoration at pilot-scale employing site-specific rationales for small-patch degraded mangroves in indian sundarbans. *Sci. Rep.*, 14(1): 12952.

Ray, P., V. Lakshmanan, J.L. Labbé and K.D. Craven. 2020. Microbe to microbiome: A paradigm shift in the application of microorganisms for sustainable agriculture. *Front. Microbiol.*, 11: 622926.

Raza, A., N. Zahra, M.B. Hafeez, M. Ahmad, S. Iqbal, K. Shaukat and G. Ahmad. 2020. Nitrogen fixation of legumes: Biology and physiology. Springer, Singapore.

Raza, T., M.F. Qadir, K.S. Khan, N.S. Eash, M. Yousuf, S. Chatterjee, R. Manzoor, S. ur Rehman and J.N. Oetting. 2023. Unrevealing the potential of microbes in decomposition of organic matter and release of carbon in the ecosystem. *J. Environ. Manag.*, 344: 118529.

Robinson, J.M., R. Hodgson, S.L. Krauss, C. Liddicoat, A.A. Malik, B.C. Martin, J.J. Mohr, D. Moreno-Mateos, M. Muñoz-Rojas and S.D. Peddle. 2023. Opportunities and challenges for microbiomics in ecosystem restoration. *Trends Ecol. Evol.*, 38(12): 1189-1202.

Rochange, S., S. Goormachtig, J.A. Lopez-Raez and C. Gutjahr. 2019. The role of strigolactones in plant–microbe interactions. *Springer*, Cham.

Rosier, A., F.H. Medeiros and H.P. Bais. 2018. Defining plant growth promoting rhizobacteria molecular and biochemical networks in beneficial plant-microbe interactions. *Plant Soil*, 428(1-2): 35-55.

Salam, U., S. Ullah, Z.H. Tang, A.A. Elateeq, Y. Khan, J. Khan, A. Khan and S. Ali. 2023. Plant metabolomics: An overview of the role of primary and secondary metabolites against different environmental stress factors. *Life*, 13(3): 706.

Sanchez, S. and A.L. Demain. 2008. Metabolic regulation and overproduction of primary metabolites. *Microb. Biotech.*, 1(4): 283-319.

Saraf, M., U. Pandya and A. Thakkar. 2014. Role of allelochemicals in plant growth promoting rhizobacteria for biocontrol of phytopathogens. *Microbiol. Res.*, 169(1): 18-29.

Saud, S., Z. Jiang and S. Fahad. 2023. Significance and exploitation of rhizosphere chemical signaling metabolites for enhancing soil nutrient transformation. *J. Soil. Sci. Plant Nut.*, 23(4): 4827-4842.

Schroeder, M. and D. Janos. 2005. Plant growth, phosphorus nutrition, and root morphological responses to arbuscular mycorrhizas, phosphorus fertilization, and intraspecific density. *Mycorrhiza*, 15(3): 203-216.

Sekhohola-Dlamini, L.M., O.M. Keshinro, W.L. Masudi and A.K. Cowan. 2022. Elaboration of a phytoremediation strategy for successful and sustainable rehabilitation of disturbed and degraded land. *Minerals-Basel.*, 12(2): 111.

Selosse, M.A., E. Baudoin and P. Vandenkoornhuyse. 2004. Symbiotic microorganisms, a key for ecological success and protection of plants. *Compt. Rendus Biol.*, 327(7): 639-648.

Shade, A., H. Peter, S.D. Allison, D.L. Baho, M. Berga, H. Bürgmann, D.H. Huber, S. Langenheder, J.T. Lennon and J.B. Martiny. 2012. Fundamentals of microbial community resistance and resilience. *Front. Microb.*, 3: 417.

Shah, A. and D.L. Smith. 2020. Flavonoids in agriculture: Chemistry and roles in, biotic and abiotic stress responses, and microbial associations. *Agron.-Basel.*, 10(8): 1209.

Sharma, S.B., R.Z. Sayyed, M.H. Trivedi and T.A. Gobi. 2013. Phosphate solubilizing microbes: Sustainable approach for managing phosphorus deficiency in agricultural soils. *SpringerPlus*, 2: 1-14.

Simenstad, C., D. Reed and M. Ford. 2006. When is restoration not?: Incorporating landscape-scale processes to restore self-sustaining ecosystems in coastal wetland restoration. *Ecol. Eng.*, 26(1): 27-39.

Singh, A.K., A. Sisodia, V. Sisodia and M. Padhi. 2019. Role of microbes in restoration ecology and ecosystem services. In: New and future developments in microbial biotechnology and bioengineering. *Elsevier*: pp: 57-68.

Singh, N., K. Sachan, M. BP, N. Panotra and D. Katiyar. 2024. Building soil health and fertility through organic amendments and practices: A review. *Asian J. Soil Sci. Plant Nutr.*, 10(1): 175-197.

Singh Rawat, V., J. Kaur, S. Bhagwat, M. Arora Pandit and C. Dogra Rawat. 2023. Deploying microbes as drivers and indicators in ecological restoration. *Restor. Ecol.*, 31(1): e13688.

Singla, P. 2020. Plant synthetic biology: A paradigm shift targeting stress mitigation, reduction of ecological footprints and sustainable transformation in agriculture. *Plant Stress Biology: Strategies and Trends*: 435-489.

Singla, P. and N. Garg. 2017. Plant flavonoids: Key players in signaling, establishment, and regulation of rhizobial and mycorrhizal endosymbioses. *Mycorrhiza-Function, Diversity, State of the Art*, 133-176.

Siqueira, J.O., M.G. Nair, R. Hammerschmidt, G.R. Safir and A.R. Putnam. 1991. Significance of phenolic compounds in plant-soil-microbial systems. *Crit. Rev. Plant Sci.*, 10(1): 63-121.

Smith, R., R. Shiel, R. Bardgett, D. Millward, P. Corkhill, G. Rolph, P. Hobbs and S. Peacock. 2003. Soil microbial community, fertility, vegetation and diversity as targets in the restoration management of a meadow grassland. *J. Appl. Ecol.*, 40(1): 51-64.

Smith, S.E., I.C. Anderson and F.A. Smith. 2015. Mycorrhizal associations and phosphorus acquisition: From cells to ecosystems. *Annual plant reviews: Phosphorus metabolism in plants*, 48: 409-439.

Spaepen, S., J. Vanderleyden and Y. Okon. 2009. Plant growth-promoting actions of rhizobacteria. *Adv. Bot. Res.*, 51: 283-320.

Stanturf, J.A., B.J. Palik and R.K. Dumroese. 2014. Contemporary forest restoration: A review emphasizing function. *Forest Ecol. Manag.*, 331: 292-323.

Stevenson, P.C., S.W. Nicolson and G.A. Wright. 2017. Plant secondary metabolites in nectar: Impacts on pollinators and ecological functions. *Func. Ecol.*, 31(1): 65-75.

Su, Y., J. Wang, W. Gao, R. Wang, W. Yang, H. Zhang, L. Huang and L. Guo. 2023. Dynamic metabolites: A bridge between plants and microbes. *Sci. Total Environ.*, 899: 165612.

Sujata, D. and G. Nibha. 2011. Microbial bioinoculants and their role in plant growth and development. *Int. J. Biotech. Mol. Biol. Res.*, 2(13).

Suman, J., A. Rakshit, S.D. Ogireddy, S. Singh, C. Gupta and J. Chandrakala. 2022. Microbiome as a key player in sustainable agriculture and human health. *Front. Soil Sci.*, 2: 821589.

Sun, Y., X. Xiong, M. He, Z. Xu, D. Hou, W. Zhang, Y.S. Ok, J. Rinklebe, L. Wang and D.C. Tsang. 2021. Roles of biochar-derived dissolved organic matter in soil amendment and environmental remediation: A critical review. *Chem. Eng. J.*, 424: 130387.

Tarkka, M., S. Schrey and R. Hampp. 2008. Plant associated soil micro-organisms. In: Molecular mechanisms of plant and microbe coexistence. *Springer*: pp: 3-51.

Temperton, V.M., N. Buchmann, E. Buisson, G. Durigan, Ł. Kazmierczak, M.P. Perring, M. de Sá Dechoum, J.W. Veldman and G.E. Overbeck, 2019. Step back from the forest and step up to the bonn challenge: How a broad ecological perspective can promote successful landscape restoration. *Restor. Ecol.*, 27(4): 705-719.

Tiku, A.R. 2018. Antimicrobial compounds and their role in plant defense. *Mol. Aspects Plant-Pathog. Interac.*, 283-307.

Timmis, K. and J.L. Ramos. 2021. The soil crisis: The need to treat as a global health problem and the pivotal role of microbes in prophylaxis and therapy. Wiley Online Library: pp: 769-797.

Trivedi, P., B.D. Batista, K.E. Bazany and B.K. Singh. 2022. Plant–microbiome interactions under a changing world: Responses, consequences and perspectives. *New Phytol.*, 234(6): 1951-1959.

Usharani, K., K. Roopashree and D. Naik. 2019. Role of soil physical, chemical and biological properties for soil health improvement and sustainable agriculture. *J. Pharm. Phytochem.*, 8(5): 1256-1267.

Vishwakarma, K., N. Kumar, C. Shandilya, S. Mohapatra, S. Bhayana and A. Varma. 2020. Revisiting plant–microbe interactions and microbial consortia application for enhancing sustainable agriculture: A review. *Front. Microbiol.*, 11: 560406.

Vithanage, U.Y. 2023. Investigation of the role of root flavonoids in the interaction of chickpea with nitrogen-fixing symbionts and parasitic nematodes. The Australian National University (Australia): pp: 1-24.

Vives-Peris, V., C. De Ollas, A. Gómez-Cadenas and R.M. Pérez-Clemente. 2020. Root exudates: From plant to rhizosphere and beyond. *Plant Cell Rep.*, 39(1): 3-17.

Wahab, A., M. Muhammad, A. Munir, G. Abdi, W. Zaman, A. Ayaz, C. Khizar and S.P.P. Reddy. 2023. Role of arbuscular mycorrhizal fungi in regulating growth, enhancing productivity, and potentially influencing ecosystems under abiotic and biotic stresses. *Plants*, 12(17): 3102.

Wang, F., L. Zhang, J. Zhou, Z. Rengel, T.S. George and G. Feng. 2022. Exploring the secrets of hyphosphere of arbuscular mycorrhizal fungi: Processes and ecological functions. *Plant Soil*, 481(1): 1-22.

Xu, L., Y. Zhang, N. Zarif, H. Li, D. Cui, J. Yu, J. Duan, C. Li and Q. Wang. 2024. Effects of low light, interspecific competition, and their combination on flavonoid exudation patterns and rhizosphere fungal community in juglans mandshurica and fraxinus mandshurica roots. *Plant Soil,* 1-19.

Yang, L., K.S. Wen, X. Ruan, Y.X. Zhao, F. Wei and Q. Wang. 2018. Response of plant secondary metabolites to environmental factors. *Molecules*, 23(4): 762.

Yeates, R.M. 2018. Development of a rhizosheath selection tool for screening perennial ryegrass (*Lolium perenne* L.) for reduced root competition against white clover (*Trifolium repens* L.) for soil phosphorus. The University of Waikato.

Yeshi, K., D. Crayn, E. Ritmejerytė and P. Wangchuk. 2022. Plant secondary metabolites produced in response to abiotic stresses has potential application in pharmaceutical product development. *Molecules*, 27(1): 313.

Younis, T., A. Khan and Z.K. Shinwari. 2024. Plant growth promoting potential of endophytic bacteria isolated from the roots of *Berberis lycium* royle. *Pak. J. Bot.*, 56(6): 2433-2440.

Zahran, H.H. 1999. Rhizobium-legume symbiosis and nitrogen fixation under severe conditions and in an arid climate. *Microbiol. Mol. Biol. Rev.*, 63(4): 968-989.

Zálešák, F., D.J.Y.D. Bon and J. Pospíšil. 2019. Lignans and neolignans: Plant secondary metabolites as a reservoir of biologically active substances. *Pharm. Res.*, 146: 104284.

Zandi, P. and E. Schnug. 2022. Reactive oxygen species, antioxidant responses and implications from a microbial modulation perspective. *Biology*, 11(2): 155.

Zhao, S. and M. Riaz. 2024. Plant–soil interactions and nutrient cycling dynamics in tropical rainforests. In: Environment, climate, plant and vegetation growth. Springer: pp: 229-264.

Zhou, J., H. Zang, S. Loeppmann, M. Gube, Y. Kuzyakov and J. Pausch 2020. Arbuscular mycorrhiza enhances rhizodeposition and reduces the rhizosphere priming effect on the decomposition of soil organic matter. *Soil Biol. Biochem.*, 140: 107641.

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