Trends in Plant Science

Special issue: Root biology and soil health for a sustainable future II

Review

Exploitation of rhizosphere microbiome biodiversity in plant breeding

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Climate change-induced stresses are perceived by plants at the root–soil interface, where they are alleviated through interactions between the host plant and the rhizosphere microbiome. The recruitment of specific microbiomes helps mitigate stress, increases resistance to pathogens, and promotes plant growth, development, and reproduction. The structure of the rhizosphere microbiome is shaped by crop domestication and variations in ploidy levels. Here we list key genes that regulate rhizosphere microbiomes and host genetic traits. We also discuss the prospects for rigorous analysis of symbiotic interactions, research needs, and strategies for systematically utilizing microbe–crop interactions to improve crop performance. Finally, we highlight challenges of maintaining live rhizosphere microbiome collections and mining heritable variability to enhance interactions between host plants and their rhizosphere microbiomes.

Rhizosphere microbiomes

The concept of plant **holobiont** (see Glossary) has been around for decades, but has recently gained significance due to the strong interdependence between plants and their microbiomes. This plant–microbiome interaction presents a valuable opportunity for manipulating both plant and microbiome genomes to enhance plant growth, improve plant health, and reduce the environmental impact of crops. Hence, harnessing the potential of the plant-associated microbiome brings us closer to achieving agricultural sustainability. While the phyllosphere (the aboveground plant parts) constitutes the largest microbial habitat on planet Earth, the microbiome it harbors is exposed to severe abiotic and biotic constraints, making it heterogeneous and unstable [1]. By contrast, the **rhizosphere**, a hotspot of microbial activity, offers a relatively stable environment with buffered fluctuations, thereby being the system of choice when attempting microbiome engineering. This zone harbors a rich range of diverse microorganisms, including bacteria, followed by fungi, viruses, and phages [2]. In this review, we have restricted ourselves to the two most dominant groups in the rhizosphere: bacteria and fungi. Extensive research has identified biotic and abiotic factors that shape the rhizospheric microbial communities. The tripartite interaction between the plant, the microbiome, and the environment determines the diversity of the rhizospheric microbiome [3,4]. Factors such as plant species, genotype, and rhizodeposition profile play a crucial role in recruiting specific rhizospheric microorganisms; in addition, the multitude of interactions, including competition and **symbiosis**, among the microbial members impact the successful colonization of this zone [5]. Important drivers of rhizospheric microbial composition and diversity include edaphic factors, such as soil type, pH, and nutrient status, as well as climatic variables, such as temperature, light intensity, and precipitation (moisture content) [6,7]. Additionally, **anthropogenic** activities have resulted in major shifts in the plant microbiome, resulting in altered diversity and resilience [8]. These changes can ultimately result in disease outbreaks and adversely affect the overall functioning of ecosystems [9]. In fact,

Highlights

Characterizing the root microbiome in wild and domesticated plants and identifying beneficial bacteria and fungi that promote growth and confer resistance to diseases, pests, and abiotic stresses offers a promising path for crop improvement.

Key genes regulating the assembly and composition of the rhizosphere microbiome have been identified in plant genomes, influencing root morphology, metabolism, and exudates, nutrient uptake, and immune responses.

Allopolyploidization may have led to more diverse rhizosphere microbiomes and, hence, to a broader adaptation than the diploid progenitors. Synthetic allopolyploids can serve as a novel genetic resource for breeding.

Conservation of wild and domesticated plants and microbial genetic resources is required for the successful development of more resilient cropping systems.

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modern agriculture has been tagged as a prime cause for the deteriorating diversity of soil microbial communities [10,11]. Notably, the relevance of these effectors varies spatiotemporally [12].

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Domestication and ploidy impact the composition and diversity of rhizosphere microbiomes

Domestication and **polyploidization** are two processes that have strongly affected plants, including their genetic diversity and cellular, biochemical, and physiological functions, from the level of the genome to the ecosystem. Changes in ploidy have occurred frequently throughout the millions of years of the evolutionary history of the plant kingdom [13]. By contrast, domestication is thought to have started only about 10 000–12 000 years ago [14]. Humans played a significant role in the domestication process from its initial steps to the present, as they sought to adapt crops to variable environments, and evolving human needs over time [15,16]. Although both diploid and polyploid crops are successful, polyploidy is generally thought to provide significant evolutionary advantages and it is not surprising that polyploidization has also played a significant role in domestication.

In a study of the interaction between an allotetraploid relative of soybean (*Glycine dolichocarpa*) and novel rhizobial symbionts (including NGR234), Powell and Doyle [17] concluded that the allotetraploid had an increased capacity for rhizobial interactions compared with its diploid ancestors, *Glycine tomentella* and *Glycine syndetika*, Furthermore, Powell and Doyle [18] observed that the allotetraploid had reduced stress-correlated transcription and enhanced transcription of hormonal signaling genes, which are important in nodulation. Rhizosphere microbiota of rapeseed (*Brassica napus*, AC genome) had a higher diversity than those of its two diploid progenitors (*Brassica rapa*, A genome; *Brassica oleracea*, C genome). This suggests that synthetic rapeseed allopolyploids could be a potential source of additional genetic diversity for the improvement of domesticated allopolyploids because of additional microbiota [19]. The increased diversity observed in polyploids may explain their broader adaptability compared with their diploid relatives. By contrast, Wipf and Coleman-Derr [20] observed only minor differences in the corresponding microbiomes between wild and domesticated wheat types across three ploidy levels.

Studies on the effect of domestication on the **rhizosphere microbiome** have three specific emphases, which align with well-known domestication triangle concept, which includes plants, biotic and abiotic environments, and human agency [15,21]:

(i) Differences between gene pools (wild ancestors, **landraces**, and modern cultivars): diploid to tetraploid to hexaploid wheat [22–24], barley [25], rice [26], common bean [27], soybean [28,29], and Lima bean [30].
(ii) Contrasting soil environments: sandy versus loamy soil in tetraploid wheat [23], nitrogen fertilization in *Trifolium* spp. [31], native inoculants in cowpea [32,33], and soil nutrient availability in potato [34].
(iii) Varying management by humans: native versus agricultural soil [35] and organic versus conventional cropping [36] in common bean, forest versus agricultural soil in soybean [28], and agricultural (maize) versus prairie (*Andropogon gerardii*), and wild (teosinte) soils in maize [37].

Overall, identifying generalizable evidence that explains changes in the rhizosphere microbiome attributable to domestication is difficult because there is considerable variation in the microbiome's composition. Other factors include the species, genotype within species, developmental stage (vegetative vs. reproductive), plant compartment (e.g., rhizosphere and root), **root exudates**, soil type and microbial population, and crop management. Some form of experimental standardization in the experimental conditions is valuable to make results directly comparable.

Mining heritable variability for rhizosphere microbiome across germplasm and environments

In both agricultural and natural environments, the symbiotic association between organisms of different kingdoms is well known. Almost all animals (including insects) have gut microbiomes that allow the host to metabolize and absorb a wide range of foods. Lichens necessarily involve symbiosis between a specific photosynthetic algae or cyanobacteria producing carbohydrates and a fungus [38]. For other plants, the rhizosphere, with interactions between plants and soil microorganisms influence nutrient uptake, abiotic and biotic stress resistance, and overall plant growth. There is increasing interest in understanding the nature and genetic basis of plant–microbiome associations, particularly the heritable variability within germplasms that can be harnessed to develop crops with optimized microbial communities for enhanced resilience and yield.

The roots of almost all higher plants can have a close, symbiotic, relationship with arbuscular mycorrhizal fungi (AMF). Carbohydrates are supplied to the fungi from photosynthesis, while the fungi enhance the uptake of water and nutrients (in particular phosphates). AMF are obligate symbionts, but most host plants can live without the fungi. Marram grass (*Ammophila* spp.) typically growing on coastal sand dunes, with low nutrients, salt, waterlogging, or desiccation, are a good example where establishment is very poor in sterilized sand but mutualism between the plant and fungi allow establishment and contributes to ecological succession of species in this demanding ecosystem [39]. Rhizobia could be exploited to enhance agricultural production through yield increase in existing fields, although some areas (such as dunes) may be sites of biodiversity, environmental sensitivity, or provide ecosystem services such as flood protection, so may not be appropriate for food production.

In legumes, nodulation of the roots is well known as a major symbiosis, with the plant gaining fixed nitrogen while the fungi gain fixed carbon to grow. As early as 206 BC–8 AD, Fan Shengzhi Shu recognized the value of crop rotation (http://en.chinaculture.org/library/2008-02/08/content_22469.htm) where the inclusion of legumes gave substantial advantages to subsequent non-nitrogen fixing crops. Today, legumes require little nitrogen fertilizer and following crops benefit from the residual nitrogen. Many trials have been carried out involving mixtures of legumes and, particularly, grasses including both cereals and forages, while a number of commercial inoculants of legume nodulation bacteria (rhizobia) have been marketed as cultures or seed treatments. Over decades, successful outcomes have been reported for yield and production cost, but none has been adopted widely.

With the genomics revolution and opportunity to identify the genetic nature and variability of rhizosphere microbiomes, there are huge opportunities to identify plant genetic factors, fungal species and genotypes, and their interactions. **Metagenomics** of soils provides a comprehensive view of microbial diversity, and transcriptomics can show how host genes influence microbial recruitment and function. Can **genome-wide association studies (GWAS)** link genetic loci in crop genotypes and specific microbial traits in the rhizosphere to crop performance?

Field-scale experiments are needed to examine interactions of crop genotype, various soil microbiomes, and environmental variability. By conducting experiments across multiple environments, researchers can identify genotype-by-environment (G×E) interactions, with potential to identify appropriate crop genotype and microbial genotype pairs or groups with enhanced performance. It is clear that plant traits such as **root architecture**, exudation profiles, and immune responses, are genotype-specific characters that influence rhizosphere assemblages through microbial recruitment and community structure. Breeding programs might target specific traits

Glossary

Anthropogenic: environmental change caused or influenced by people, either directly or indirectly.

Chemostatic: microbes maintain a balanced response to the plant's signals, possibly adjusting their growth, nutrient consumption, or metabolic activity according to the signalization received from the plant.

Cry for help theory: plants under stress shift their exudation patterns to release specific chemicals that attract beneficial microbes capable of overcoming stress.

Domestication: a coevolutionary process that arises from a specialized mutualism, in which one species (e.g., humans) controls the fitness of another (e.g., plants) to gain resources and/or services.

Genome-wide association studies (GWAS): a research approach to Identify genomic variants significantly associated with trait expression based on existing, diverse populations with limited linkage disequilibrium compared with bi- or multi-parental populations.

Genomic selection (GS): marker-assisted selection using all SNPs covering the whole genome, facilitating rapid selection of superior genotypes and accelerating the breeding cycle.

Glucosinolates: S- and N-containing compounds derived from glucose and various amino acids possessing a range of bioactivities in *Brassica* plant family.

Heterosis: superior performance of F_1 hybrid over its parental lines.

Holobiont: colonization of the rhizosphere environment of the host plant with bacteria, fungi, and viruses for mutualistic symbiosis.

Immunity: innate or induced capacity of plants to eliminate pathogens.

Inbreeding depression: inferior performance of an offspring as result of continuous breeding between closely related individuals of a species.

Landraces: locally adapted traditional varieties of domesticated plants developed over time through natural selection.

Metagenomics: a suite of genomic technologies and bioinformatics tools to directly access the genetic content of entire communities of organisms.

Operational taxonomic unit (OTU): a group of organisms that are closely related and are grouped together based on the similarity of their DNA sequences.

that favor interactions with beneficial microbiomes. Thus, mining heritable variability for rhizosphere microbiomes across germplasms and environments holds promise for improved agriculture, integrating microbiome research with plant breeding [40].

Key genes regulating rhizosphere microbiomes and host-associated genetic variation

Plant roots interact with various microbes in the rhizosphere [41] and many of these interactions affect plant growth and fitness [42,43]. The outcome of plant root–microbiome interactions is determined by multiple factors, including host genetics, climatic and edaphic factors, and rhizosphere properties [44–47]. In recent years, studies have shown that host genetics, which regulates root architecture, exudates, immune response, and nutrient uptake, influences the composition and structure of the rhizospheric microbiome [48,49]. For example, genes associated with root and root hair development in different plant species potentially shape the composition and activity of the microbial community by changing root exudate profiles. In *Arabidopsis*, *AXR2* and *RHD6* are key genes in root hair formation, increasing root surface area and altering root-mediated exudates that potentially structure the rhizosphere microbial community [50,51]. In addition, genes *RTH6*, *LRT1*, *RUM1*, and *RTCs* related to root development in maize also shift the structural composition of root-associated microbes [49,52].

Genes that regulate the uptake and transport of nutrients, such as ammonium or nitrates, *NRT1.1* [53], and *PHT1* [54], also potentially alter root-associated microbiota by selectively recruiting nitrogen-fixing and phosphorus-solubilizing bacteria. Plant genes such as *FNS* and *C2* that regulate the biosynthesis of secondary metabolites (e.g., flavonoids in maize) [55] and *ABC* transporter genes [56,57], which transport endogenous secondary metabolites, significantly reshape the structure of microbial communities.

The composition of the rhizosphere microbiome is also influenced by plant defense-related genes. Examples are the *flagellin sensing gene2* (*FLS2*) [58,59] and *NLR* [60,61], which act as decoys to recognize microbially derived molecules, substantially altering rhizosphere microbial diversity by modulating the plant immune response, which may affect the availability of nutrients and metabolites. Another example is the protein NPR1 governing defense response genes related to salicylic acid-mediated systemic acquired resistance (SAR) that alters the structure of the rhizospheric microbial community. Moreover, the compositional structure of these microbiomes is influenced by many plant **transcription factors (TFs)**, such as MYB72 [62], WAK2 [63], and WRKY [64], which regulate the host immune system in response to pathogens or abiotic stress.

Host-associated variations of plant genes play an important role in reshaping plant roots and associated microbes. In recent years, an increasing number of GWAS have identified loci and quantitative trait loci (QTL) associated with variation in microbial abundance and diversity in *Arabidopsis* [65], barley [60], foxtail millet [48], and sorghum [66]. For example, barley sibling lines with allelic variations on the QRMC-3HS chromosome recruit different microbial taxa [60]. Variation in the relative abundance of heritable taxa also represents, in part, a dimension of host-associated genetic variation [67].

Integrated breeding approaches involving host (plant) and rhizosphere microbiome genes to enhance food/nutritional security and environmental sustainability in global south

Beneficial plant and microbiome traits lost through domestication and genetic improvement
The genetic bottleneck of crop domestication is widely accepted: individual plants gain mutations for critical domestication characters (e.g., non-dehiscence of harvested seeds; gigantism of

Polyploidization: a condition where an organism has more than two complete sets of chromosomes.
Recombinant inbred line (RILs): a powerful tool for genetic mapping originated from biparental or complex crosses by single seed descent method.
Rhizosphere: the narrow region of soil surrounding plant roots where complex interactions between the plant, soil, and microorganisms occur.
Rhizosphere microbiome: community of microorganisms surrounding plant roots.
Root architecture: spatial configuration of a root system in the soil, including root distribution with depth, root topology, and root morphology.
Root exudate: a complex mixture of organic compounds, including amino acids, organic acids, and simple sugars released by plant roots into the soil.
Symbiosis: a close and prolonged mutualistic association between two or more different biological species.
SynCom: a cutting-edge technology involving co-culturing multiple taxa under well-defined conditions to mimic the structure and function of a microbiome.
Terroir: a set of growing conditions, including cultivation practices and environmental conditions, associated with a certain geographic location and its influence on the product's chemistry.
Transcription factor (TF): a protein that regulates the transcription of genes, or the process of copying DNA into RNA.
Volatile organic compounds (VOCs): small, gaseous molecules produced and released by microorganisms, such as bacteria and fungi, allowing microbes to interact with their environment, including plants.

harvested part or change in harvest index; uniform germination, etc.), which then come together, often via hybridization involving only a small part of the genetic diversity that is represented in the whole species. Genomic analysis of the domesticate will often identify a domestication signature, a 'selective sweep' with reduced genetic variation around the chromosomal loci of the domestication genes [16,68]. This selection, whether ancient or modern, by farmers, breeders, or researchers, almost never considers the soil microbiome and will often be carried out at a single plot or soil type. Later, when a selection is grown in multiple locations [69], it will have various soil microbiomes without the benefit of systematic analysis of the performance with known microbiomes.

Unlocking the crosstalk between plants and microorganisms in the rhizosphere

The plant–microbial interactions in the rhizosphere are primarily driven by molecular signaling allowing the recruitment of specific microbiome [70]. This microbial recruitment is controlled by root exudation, releasing multiple classes of compounds and signaling molecules [71], involving a biochemical crosstalk between plants and microorganisms [72,73]. Roots release sugars and organic compounds that promote microbial enrichment in the rhizosphere [74]. Previous studies have identified distinct root exudates involved in plant–microbe crosstalk, such as flavonoids [75], alanine [76], chitinase [77], citric acid [78], and succinic acid [79]. Another important mechanism is the release of **volatile organic compounds (VOCs)** acting as signals in plant–microbe interactions [80]. Interestingly, plants recruit their rhizosphere microbiome to help them in supporting against biotic and abiotic stressors. When under biotic and abiotic danger, the plants start the recruitment of a specific microbiome to protect them [7]. There is a phenomenon known as the '**cry for help**' **theory** [81] where plants signal a selective recruitment of protective microbes [82]. For example, roots release specific compounds such as coumarins and oxylipins to recruit microbiomes that act against pathogens in the rhizosphere [62,83].

Although the different root exudate mechanisms involving the crosstalk between plants (varieties, landraces, or in the wild) and microorganisms have been studied, there are several gaps, such as the variation and composition across domesticated, and improved genotypes, different stages of plant development, and different plant compartments or organs. These features are important for designing strategies to utilize plant signaling for recruiting specific microbiomes. Additionally, the microbiome recruited by the rhizosphere can be vertically transmitted [84]. Indeed, previous studies have found that vertical transmission from the rhizosphere to seeds and progeny varies from 5% to 70% [85,86]. Therefore, understanding the potential of microbial vertical transmission associated with specific roles of molecular signaling in recruiting beneficial microbial communities in the rhizosphere can be useful for plant breeding [87].

Breeding environments influencing rhizosphere microbiomes

Millions of years of coevolution shaped plant–microbe associations, which could have been lost due to domestication and genetic improvement. Assessment of root-associated microbiomes at the seedling stage in wheat revealed that microbial taxa were highest in landraces adapted in low-input systems, while these were lowest in ancestors evolved in native soils. The microbial communities of modern wheat were different from those of landraces and wild ancestors. Traditional cultivars were enriched with *Acidobacteria* and *Actinobacteria*, while modern wheat with *Candidatus Saccharibacteria*, *Verrucomicrobia*, and *Firmicutes*. *Fusarium*, *Neoascochyta*, and *Microdochium*, among fungi, were enriched in modern cultivars, thereby suggesting that genetic improvement has significantly impacted root microbiota, both bacteria and fungi [88].

Organic and inorganic production systems also influence rhizosphere microbiome composition and diversity, which in turn affects plant response to growth and reproduction, stresses, and

nutritional quality of edible products. A comparative assessment of snap bean (*Phaseolus vulgaris*) **recombinant inbred lines (RILs)** evaluated under an organic production system showed that breeding environment (organic vs. conventional production system) of crops significantly altered the microbiome community composition, while the fungal communities varied between breeding histories and parentage [36].

Soil microbiomes influencing flavor chemistry of fruits and seeds

Cultivation practices and environmental conditions within a geographic location, often termed as **terroir**, may affect the chemistry of plants' edible produce, necessitating the need to optimize farm conditions to harvest maximum quality. Analysis of ripe tomato fruits harvested from plants grown in soil and hydroponic environments revealed that fruits harvested from soil had significantly higher sugar content. Hydroponically harvested fruits were superior in organic acids. The cultivation practices significantly shaped the bacterial community composition, with bacterial communities in hydroponic tomatoes more variable than soil-grown tomatoes. The bacterial species in soil-grown tomatoes correlated with higher concentrations of 'green' or 'pungent' volatiles. The greatest sweetness of 'Solarino' tomatoes correlated with aroma-related volatiles, fructose, and glucose, indicating that microbiota-related accumulation of flavor and aroma compounds are strongly dependent on the cultivation substrate and approach [89].

The differences in rhizosphere microbiomes may impact seed **glucosinolates** in *Brassica* species. A greenhouse study involving mustard plants (*Brassica juncea*) and distinct soil microbial communities established the links between the rhizosphere microbial community composition and the concentration of the main glucosinolate, allyl, in seeds. Specific rhizosphere taxa predictive of seed allyl concentration were detected. The bacterial functional genes associated with sulfur metabolism partly explained the observed associations between specific rhizosphere and seed allyl concentrations [90].

A consortium of microbes (Box 1) isolated from tea roots enhanced ammonia uptake to facilitate the synthesis of theanine, a key determinant of tea taste. A comparative assessment of root microbiomes involving high- and low-theanine tea accessions unfolded a specific group of microbes that modulated N_2-metabolism to influence theanine levels in tea. The application of synthetic communities (**SynComs)** mirroring the microbe population composition found in high theanine roots resulted in a significant increase in the theanine content of tea plants [91].

Root microbiome-based inbreeding depression and heterosis, genomic selection, and tradeoffs

The host plant significantly influences its associated microbial community composition [60], which has been molded by both plant domestication and crop diversification. Similarly, soil microbiomes play a crucial role in shaping the characteristics of their host plants. **Inbreeding depression** can diminish individual fitness and understanding its impact on population growth and viability can be facilitated through the availability of genomic data [92]. Incorporating this information into a theory-based hierarchical framework could potentially predict emergent behaviors that stem from interactions between individual traits [93]. In this context, Yang *et al*. [94] employed a microbiome-informed **genomic selection (GS)** strategy for selecting nitrogen (N)-related traits in maize. Their findings indicate that this method outperforms traditional GEBV modeling that relies solely on crop data for assessing plant growth and N response traits, especially under low N. This suggests that beneficial microbes may enhance N nutrient uptake under stress.

Liu *et al*. [95] recently highlighted the phenomenon of microbiome-induced **heterosis** by observing distinct and varied seed microbiomes in rice hybrids, which led to superior seed germination compared with their parents. Wagner *et al*. [96] showed that heterosis for root biomass (among

Box 1. Conservation and cataloguing strategies for maintaining a live collection of beneficial rhizosphere microbiomes and the challenges involved

In addition to their crucial role in improving plant growth and overall health [115,116], these rhizospheric microbes also harbor novel metabolites and genes that have potential applications in the biotech industry and the environment [117,118]. However, the degradation of the agroecosystem due to various factors has led to a loss of microbial diversity in the rhizosphere and limited their utilization in agriculture and industry to meet human needs [119]. Hence, conservation and cataloguing of these microbes with their functional traits plays a crucial role in sustainable agriculture, promoting research and fostering innovation in the biotech industry [120,121].

Microbial culture collections and repositories were begun in Prague at the end of the 19th century [122] and, a few years later, the concept of culture collection was extended to other European countries. Currently, 789 culture collections from 77 countries are registered with the World Federation of Culture Collections (WFCC, https://www.wfcc.info/) to protect the microbial diversity with an important role in agriculture, public health, and food supply [123,124]. In addition, there are international centers, including ICARDA (https://genebanks.cgiar.org/genebanks/icarda/) and ICRISAT (https://oar.icrisat.org/987/), which deal with the culture collection and conservation of rhizobium strains isolated mainly from legume. Over the years, various *ex situ* preservation methods, including repeated sub-cultivation, agar beads [125], storage in sterile soil, spray-drying, storage in silica gel, cryopreservation, and lyophilization [126] have been developed to preserve microbial collections. However, each strategy has its own advantages and challenges, as the response to preservations varies between and within species [127]. *In situ* preservation is used to preserve entire microbial communities together with their habitat. Although this strategy effectively preserves the integrity of the microbial ecosystem, its applications are limited by capacity constraints [119,128].

Advanced genomic, metagenomics, and bioinformatic techniques are essential for the characterization and cataloguing of microbial strains for future use. However, the high costs associated with these techniques and the lack of a standardized cataloguing protocol hinder microbial cataloguing efforts and make it difficult to document microbial diversity across different repositories [129–131]. In addition, biosafety concerns and the ethical dilemma associated with patenting microbial resources limit the efficiency of microbial cataloguing activities [132,133]. Therefore, improved culture collections and cataloguing strategies are critical to fully exploit the potential applications of these rhizospheric microbiomes in sustainable agriculture.

other traits) in maize is contingent upon the surrounding underground microbial environment. Despite ongoing inquiries into the mechanisms behind this heterosis within the endophytic microbiome and the reasons for the hybrid microbiota's advantageous traits, evidence suggests that hybridization itself affects both the rhizosphere and seed endophytic microbiome compositions. Furthermore, the resulting microbiome following hybridization appears to be transmissible from the initial stage to subsequent generations [97].

Immunity may have an adverse impact on plant growth and development as well on rhizosphere microbiomes. Autoimmunity in *Arabidopsis phytosulfokine receptor1* (*pskr1*) mutant displays stunted plant growth, reduced defense-related gene expression, and reduced rhizosphere bacterial growth in response to growth-promoting *Pseudomonas fluorescens* [98]. *PSKR1* regulates the growth-defense tradeoff during *Pseudomonas* colonization by upregulating plant photosynthesis and root growth, but suppressing salicylic-acid-mediated defenses. *pskr1* stunting and restoration of bacterial growth are salicylic acid dependent. Thus, *Pseudomonas* induces *PSKR1* expression in roots mediating tradeoff by manipulating plant signaling to promote *Pseudomonas* colonization.

Resistance breeding to soil-borne diseases impacts rhizosphere microbiome community

Soil-borne diseases caused by various pathogens, mainly fungi, viruses, and nematodes, pose a significant challenge to agriculture. These pathogens use plants as hosts for their development and the soil as a suitable environment for both their spread and long-term survival [99]. To protect plants against these pathogens, breeders employ strategies to confer resistance in plants. These strategies generally involve crossing susceptible and resistant genotypes to obtain resistant sources [100] and identifying key genes involved in resistance mechanisms [101]. Both strategies lead to changes in the genetic makeup of plants, which can have consequences for the

rhizosphere microbiome. Additionally, plant breeders often overlook the importance of root traits and the rhizosphere microbiome in breeding programs. However, some studies have observed modifications in root traits during plant breeding [102,103], particularly in relation to the quality and quantity of exudates, which affect the recruitment of microbial taxa in the rhizosphere [36,104]. This is important because previous studies have shown the crucial role of the rhizosphere microbiome as the first line of defense for plants against pathogen invasion [105–107]. For instance, Mendes *et al*. [105] assessed the effect of breeding common bean for resistance against *Fusarium oxysporum*. They observed that resistance breeding altered the rhizosphere microbiome and recruited specific beneficial bacterial genera that exhibit antifungal traits against *F. oxysporum*. Later, Lazcano *et al*. [107] observed differences in the rhizosphere microbiome when comparing strawberry genotypes susceptible and resistant to *Verticillium dahliae* and *Macrophomina phaseolina*. The authors found higher abundances of known biocontrol microorganisms, such as *Burkholderia* and *Pseudomonas*, in the rhizosphere of the resistant genotype. Thus, available studies report significant changes in root traits during plant breeding for resistance, which stimulate plants to recruit specific microbial groups within the rhizosphere. These beneficial and specific microbes play crucial roles in helping plants defend against pathogens.

Developing a genotype–phenotype map involving host and symbiotic extended phenotype

The intricate relationships between plant hosts and their associated microbes are well-documented, yet the mechanisms through which plants influence these relationships remain largely unknown [108]. Plant genotypes significantly impact the structure of soil microbial communities, consequently affecting soil carbon stock compositions [109]. Hence, the soil microbiome, encompassing the collective genomes of all microorganisms present, can be considered the 'extended phenotype' of a specific plant host, potentially varying under selective pressures. This concept, termed the 'extended phenotype', was introduced by evolutionary biologist Dawkins [110] to describe all environmental impacts exerted by a gene, both within and beyond the organism's body. Changes in chromosomal regions (including structural variations) during cultivar development could influence this extended microbiome phenotype.

A GWAS utilizing metagenomic data to define and quantify **operational taxonomic units (OTUs)** offers a robust, unbiased method for identifying microbes sensitive to host genotype and linking them to genetic loci influencing their colonization [111]. For instance, research by Bergelson *et al*. [112] identified potential genes involved in plant immunity that affect microbiome traits in *Arabidopsis*. They also suggested that root microbiomes might rely on genes governing root and root hair development. Similarly, GWAS has been instrumental in uncovering plant loci responsible for the heritability of the leaf microbiome in maize [113] and rice [114], as well as the rhizosphere microbiome in sorghum [66]. Further bioinformatic analysis of metagenomic data aids in comprehending the variations in OTU richness associated with each genotype.

Concluding remarks

Recent studies in plant breeding have shown that both plant genotype and the associated microbiome are important to obtain superior crop cultivars. Indeed, an understanding of the concept of plant holobiont, which includes rhizosphere microbiomes, confirms that microbes contribute to plant growth and development, improve plant health, reduce environmental impacts, and enhance nutritional quality of food crops. Rhizosphere microbiomes provide stable environments with buffered fluctuations (i.e., functional traits involved in abiotic stress adaptation), and microbiome-induced variations are heritable across germplasms and environments. Hence, it is essential to exploit both host (plant) and microbiome genetics to achieve resource-use efficient, and productive and nutritious crops, through plant breeding (Figure 1).

Outstanding questions

What approach should one follow to integrate knowledge gained from host (plant) and rhizosphere microbiome genetics to harness mutualistic symbioses in plant breeding?

Can genomics be applied, potentially with GWAS-type analysis of crop and rhizosphere, to identify favorable crop–microbiome interactions?

What crop- and environment-specific synthetic communities (SynComs) are ideal to identify and harness mutualistic symbiosis to make food crops resilient to stress, maintain/increase productivity, and improve nutritional quality?

What are the optimum conditions to maintain live collections of rhizosphere microbiomes in genebanks and could long-term conservation bring changes in their genetic makeup?

What genomic studies of biodiversity in the rhizosphere of diverse crops, and natural species or communities from various environments, are required?

Is there sufficient knowledge to quantify the effects of soil, environment, and crop management practices on the rhizosphere microbiome to develop an accurate and predictable model to regulate the rhizosphere microbiome mechanisms, enhancing agricultural production in harsh environments?

What host (plant) traits favor mutualistic interaction with beneficial rhizosphere microbiomes?

What is the potential of microbiome vertical transmission in recruiting beneficial microbial communities in the rhizosphere?

What procedural assay (throughput screen for large-scale evaluation of breeding populations) and statistical protocol follow to initiate rhizosphere microbiome-assisted plant breeding, considering genotype × environment interactions?

Are genomic selection and gene editing options to retrieve missing functional rhizosphere microbiomes in crop domesticates, or should these be integrated into new crops as a part of *de novo* domestication?

Future studies should focus on mapping rhizospheres from contrasting terroirs to identify characteristic microbial signatures for developing biomarkers that uniquely define and characterize crop production habitats. Additionally, it is important to develop and catalogue rhizosphere microbiota-derived consortia for *in situ* conservation tailored to specific crops and environments. A quantitative assessment should be conducted to identify microorganisms from contrasting genotypes and environments to develop crop- and environment-specific SynComs. A two-pronged strategy should be adopted for the precise management and exploitation of environment- and plant genetic-dominated rhizosphere microbiomes. We should also adapt a paradigm shift for more holistic microbiome research to harness heritable variations associated with host (plant) and rhizosphere microbiome genetics. We should develop a network of microbe conservation genebank for futuristic plant breeding strategies. It will also be important to promote collaboration among molecular biologists/plant breeders, industry researchers, farmers, and traders involved in the conservation, development, and marketing of rhizosphere microbiome-based products. Strengthening government policy support for researchers will help unlock plant–microbe

Where new approaches to exploit enhanced rhizospheres (composition and management) are effective, how will these be adopted by both small-holder and commercial farmers?

What agronomic approaches (e.g., inoculations) can further complement and enhance plant–rhizosphere interactions?
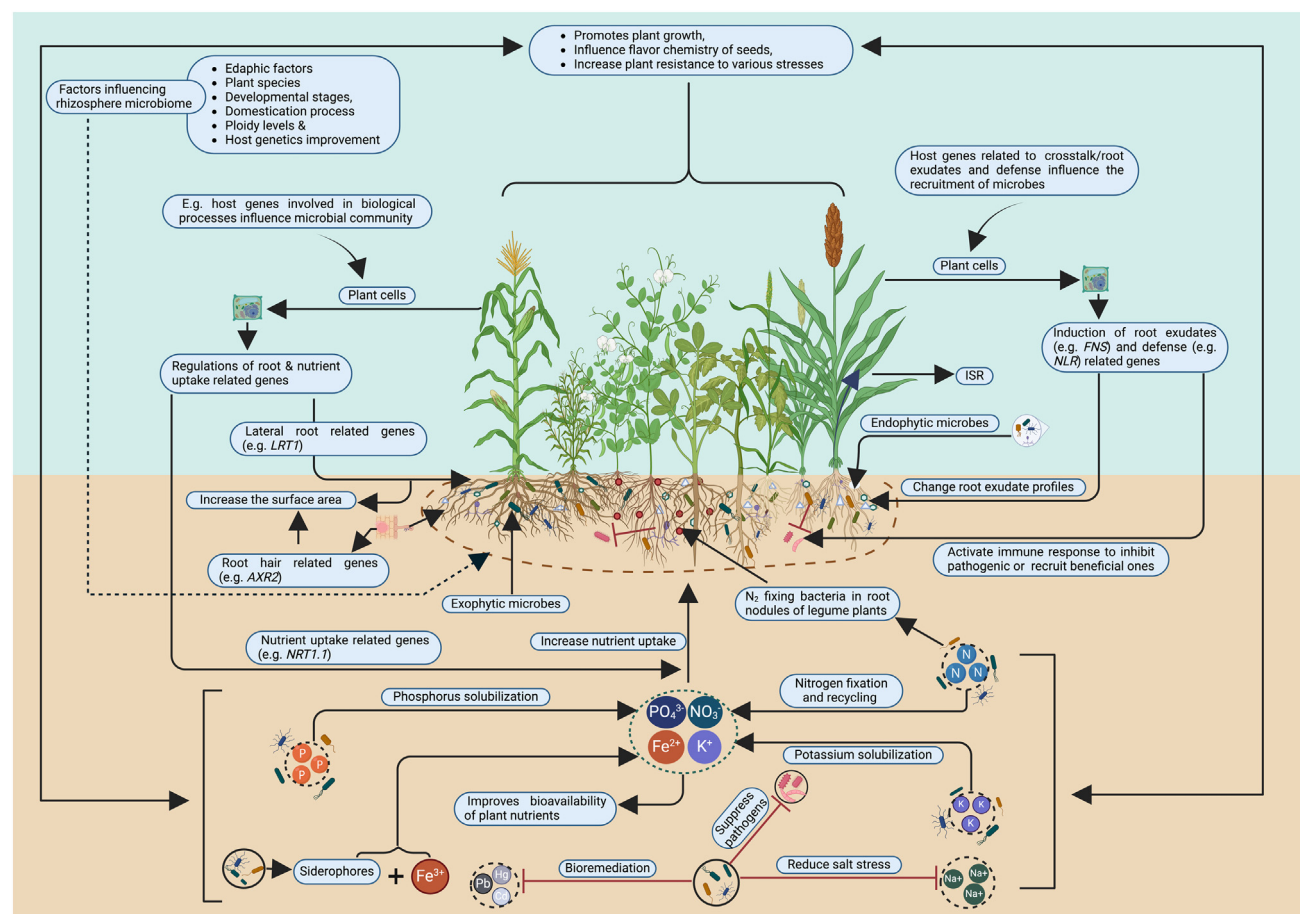
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Figure 1. Schematic representation of the rhizosphere microbiome's role in promoting plant growth and enhancing tolerance to various stress factors. Factors such as host genetics, edaphic conditions, plant developmental stages, and domestication processes influence the composition and diversity of these microorganisms in the rhizosphere. Microbial contributions to plants, including nutrient acquisition (e.g., nitrogen fixation and phosphorus solubilization) and induction of systemic resistance are indicated by black arrows (↑). By contrast, pathogen inhibition, salt reduction (Na+), and bioremediation of heavy metals (e.g., Cd and Pb) are shown with red blunt lines (⊣). This figure highlights the interplay between plant genetics and rhizosphere microbial communities (which may be **chemostatic**, top right) in influencing nutrient cycling, stress resilience, and pathogen suppression. Abbreviation: ISR, induced systemic resistance. Figure created using Biorender.com.

interactions and encourage farmers to adopt eco-friendly agricultural practices to restore soil and plant health, plant nutrition, and ecosystem health. Finally, improving rhizosphere-crop associations with research-based approaches will play an important role in both mitigation (increasing the sustainability of farming and reduction of greenhouse gas emissions) and adaptation (to altered conditions) of agriculture under a changing climate (see Outstanding questions).

Author contributions

S.L.D.: conceptualization, investigation, writing – original draft, and writing – review and editing + editing graphical abstract; R.R.V. and B.G.K.: investigation, writing – original draft, and writing – review and editing + drawing a graphical abstract; P.G.: investigation, writing – original draft, and writing – review and editing + editing graphical abstract; P.H-H.: investigation, writing – original draft, and writing – review and editing; A.S.F.A.: investigation, writing – original draft, and writing – review and editing + editing graphical abstract; S.S.: investigation, writing – original draft, and writing – review and editing + editing graphical abstract; R.O.: conceptualization, project administration, investigation, writing – original draft, and writing – review and editing. All authors contributed to the article and approved the manuscript for submission.

Declaration of interests

No interests are declared.

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