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REVIEW ARTICLE

Exploration of soil operative resistance factors: modulators of plant ecophysiological responses

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Abstract
The increasing intensity of environmental stresses presents significant challenges to modern agriculture. The assorted group of all environmental stress-related genes and mechanisms carried out by various soil-inhabiting microorganisms could readily contribute to resistance in crop plants represented as soil resistance factors (SRFs). It is essential to have a profound knowledge of the SRFs and their interaction with current basic challenges to develop appropriate strategies that effectively improve plant growth. Modern soil microbiological research is dedicated to understanding the relationship between the organization of gene and their function involved in various environmental processes. A significant fraction of the scientific community is primarily engaged in developing culture-independent techniques as a substantial (99%) portion of soil is still not cultivable in laboratory conditions. However, the SRFs and their exploitation are still in their commencement. The metagenomic method has proven to be a strong methodological tool for soil microbiome and SRF analysis. However, obtaining the appropriate detail of any particular gene that can completely characterize the intricacy of soil metagenomes and interpret meaningful conclusions about the native microbial communities is challenging. This review provides an overview of the metagenomic methods employed to gain insights into specific genes in soil microbiomes that confer resistance to abiotic and biotic stresses on crops.

Keywords Soil resistance factors · Metagenomics · Rhizosphere · Microbial diversity · Abiotic/biotic stress

Introduction

A rapidly growing population with a gradual decrease in the arable land area has recently evoked concerns about food security worldwide. Moreover, crop production is fronting various abiotic and biotic stresses in the agricultural system. A few reports estimated that about 70% of global crop production is reduced due to abiotic stresses such as temperature, drought, and salinity (Bowerman et al. 2023). Whenever plants encounter different abiotic stresses, i.e., drought, salinity, and low/high temperature, they become more susceptible to infections caused by bacterial/fungal pathogens, insects, and weeds (Das Laha et al. 2024; Peters et al. 2014). To contradict this situation there are several integrated management practices such as selecting early-maturing/short-duration along with abiotic resistant/tolerant crop varieties, disease-free and healthy seeds, and seed treatment. Among these management practices, the role of beneficial soil microorganisms as a cost-effective and environment-friendly tool can't be overlooked. Microorganisms dwelling in the soil play a vital role in agriculture by improving soil health and plant nutrition (Ding et al. 2024; Semwal et al. 2023; Misra et al. 2017). To this end, the scientific community intends to enhance agricultural output by managing soil microorganisms appropriately as low-input biotechnology while maintaining biodiversity (Jyoti et al. 2024; Zolla et al. 2013). Nowadays, agricultural research primarily depends on analyzing and managing the root-associated microbiome crucial for tackling economic and environmental sustainability problems. Moreover, studies demonstrating soil microbial ecology and its effect on plant physiology have provided an important platform for the present study region (Morris and Blackwood 2024; Mishra et al. 2023). Large and diverse communities residing in soil impart essential benefits to plant growth functions through

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nutrient mobilization and minimizing the harmful effects of environmental stresses. These communities are designated as "soil microbial biomass" *in toto* and the active members, i.e., viruses, archaea, bacteria, nematodes, fungi, oomycetes, arthropods, protozoa, and algae are involved in essential soil functions (Philippot et al. 2024; Zhang et al. 2024a, b). The enormous intricacy of soil microbial processes with an inappropriate estimation of their functional aspects has defied our knowledge of microbial influence. To characterize complicated soil microbial diversity, extensive research is needed to explore the particular features and their soil management implications for better crop production. In this context, culture-dependent techniques have limited access to estimate only 1% of the total soil microbes by culturing them in vitro while the rest (99%) is still unexplored (Anthony et al. 2023). Therefore, culture-independent techniques have appeared as a tool to examine the microbial community structure present in soil by analyzing existing metagenomes. The novel sequencing methods have explored the soil microbiomes and their respective functions with higher resolution and coverage making better options for agricultural management practices (Pinto and Bhatt 2024).

This review emphasizes exploring the soil microbial diversity, their interrelated functions, and resistance factors through metagenomics, helping crop plants to withstand abiotic and biotic stress. In this regard, various efforts associated with microbe-mediated enhanced plant growth under different biotic and abiotic stress have been attempted to describe.

Rhizospheric soil and its utility

The rhizosphere is a dynamic microenvironment established by the interaction of plant roots and microorganisms (Dixit et al. 2021; White et al. 2017). The chemical interplay between plant roots and associated microorganisms is considered to be directly or indirectly associated with plant growth (Dixit et al. 2023; Gupta et al. 2023). Exudate from plant roots exerts selective pressure drawing specific microorganisms adapted to utilize plant compounds. This phenomenon helps to create an aura of specialized microorganisms acquainted with a similar environment within the rhizosphere. These special classes of microorganisms carry various attributes that help confer resistance to crop plants against abiotic and biotic stresses (Table 1). Therefore, the potential of microorganisms could be harnessed to unravel the soil resistance factors and their role in sustainable agriculture by counteracting various environmental challenges (Solomon et al. 2023).

Table 1 List of factors analyzed by metagenomics conferring resistance against different abiotic/biotic stress

Stress	Members	Resistance factor	Function	References
Salt	Proteobacteria, Actinobacteria, Gemmatimonadetes, Bacteroidetes, Firmicutes, and Acidobacteria	*BCAA_ABCtp*, *GSDH*, *STK_Pknb*, and *duf3445* genes	Osmotolerance	Ahmed et al. (2018)
Drought	Actinobacteria, Proteobacteria, Cyanobacteria and Bacteroidetes	*desR*, *desk*, *oxyR*, *perR*, *cydA*, *cydB*, *fnr*, *arcB*, and *opuE*	Temperature regulation Oxidative stress tolerance Proline uptake	Phuong et al. (2016)
Temperature	α- Proteobacteria, Cyanobacteria, and, Actinobacteria	Genes coding for functional responses to environmental stress, and sigma B genes *desR* and *desK*	Cryoprotection, and Osmotolerance	Varin et al. (2011)
	Actinobacteria, Proteobacteria, Cyanobacteria and, Bacteroidetes		Temperature regulation	Mascher et al. (2006)
pH	α-, β-, γ-, and Ɛ- Proteobacteria, Flavobacteria, Bacteroidetes, Sphingobacteria, and Flexibacter	*ABCTPP*, *TMSRP1*, and *TLSRP*	Osmotolerance	Verma et al. (2018)
Heavy metals	α-, β-, and γ- Proteobacteria	*NarK*, *CzcABC*, and *CzcD*	Ion toxic stress tolerance	Hemme et al. (2010)
Phytopathogens	Mesorhizobium, Bradyrhizobium, Streptomyces	*pchB,* genes coding for β-1,3-glucanase, and chitinase	Plant disease suppression	Tsurumaru et al. (2015)
	Proteobacteria, Firmicutes, and Actinobacteria	NRPS genes	Protection against fungal infection	Mendes et al. (2011)

Soil resistance factors: a critical factor for plant physiological response

Soil represents the most complex environment regarding microbial diversity. The microbial abundance in the soil is directly or indirectly modulated by grown host crops. In particular, grassland or cultivated soil contains about 10^9 prokaryotic cells gram^{-1}. The soil microbial composition is a significant variable in distinct agricultural systems because it is accountable for nutrient assimilation in the soil which can enhance plant productivity (Misra et al. 2017; Lugtenberg 2015). In addition, studies on soil microbial ecology and its impact on plant physiology and productivity represent an emerging field of interest (Dubey and Misra 2024; Misra et al. 2017; Owen et al. 2015). The rhizosphere is one of the intriguing microbial habitats for fundamental and applied environmental microbiological research as it consists of the tripartite interaction of soil, plants, and microorganisms. The rhizospheric soil demonstrates extensive root colonization and displays higher microbial activities than bulk soil (Misra et al. 2017). The significance of rhizosphere for plant growth and soil ecology had already been understood in the early times of microbiology as an environment rich in varied microbial communities. The microbial diversity in the soil is important for maintaining good soil health as these microorganisms contribute to varied crucial functions such as elemental cycles, soil formation, toxin elimination, and others (Wu et al. 2023). Traditionally, the analysis of bacterial populations and diversity has started with sampling from environmental sources (Lemke and DeSalle 2023). This method has constraints due to its restricted capacity to cultivate a wide range of bacterial species. Unknown conditions for the growth demands of many microorganisms and the existence of cells in a sustainable but non-cultivable condition represent less than 1% of the microbial diversity acquired through standard cultivation methods (Wei et al. 2021; Nichols 2007). In addition, genomic studies comprising cloning the entire genome of a single microorganism demonstrated inadequacy in achieving comprehensive microbial diversity because of the possible interaction of microorganisms with other habitats and sometimes with native microbial populations within the community (Li et al. 2024a, b; Misra et al. 2017). However, advanced sequencing methods with high-performance evaluation have led the scientific community to acquire alternatives to combat this issue. The pace of genomic research in microbial ecology and environmental microbiology is accelerating. A sample can now be obtained from the habitat(s) and sequenced directly from the environment. The collection of genomes from a particular habitat is defined as 'metagenome', and the study about it is known as 'metagenomic studies' or shortly as 'metagenomics' (Handelsman et al. 1998). Metagenomics can overcome the limitations of normal genomics, as the data can be attained directly from the environment where they exist with their natural habitats (Chen 2024). This novel field of study is increasing rapidly to study uncultured microorganisms to comprehend the diversity of microbes, their functions, collaboration, and development in environments such as soil, water, ancient animal remains, or the digestive system of animals and humans (de Bruijn 2011). Although, the significance of microbial communities in such systems is well acknowledged, however, a more detailed understanding is required to gain the possible underlying mechanism.

Metagenomics: a tool to understand soil microbiome

Metagenomics is a tool that enables the user to obtain data related to the niche division of microbial species exhibiting plant growth promoting (PGP), biocontrol, antibiotic-producing, and xenobiotic mitigating attributes. A report on potato endophytes indicates that PCR analysis has identified two types of ACC-deaminase genes (*acdS*) that are homologous to those found in *Pseudomonas fluorescens* demonstrating stress alleviation (Nikolic et al. 2011). An *acdR* gene (transcriptional regulator) was identified upstream of the acdS operon of the uncultivated endophyte population through clone analysis in metagenomics libraries (Nikolic et al. 2011). Also, a metagenomic library of pond water demonstrating clones of *Escherichia coli* identified certain salt-tolerance genes by growing uncultivable bacterial colonies at inhibitory concentrations of NaCl (750 mM). Genes from two clones that encode proteins resembling a putative general stress protein (GspM) containing a GsiB domain, along with a putative enoyl-CoA hydratase (EchM), were found to play a role in salt tolerance (Kapardar et al. 2010). These genes could prove to be of great importance in developing salt-tolerant bacteria and transgenic plants. Furthermore, the metagenome of acid mine drainage contains genes responsible for survival at low temperatures, such as anti-freeze proteins, cold-shock proteins, compatible solute production pathways, and mechanisms for maintaining pH homeostasis (Liljeqvist et al. 2015). These studies could decipher novel functions and underlying mechanism(s) for cold-stress mitigation. Moreover, due to a lack of proper cultivation practices, the potential role of endophytic microbes is largely unexplored and hence represents only a fraction of the whole microbial community that resides in the root endosphere. Earlier, Sessitsch et al. (2012) characterized the endophytic bacterial inhabitants of rice roots using a metagenomic approach. Metagenomic sequences derived from the root endosphere indicated that metabolic processes

such as quorum sensing and ROS detoxification demonstrated enhanced plant stress resistance. (Sessitsch et al. 2012). Microbial communities play a crucial role in maintaining plant health and productivity (Fig. 1). Holistic methods like metagenomics, metatranscriptomics, and metaproteomics are conducive to knowing the soil resistance factors and describing their diversity and function. Metagenomics analysis may also uncover the functionality of the particular metabolic process involved in stress amelioration (Turner et al. 2013). Profiling microbial diversity and colonization studies utilizing metagenomics can also provide insights into the quantitative colonization of a specific host in response to stress factors. Integrating the analysis of microbial diversity with metatranscriptomic approaches can yield valuable insights into the changes induced by stressors (Turner et al. 2013). These combined analysis significantly contributed to understanding how stressor influences are mitigated during the colonization process.

In addition, profiling of microbial functional (*amoA* gene: Nitrifying bacteria; *nifH* gene: Nitrogen-fixing bacteria) and taxonomic (16S rRNA gene: Bacteria and archaea; ITS or 18S rRNA gene: Fungi) genes in the soil can be achieved by utilizing high-throughput sequencing of marker gene tags (iTAG) (Kashani et al. 2024). Plant-associated microbiomes can also be deciphered by applying comparative metatranscriptomics to reveal kingdom-level variances in the dynamic rhizosphere microbiome of host crops (Ortúzar et al. 2024). The root phenotyping method for studying plant responses to different abiotic and biotic conditions, and microbial interactions, shows significant potential for enhancing the understanding of crop resilience (Balestrini et al. 2024).

Microbial expression profiles in the soil

Salinity

The microorganisms enriched with the plentitude of phytobeneficial properties show resistance against varied environmental stresses, termed Plant growth-promoting rhizobacteria (PGPR). Several researchers have identified novel genes encoding proteins related to osmoadaptation such as a glycerol transporter and a proton pump from the microbial

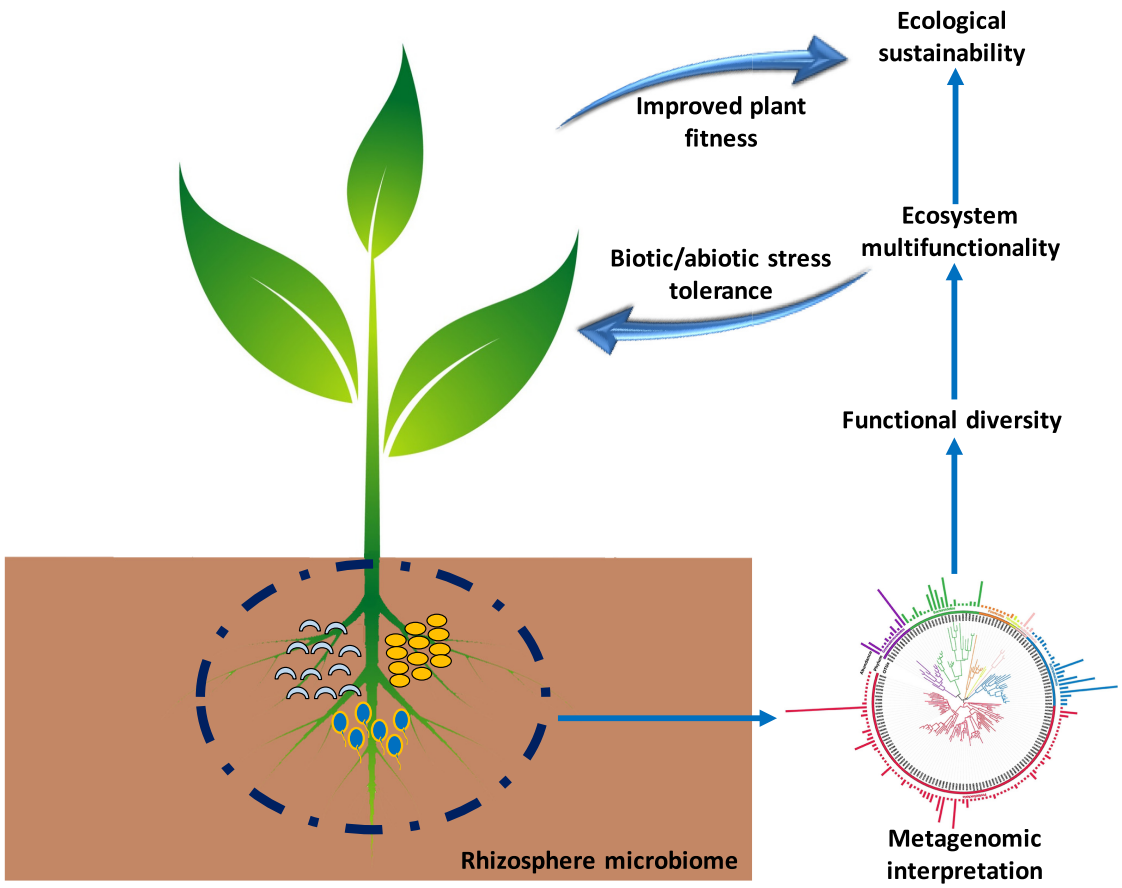

Fig. 1 Illustration depicting the importance of metagenomic research for sustainable ecosystem

populations of a moderate salinity rhizosphere and brine from the Es Trenc saltern (Mallorca, Spain), which could confer increased salt resistance to *Escherichia coli* (Mirete et al. 2015). Furthermore, the root microbiota of halotolerant seepweed *Suaeda salsa* was also explored to gain knowledge about the rhizospheric and endophytic bacteria associated with *S. salsa* contributing to salinity acclimatization, nutrient solubilization, and competitive root colonization. These results also revealed that an ecological patterned root-microbial interaction strategy has been adopted in *S. salsa* and non-host plants to confront soil salinity (Yuan et al. 2016). In addition, previous reports demonstrated IST to salt stress in soybeans by the inoculating PGPR strains *Pseudomonas* sp. and *Bacillus* sp. through proline content enhancement and lipoxygenase activity (Kumari et al. 2015). The addition of proBA genes from the rhizobacterial strain *Bacillus subtilis* into *A. thaliana* led to the production of elevated levels of free proline, which enhanced osmotic stress tolerance in the transgenic plants (Chen et al. 2007). Similarly, maize (*Zea mays*) plants inoculated with *Rhizobium* and *Pseudomonas* exhibited increased proline production, decreased electrolyte leakage, maintained relative water content in leaves, and selective uptake of K^+ ions, collectively contributing to enhanced salt tolerance. (Bano and Fatima 2009). Moreover, trehalose metabolism in PGPR plays a crucial role in enhancing plant growth, yield, and tolerance to environmental stresses (Duan et al. 2013).

Drought

Drought stress is considered to be a chief constraint limiting agricultural production worldwide. PGPR are beneficial rhizosphere colonizing microorganisms that exhibit drought tolerance by the production of 1-aminocyclopropane- 1-carboxylate (ACC) deaminase, phytohormones, volatile compounds, exopolysaccharides (EPS) (Misra et al. 2017). Besides these phytobeneficial attributes, PGPR acquires resistance against drought stress by upregulation or down-regulation of stress-responsive genes and modification in root morphology. Earlier reports have demonstrated that augmentation of the drought-responsive gene EARLY RESPONSE TO DEHYDRATION15 (*ERD15*) from *Paenibacillus polymyxa* B2 resulted in enhanced drought tolerance of *Arabidopsis thaliana* (Timmusk and Wagner 1999). Also, pepper plants treated with *B. licheniformis* K11 showed resistance against drought stress by increased accumulation of proteins encoding specific genes of *Cadhn*, *VA*, *sHSP*, and *CaPR-10* (Lim and Kim 2013). Rhizobacteria-induced drought endurance and resilience (RIDER) induces microbe-mediated plant responses including phytohormone modulation, and production of defense-related proteins and enzymes, antioxidants, and exopolysaccharides. These strategies enhance plants' toughness against abiotic stresses (Kaushal and Wani 2016). Previously, Koussevitzky et al. (2008) demonstrated that PGPR-mediated upregulation of the *Apx1* gene induces drought stress tolerance in *Arabidopsis*. Moreover, ectoine has been reported as a compatible osmolyte mainly responsible for conferring salt tolerance in *Halomonas elongata* (Nakayama et al. 2000). Introducing the genes involved in ectoine biosynthesis into the tobacco plant (*Nicotiana tabacum* L.) resulted in enhanced tolerance to hyperosmotic shock demonstrating normal growth under these conditions (Nakayama et al. 2000).

Temperature

High temperature (e.g., heat shock) is a critical environmental challenge to plant and microbial growth and homeostasis. Finding PGPR strains that allow plant growth at higher temperatures would potentially expand the global range of crop cultivation, particularly regarding future climate scenarios. Interventions of PGPR that improve plant thermal stress are less known. However, previous research has discussed the isolation and selection of PGPR strains that are heat tolerant up to 60 °C (e.g., rhizobial isolates) (Rodriguez et al. 2008). However, several reports have studied the application of PGPR to alleviate the side effects of low-temperature stress on plant growth (Ait Barka et al. 2006; Dimkpa et al. 2009). Plants respond to cold acclimation or hardening through changes in their physiological properties including an increase in sugar, proline, and anthocyanin contents (Dimkpa et al. 2009). Previous report established that grapevine plants treated with *Bacillus phytofirmans* strain PsJN accumulated higher levels of carbohydrates, proline, and phenols, and showed elevated rates of photosynthesis and starch deposition as compared to control plants during cold stress (Ait Barka et al. 2006). Furthermore, in the same study, treated grapevine exhibited a lower rate of biomass reduction and electrolyte leakage (an indicator of cell membrane injury) during cold treatment at 4 °C, and PGPR inoculation also promoted post-chilling recovery. Similarly, Srivastava et al. (2008) studied a thermotolerant PGPR strain *Pseudomonas putida* isolated from the drought-stressed rhizospheric soil of chickpea exhibiting excess production of stress sigma (S) (*RpoS*) under high-temperature stress. Also, previous research demonstrated that the inoculation of a thermotolerant *Pseudomonas* sp. strain significantly induced thermotolerance in sorghum seedlings (Ali et al. 2009). Moreover, AMK-P6 also exhibited improved plant biomass as well as biochemical status in terms of proline, sugar, amino acid, and chlorophyll contents (Ali et al. 2009). Likewise, a previous report related to PGPR-mediated thermotolerance to crop plants established that *Burkholderia phytofirmans* colonizes the grapevine endosphere while protecting it against cold and heat stress (Compant et al. 2005).

pH and heavy metals

Extreme pH and heavy metal concentrations are other abiotic factors that may adversely affect plant growth (Dixit et al. 2021). Soils exhibiting low, or high pH levels, as well as contaminated soils, present significant challenges to agricultural sustainability. In the context of pH stress, it was observed that foliar injuries on corn plants growing in low-pH soil were significantly ameliorated with the treatment of 2,4-diacetyl phloroglucinol (DAPG)-producing strain of *P. fluorescens* (Raudales et al. 2009). Recently, Kar et al. (2024) have demonstrated the plant growth-promoting effect of isolated alkaline-tolerant bacterial strains of varied genera including *Enterobacter*, *Bacillus*, *Stenotrophomonas*, and *Lysinibacillus* under alkaline stress conditions. Moreover, a rhizobacterial strain *Ochrobactrum* sp. has been reported to restitute the soil alkalinity by producing organic acids hence promoting the growth of maize plants under high pH soil conditions (Mishra et al. 2023).

Heavy metals like arsenic (As), chromium (Cr), cadmium (Cd), mercury (Hg), copper (Cu), nickel (Ni), and lead (Pb) significantly affect microbial and plant physiology beyond threshold levels (Majhi et al. 2023). Heavy metal contamination in soil considerably affects the remediation potential of plants, however, the microbial intervention may augment phytoremediation and is therefore termed microbe-assisted phytoremediation (Glick 2003; Jamil et al. 2014). The role of PGPR is well established in protecting the host crops from heavy-metal toxicity (Majhi et al. 2023; Shinwari et al. 2015). Numerous PGPR genera comprising *Mesorhizobium, Rhizobium, Sinorhizobium, Bradyrhizobium, Achromobacter, Azotobacter, Pseudomonas,* and *Bacillus* have bioremediating ability (Majhi et al. 2023; Shinwari et al. 2015). An earlier report has demonstrated the ability of *Bacillus licheniformis* to improve seed germination and biochemical attributes of rice by protecting it against Ni stress (Jamil et al. 2014). Also, PGPR has developed distinct mechanisms to utilize, mobilize, and transform heavy metals, making them endurable, potentially useful, or inactive. The PGPR-mediated heavy metal tolerance may encompass the following mechanisms: (a) exclusion through the efflux pumps, (b) Elimination of the metals from target sites, (c) Inactivation by complex formation, and (d) Bioconversion to a less toxic redox state (Tak et al. 2013).

Phytopathogens

Plant diseases are responsible for annual crop losses at a total value of more than 200 billion (Venbrux et al. 2023). Developing biotic stress-tolerant plants through breeding methods may take many years and recognition of genetically modified crops is still a concern in the European Union (Yadav et al. 2024). Moreover, the consumers negatively adopt the excessive usage of agrochemicals for disease management (Misra et al. 2017). Therefore, utilizing phytobeneficial microbes as a biocontrol is considered to be an environment-friendly alternative approach by the research communities (Misra et al. 2017; Pérez-García et al. 2011). Microbe-mediated biocontrol of plant pathogens is a natural process comprising different strategies such as secondary metabolite production and synthesis of allelochemical (Benaissa 2024). In comparison to microbes, agrochemicals are not location-specific and sometimes remain unreachable to the host plant. Apart from their specificity to location, the molecules from the biological origin are biodegradable (Benaissa 2024). Studies related to rhizobacteria are not only limited to the biocontrol of microbial pathogens but also control weeds and insects (Ayyub et al. 2024; Jian et al. 2024). Soils demonstrating disease symptoms are termed conducive soils while suppressive soils characterized by the presence of disease-suppressing microbes (Khatri et al. 2024). Combining small quantities of suppressive soil with a larger volume of conducive soil renders the latter suppressive (Khatri et al. 2024). Microbe-mediated control of plant diseases is a complex process involving indigenous microbiomes and plant growth substrates. Several findings popularize the usage of microbe-based formulations and protect the environment by minimizing chemical pesticide usage (Behl et al. 2024).

Variation in soil operative resistance

Soil bacteria inherently demonstrate resistance factors as a means of competition and survivability, accompanied by the evolution and exchange of various resistance mechanisms through horizontal gene transfer. Most studies on bacterial resistance elements in soil ecosystems have focused on human-impacted environments, leaving a gap in knowledge about unexplored areas, where the resistome may reflect inherited gene diversity. An earlier study by Wang et al. (2020) investigated the distribution of resistance factors in saline-alkali soils under greenhouse conditions. They reported that soil resistance factors vary with the soil types having complex diversity and relative abundance in saline-alkali soils. This study also explained the effective role of heavy metals and soil physicochemical parameters in affirming the distribution of soil resistance factors. Recently, Xu et al. (2022) also established the central role of soil salt concentration in determining the spread of soil resistance factors. This study proposed that the enhanced transfer of resistance genes was likely associated with the overproduction of intracellular reactive oxygen species and the heightened activity of DNA repair enzymes involved in the SOS response system. Moreover, this study highlighted that soil salinity-sodicity reshapes the spreading of resistance factors

in the soil and community framework of microbes. However, several researchers utilized shotgun metagenomics techniques to decipher the resistance factors under permafrost soil conditions (Van Goethem et al. 2018).

Soil molecular insights and agricultural productivity and resilience

Soil microbiomes are structured differently among varied host plant and their genotype. An earlier study demonstrated the potential role of numerous candidate genes in shaping the microbial community structure (Crespo-Piazuelo et al. 2019). Moreover, the interaction between soil physicochemical properties and plant root exudates also plays a crucial role in designing the soil microbial community structure (Stringlis et al. 2018). Microbial communities serve as both agents and sources of insight into biogeochemical cycles, nutrient dynamics, and metabolic activities. Metagenomics is likely employed as a tool for detecting pathogens in agriculture (Misra et al. 2017). Synthetic metagenomics entails identifying novel genes by exploring sequence databases and metagenomics data for a specific gene of interest. Through this method, methyl halide transferase enzyme was identified which is extensively used for biofuel production in the agricultural sectors (Culligan et al. 2014). Also, metagenomics revealed the existence of microbial genes encoding novel bio-compounds having antimicrobial properties. Previous studies have indicated that agricultural productivity and defense could be improved by fortifying the soil microbiomes by applying volatile compounds and imitating microbial quorum sensing (Kwak et al. 2018; Schulz-Bohm et al. 2018). Further, the signaling molecules in the soil microbiomes can also be utilized to selectively promote nutrient acquisition and phytopathogen defense (Papenfort and Bassler 2016). Plant–microbe assemblage can also be engineered to accomplish Symbiotic Signaling Pathway (SYM) in crops ultimately inducing signaling molecules for enhanced productivity (Hao et al. 2024). Existing research also specified that higher agricultural yield could be possible through the higher abundance of phosphorus (P) solubilizing (*gcd* and *ppa*) and phosphorus mineralizing (*phoD*, *phy*, and *ugpQ*) genes in the soil (Kong et al. 2024). Several reports have confirmed the presence of microbial genes encoding root colonization, stress response, motility, and organic compound secretions in soil for supplementing plant growth (Xu et al. 2018). Enhanced plant growth can also be attributed to microbial genes responsible for P-solubilization, nitrogen fixation, iron sequestration, and biocontrol activity (Li et al. 2019). Additionally, Symanczik et al. (2020) and Fan et al. (2023) have confirmed the regulation of drought stress response through the synchronized induction of the fungal (*RiMsn2*) and host plant aquaporins (AQP) genes in roots.

Contribution of rhizobacterial diversity in improving soil health

In the natural environment, plants are part of a rich ecological system comprising diverse microbial communities in the soil. The role of beneficial soil microbes such as nitrogen fixation, phosphate solubilization, nutrient mineralization, and pollutant degradation has been well recognized for improving plant growth and soil fertility (Majhi et al. 2023; Mishra et al. 2023). However, the potential of microbes associated with plants to be an alternative to synthetic products has only recently started to come into existence (Ayilara et al. 2023). With the advent of next-generation sequencing, great progress has been made in the knowledge of the composition of rhizospheric microbiomes and their dynamics. Earlier reports revealed that plants shape microbiome structures, most probably through root exudates (Wang et al. 2017). Soil microbiomes can have direct or indirect effects on many ecosystem services therefore, it is important to identify taxa (to the highest resolution possible) responsible for specific processes. With the ongoing metagenomics-based analyses of soil microbiomes, it is possible to decipher the mechanisms of plant-soil-microbe interactions along with the processes driving the alterations in microbiomes (Misra et al. 2017). It has been estimated that the abundance of beneficial microbes is positively correlated with higher soil quality, which includes improved plant growth, reduced disease incidence, and increased nutrient levels and soil enzyme activities (Wang et al. 2017) (Fig. 2). Bacterial phyla playing a crucial role in aforementioned processes have been listed in Table 2. Metagenomics analysis could yield a better understanding of the biotic and abiotic factors that control these processes. For example, determining the specific microbial taxa responsible for atmospheric nitrogen fixation improves our ability to predict the rate of nitrogen fixation in the soil.

Moreover, the soil microbial population framework is structured based on plant growth stages driven by the changes in the root exudates composition and soil pH. In a previous study, Wang et al. (2017) reported that healthy soils demonstrated high microbial diversity than bacterial wilt-infected soils. In addition, they described that the beneficial microbes including *Bacillus*, *Agromyces*, *Micromonospora*, *Pseudonocardia*, *Acremonium*, *Lysobacter*, *Mesorhizobium*, *Microvirga*, *Bradyrhizobium*, etc. have significantly increased the activities of catalase, invertase, urease, and availability of phosphorous and potassium in the healthy soils in comparison to bacterial wilt infected soils. Soil processes are directly linked with the absolute number of taxa, genes, or gene products (Xun et al. 2021). Thus, information

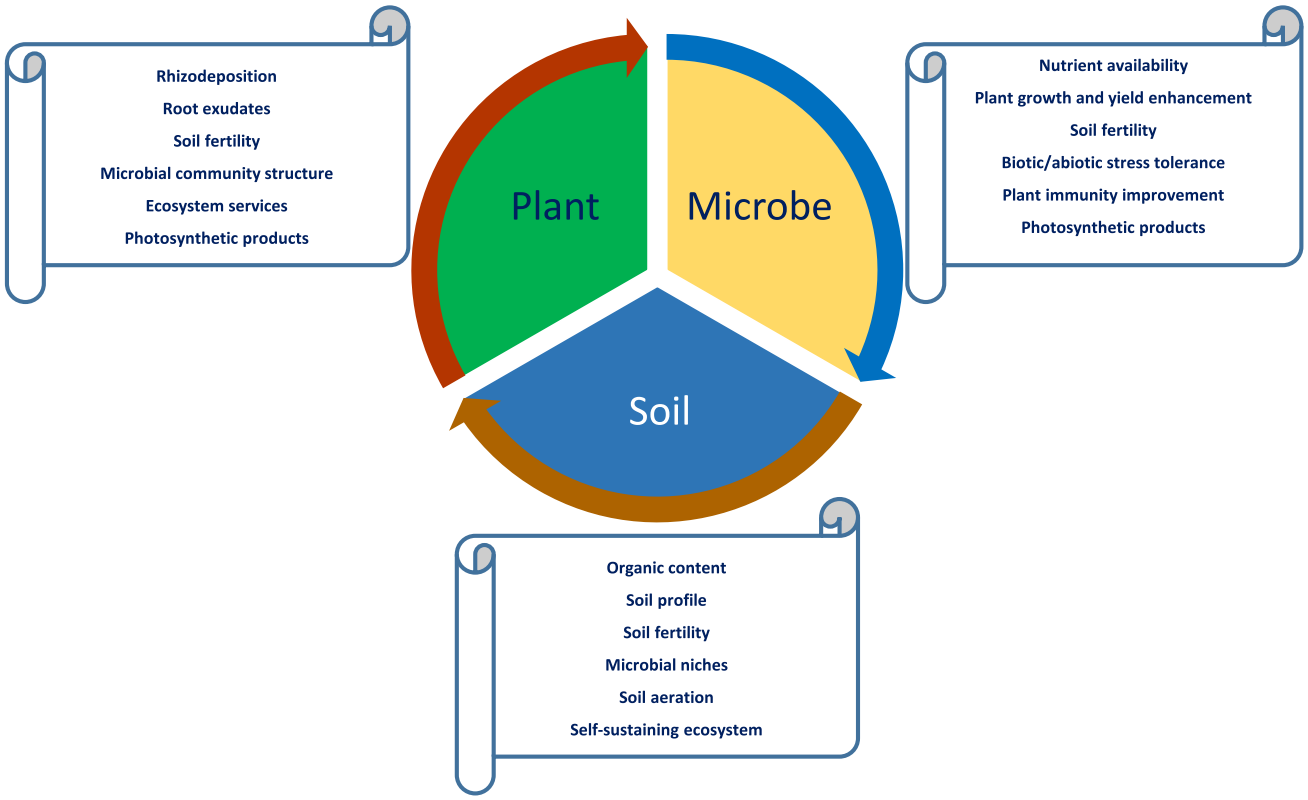

Fig. 2 Representation of ecosystem sustainability by important factors of rhizosphere

about the microbial taxa found in soil is often useful for predicting the rates of a given biogeochemical process and overcoming the challenges in linking microbiome structure to function.

Climate change and soil functions

Ecosystem multifunctionality is well regulated by soil microbiomes but the interaction of soil microbiome with soil attributes under diverse climates warrants extensive research. Alterations in precipitation patterns can significantly impact soil water balance and aeration systems, leading to subsequent changes in soil nutrient cycling and the composition of microbial communities (Suolang et al. 2024). Soil microbial activity, which is a key driver of nutrient cycling, is strongly influenced by the availability of soil water. This is particularly important because soil microorganisms play a vital role in regulating carbon cycles in terrestrial ecosystems, especially in water-limited arid environments understanding the importance of fluctuating precipitation in shaping microbial community structure. For example, numerous studies have shown that increased precipitation can enhance soil microbial diversity directly by enabling the coexistence of species with varying water tolerance strategies, and indirectly by boosting plant community productivity and composition (Wang et al. 2018). Mean annual precipitation (MAP) is a key factor influencing the structure of microbial networks, with higher precipitation leading to increased network complexity (Wang et al. 2018). Additionally, keystone taxa are well-known within these networks for their extensive interconnections and essential ecological roles in sustaining the structure of microbial communities and promoting nutrient cycling (Wang et al. 2018). The application of Molecular Ecological Network Analyses (MENA) can clarify potential changes in keystone taxa resulting from fluctuations in resource availability under varying precipitation levels (Li et al. 2024a, b). However, it is still unclear whether the relative abundance of keystone taxa increases with higher precipitation-like microbial diversity, which could have implications for the organic carbon storage of soil (Li et al. 2024a, b). Additionally, more frequent and smaller precipitation events enhance the abundance of *nosZ*, *gltBD*, *ghdhB*, and *nrtABCD* (Suolang et al. 2024).

The functioning of soil ecosystems is highly sensitive to the interplay between high temperature and soil moisture, indicating that climate change will significantly impact soil functions in the future. Gaining insight into the collective drivers of soil functions allows for more accurate predictions of the soil ecosystem's response to a quickly changing

Table 2 List of bacterial phyla involved in maintaining soil fertility

Bacterial phyla	Occurrence	Possible contribution in soil fertility	References
Acidobacteria	Low pH and nutrient-starved condition	Mitigate alkalinity stress of soil Degradation of cellulose	Bruce et al. (2010)
		Disease suppression	Xiao et al. (2018)
Actinobacteria	Soil with high sensitivity to acidic environment	Degradation of polysaccharides, protein, fats, organic acids	Baoune et al. (2018)
		Disease suppression	Mendes et al. (2011)
Armatimonadetes	High temperature condition	Improve soil physicochemical properties	Zeng et al. (2016)
Bacteroidetes	Anaerobic condition, soil with low C:N ratio, and high pH	Nutrient solubilization in the soil	Wang et al. (2017)
		Bioremediation of petroleum-contaminated soil	Shahi et al. (2016)
Chlorobi	Anaerobic and low light condition	Sulphate reduction and nitrogen fixation	Thompson et al. (2017)
Chloroflexi	Soil with high C:N ratio and low pH, high temperature, and halophilic condition	Degrade and utilize cellular compounds derived from dead biomass in soil	Kindaichi et al. (2012)
		Anaerobic ammonium oxidation	Gao et al. (2018)
		Nutrient solubilization in the soil	Krzmarzick et al. (2011)
		Glycoside hydrolysis	Kragelund et al. (2007)
Cyanobacteria	Anaerobic condition, damp soil, bare rock and soil, and even Antarctic rocks	Nitrogen fixation	Singh et al. (2016)
Fibrobacteres	Arable soil with high organic content	Cellulose degradation	Ransom-Jones et al. (2012)
Firmicutes	Extreme conditions	Degradation of lignocellulose	Bonanomi et al. (2016)
		Disease suppression	Mendes et al. (2011)
Nitrospirae	Halophilic condition	Nitrite oxidation in soil	Koch et al. (2015)
Planctomycetes	Halophilic condition	Ammonium oxidation anaerobically	Fuerst (2017)
		Glycoside hydrolysis	Kragelund et al. (2007)
Proteobacteria	Low nutrient, halophilic, low temperature condition	Bioremediation of petroleum-contaminated soil Nitrogen fixation	Shahi et al. (2016)
Thermodesulfobacteria	Thermophilic condition	Sulphate reduction in soil	Balk et al. (2015)
Thermotogae	Hyperthermophilic and anaerobic condition	Metabolize numerous organic substrates	Bhandari and Gupta (2014)
Verrucomicrobia	Low nutrient condition	Polysaccharide degradation	Cardman et al. (2014)

environment. Drought is anticipated to decrease microbial abundance and diffusion rates, leading to a reduction in enzyme activity (Wang et al. 2024). However, the overall effects of drought may be enhanced or alleviated by other factors, including soil enzyme stability, alteration in microbial community structure, etc. Consequently, the response of enzyme activity to drought varies across different soil types, drought strength, and frequency. In particular, high temperatures attracted bacteria containing the *phoD* and *phoX* genes, which encode enzymes involved in phosphoester hydrolysis, significantly accelerating organic phosphorus mineralization and directly influencing phosphorus availability in the soil (Wang et al. 2024).

Carbon dioxide is an essential greenhouse gases that significantly influence the carbon content of the terrestrial environment globally (Sporchia et al. 2024). Nitrogen enrichment also affects carbon cycling processes by altering C-cycle-related genes, particularly enhancing the Calvin cycle carbon fixation process, which results in an increased expression of the *cbbS*, *prkB*, and *cbbL* genes. Recently Wang et al. (2024) have established that nitrogen enrichment resulted in greater soil CO_2 emissions compared to control treatments. This increase was significantly correlated with carbon degradation genes (*bglA*, *per*, and *lpo*), as well as the diversity of microbial strains containing these genes. A recent study reported that the elevation of CO_2 and temperature simultaneously demonstrated increased microbial biomass carbon and nitrogen assimilation. This study also described that the total expression of the nitrogen assimilation genes *chiA*, *pepA*, *pepN*, along with urea hydrolysis gene *ureC* has enhanced in the rhizosphere under high CO_2 conditions in the soil (Zhang et al. 2024a, b).

Conclusion

Microbe-associated resistance factors in soil, including abiotic stress resistance mechanisms, efflux systems, biodegradation capabilities, microbial diversity, and symbiotic

relationships, are essential for enhancing soil fertility and resilience against environmental stresses. Plant responses to environmental stress assisted with microbe-mediated stress amelioration have been investigated based on robust biochemical, molecular, and physiological attributes. Such investigations have employed multi-omics approaches that have deepened our understanding of the mechanisms underlying microbial interactions, gene signaling, metabolic pathways, metabolite accumulation, and differential gene expression. Soil metagenomics is a powerful tool for unraveling the complex interactions between soil microbes and plants, thereby enhancing our understanding of plant physiological responses to various environmental conditions. The key insights of soil metagenomics may involve microbial functional gene analysis, soil community composition and dynamics, and stress response mechanisms.

In conclusion, it is essential to focus more on comprehensive studies aimed at identifying, characterizing traits, and assessing the compatibility of microbes and their associated factors from various environmental conditions to mitigate the impact of stresses in crop plants. It is essential to explore novel microbial attributes expressed under stressed environmental conditions. Therefore, a holistic approach including metagenomics, proteomics, and metabolomics on specific plant-soil-microbe interactions is warranted for stress tolerance/mitigation in crop plants. Moreover, there is a significant need for greater government financial support for Artificial Intelligence (AI) technologies in developing countries. Policies should encourage Climate-Smart Agriculture (CSA) practices and environmental sustainability to enhance productivity and soil ecosystem health. This can be accomplished through incentive programs that improve decision-making at the farm level, promote the use of advanced technologies, optimize resource utilization, and enhance post-harvest processes. Achieving CSA will necessitate innovative financing that links climate and agricultural funding from both the public and private sectors. It is essential for governments and local organizations to actively involve farmers and stakeholders in constructive discussions when creating and revising policies. Effective CSA policies will contribute to poverty alleviation while fostering sustainable development and economic growth.

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Declarations

Conflict of interest The author declares no conflict of interest.

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