Rhizosphere Associated Bacteria

The abundance of nutrient accumulation in rhizosphere soils has placed the rhizosphere as an "epicenter" of bacterial concentrations. Nonetheless, over the years, little attention has been given to bacterial inoculants and soil-like substrates. The reason is that many farmers and experiments have focused on chemical fertilizers as an approach to improve plant growth and yield. Therefore, we focused on assessing the application of rhizosphere soil and its associated bacteria for biotechnological applications.

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1. The Rhizosphere Soil as a Treasure Trove for Bacterial Community Concentration

The rhizosphere is known as the region of the soil that surrounds the root where biological, physical and chemical properties of the soil are modulated by plant processes. The rhizosphere is a hotspot of plant-bacteria interplay within the soil environments [1]. It is colonized by diverse bacterial communities, which are functionally and structurally controlled by soil type and texture, environmental factors and plants [2]. Studies have revealed that the plant root exudates and other rhizodeposits lure beneficial bacteria to the rhizosphere, although uninvited ones are also enticed [3]. The host plant induces selection pressure on the development of the rhizosphere microbiome, which favors and attracts a specific plant microbiota due to variations in the composition of the root exudate [4].

Odelade and Babalola [5] stated that there is a higher bacterial biomass in the rhizosphere soil compared to the bulk (rootless) soil, which is as a result of increased availability of substrates for bacterial growth through root exudates, resulting in greater population density and community structure in the root region that may be different from those in the bulk soil. This was supported by a study by De Luna, et al. [6], who stated that the bacterial cell population in 1g of rhizosphere soils is typically 10^8–10^{12}, and they surpassed that of the bulk soil, which is due to various root exudates and rhizodepositions in the root region. This high bacterial density in the rhizosphere soils has been ascribed to the high level of available substrate and humidity [7].

Reports have suggested that root exudates and various rhizodeposits perform key roles in the richness and diversity of bacterial communities in the rhizosphere. Root exudates have the most diversified nutritional composition compared to other rhizodeposits. They are also versatile in composition and influenced by the plant host and environmental factors [8]. The root exudates attract beneficial bacterial species to the rhizosphere of plants, while some unwanted bacterial species are also lured [9]. The constituents of root exudates vary between plant species and cultivars, which leads to variation in the rhizosphere bacterial community. These variations can be manipulated to create specific selective effects on the rhizosphere microbiome [10].

Dennis et al. [11] stated that root exudates carry out a limited role in controlling the bacterial communities in the rhizosphere compared to the other rhizodeposits (volatile compounds, mucilages, slough-off root cells, and lysates) due to large variations in exudate composition and dynamics shown by various studies. Collective evidence indicates that bacterial communities are oftentimes distinct from similar plant cultivars and from bulk soil, but not always. The authors classified these plants as having a delicate rhizospheric effect [12][13]. The mechanisms by which hosts winnow the ambient community to form their microbial communities are not fully understood, although plant functional traits, such as the cuticle composition, may be responsible [1]. However, shaping and establishment of the rhizosphere microbiome is a selective and dynamic process that involves several mechanisms such as signal recognition, chemotaxis, biofilm formation and antibiosis [8].

Root exudation includes the secretion of enzymes, oxygen and water, ion, mucilage and diverse carbon-containing metabolites. The plant root system produces various metabolites, while the root tips secrete most of the root exudates, which are low molecular weight organic substances (such as amino acids, amides, organic acids, sugars, enzymes,

phenolic acids and coumarin), high-molecular-weight compounds (such as proteins and mucilages) and other substances, including sterols that attract bacteria to the rhizosphere [14][15]. However, the components of the exudates vary in the amount released, molecular weight, and biochemical functions. These exudates act as attraction signals that influence the ability of bacteria to colonize the roots. To proliferate and be established in the rhizosphere, the organisms must be able to use root exudates, colonize the root or rhizosphere effectively and be able to compete with other organisms [11]. Rhizobacteria locate plant roots through cues exuded from the roots and root exudates, which stimulate Plant Growth-Promoting Rhizobacteria PGPR chemotaxis on root surfaces. Root exudates can also stimulate flagella motility in some rhizobacteria [16]. These traits are essential for the colonization of the rhizosphere.

The impact of plant roots was examined on rhizosphere and bacterial communities, and it was deduced that root length, biomass, density, volume, and surface area create distinct ecological niches for some bacterial species to improve advantageous interactions in the rhizosphere [17]. It has been established that since the root tips make the initial connection with the bulk soil, the bacterial communities and rhizodeposits are notable in maintaining the rhizosphere [18][19].

Despite variations in the dynamics and composition of root exudates, a subset of the bacterial population is designated as the core rhizosphere microbiome, which are ubiquitous across plant species and environment [4]. The microbiota uses the root exudates as a source of energy, and the common genera in the rhizosphere include *Burkholderia, Bacillus, Microbacterium, Azospirillum, Serratia, Pseudomonas, Erwinia*, *Aeromonas, Mesorhizobium, Rahnella, Acinetobacter, Enterobacter* and *Acinetobacter* [20][21]. Conventionally, bacterial species in the rhizosphere were isolated and identified using the traditional or culture-based method for isolating and classifying microorganisms. This method's main inadequacy is that it cannot identify the entire microorganism in a sample, making approximately 99% of the microorganism unknown [22]. Thus, only a few bacterial populations has been identified from the rhizosphere soils using conventional techniques, but not until the advent of next-generation sequencing techniques [23]. High-throughput sequencing has made the identification of most rhizobacteria possible and also lends credence to their functional role in the rhizosphere (Table 1).

Table 1. Bacteria present in rhizosphere soil and the techniques used in identifying them.

Technique Used	Bacteria Reported	Plant	Reference
Denaturing Gradient Gel Electrophoresis (DGGE)	*Sphingobacteriales, Flavobacteriaceae, Xanthomonadaceae, Cyanobacteria*	Lettuce, soybean, potato, maize	[24][25]
Quantitative PCR (qPCR) analysis	*Bacillus velezensis NJAU-Z9*	Pepper	[26]
G3 PhyloChip microarray analyses	*Atribacteria, Dependentiae, TM6, Latescibacteria WS3 Marinimicrobia, SAR406; Omnitrophica, OP3; BRC1. Acidobacteria, Gemmatimonadetes*, and *Tenericutes*	Wheat, barley	[20]
Restriction Fragment Length Polymorphism (RFLP)	*Azospirillum, Pseudomonas chlororaphis, P. frederiksbergensis, Bacillus aryabhattai*, and *Paenibacillus peoriae*	Maize	[15]
DNA-Stable Isotope Probing (DNA-SIP)	*Nostocales, Stigonematales, Streptomyces Bacillus, Alicyclobacillus, Clostridium. Rhizobiales, Rhodospirillale, Myxococcales*, and *Actinomycetales*	Rice	[7][27]
16S amplicon sequencing	*Proteobacteria, Actinobacteria, Bacteroidetes, Acidobacteria, Firmicutes, Verrucomicrobia, Planctomycetes, Actinobacteria, Cyanobacteria*, and *Gemmatimonadetes*	Wheat, maize, potato, soybean	[28][29]
Shotgun sequencing	*Stenotrophomonas, Rahnella, Sphingomonas, Janthinobacterium Luteibacter, Arthrobacter, Streptomyces, Bradyrhizobium, Methylobacterium, Ramlibacter, Nitrospira, Nocardioides, Geodermatophilus*, and *Burkholderia*	Soybean, sunflower, sugar beet	[14]
Culture-based	*Bacillus, Pseudomonas, Ochrobactrium, Providencia, Achromobacter, Burkholderia, and Enterobacter*	Wheat	[30]

Bacterial communities from the rhizosphere have been implicated in synthesizing extracellular hydrolytic enzymes responsible for biodegradation into the soil. Therefore, they are viewed as the leading force manipulating the terrestrial ecosystems. The abundance of nutrients in the rhizosphere not only contributes to plant growth and development but also maintains the beneficial soil bacterial community inhabiting the rhizosphere soil [1]. Some studies conducted on rhizosphere soils have reported the presence of beneficial bacterial communities essential for biotechnological applications (Table 1). Methanotrophic bacteria capable of producing methane from NH^{4+} were identified from rice paddy rhizosphere soil [31].

2. Biofertilization: The Use of Rhizosphere Bacteria as a Soil Amendment for Plant Growth Promotion

Plant growth-promoting bacteria, such as *Azospirillum*, *Rhizobium*, and *Azotobacter* enhance the growth of different plants and, thus, are used for biofertilization of many crop plants [32]. The effects of plant growth stimulation have been attributed to atmospheric nitrogen fixation, potassium and phosphate solubilization, production of plant growth hormones (auxins, gibberellins, ethylene, and cytokinins), polyamines and diverse amino acids produced by PGPR, which improve the nutritional availability of plants directly [8]. There are several factors to be considered in the formulation of biofertilizer. These factors include the choice of appropriate microorganisms with the potential to colonize plant rhizosphere, the growth profile of the bacteria, appropriate carrier and types and optimum conditions of organisms. The success of the products also depends on the method of application and storage of the formulation [33].

Any material added to a soil to improve the physical and chemical properties of the soil, such as structure, water infiltration, water permeability, aeration, and drainage, which, as a result, provides a more suitable environment for plant roots and health, is referred to as soil amendment [21]. Owning to the distinct physical and chemical properties of rhizosphere soils due to microbial activities, they are the epicenter for nutrient accumulation. However, reports on soil and soil-like substrate amendments are limited. Currently, other methods widely employed as soil amendment include the excessive application of growth enhancers, chemical fertilizers, pesticides, and soil sterilization approaches, such as fumigation with methyl bromide (MeBr). Although these treatment methods can be efficient for controlling environmental stresses, they have harmful impacts on human health and the environment and long-term adverse effects on soil health and quality [34].

Promising alternatives such as using materials like bacterial soil amenders (PGPR) integrated with soil for enhancing the physical and chemical qualities of the amended soil, consequently improve plant health, performance, and growth. Plant growth-promoting rhizobacteria can improve crop growth through various mechanisms (direct or indirect), including improving water acquisition, increasing soil nutrient bioavailability, suppressing plant diseases, and decreasing herbivore damage [35]. Cui, et al. [36] inoculated maize with *Bacillus amyloliquefaciens* B9601-Y2, which consequently controlled the impacts of *Biopolaris maydis* (southern corn leaf blight) by colonizing the main roots and root hairs and later migrating to the stems and leaves. Likewise, *Bacillus amyloliquefaciens* B9601-Y2 notably improved maize-seedling growth (height, number of leaves), and chlorophyll content.

The physical and chemical parameters of rhizosphere and bulk soils are relatively variable [37]. This is due to different bacterial interactions and high nutrient concentrations. Several studies have revealed that the rhizosphere soils have significant levels of organic carbon, nitrogen, ammonium nitrate, clay content, and soil mineral nutrients such as phosphorus, iron, zinc, magnesium, copper, manganese, sodium, calcium, and potassium compared to bulk soils due to symbiotic nitrogen fixation, root exudation of organic acids, cluster root formation, plant secretion of phosphatases, and rhizosphere pH modification [37][38]. An experiment conducted by Maseko et al. [39] showed that the rhizosphere soils had approximately two-to-three times the phosphorus, copper, sodium, and potassium compared to the bulk soils. The clay content in rhizosphere soils increases their waterlogging and soil porosity. The high concentrations of these minerals naturally increase bacterial and phosphatase activities, which could be due to root exudation and, as a result, improve plant growth and yields [38]. Considering the exclusivity of the bacterial population in the rhizosphere soils, many authors have suggested their use as soil amendments in low-input farming systems [40] (Table 4).

Table 4. The rhizosphere soil and rhizobacteria as a soil amendment.

Plant	Impact of Rhizobacteria on the Plant	Reference
Capsicum annuum L.	The soil amended with *Bacillus velezensis* improves seedling height, stem diameter, and yields compared to those pepper plants grown on un-amended soil	[26]

Plant	Impact of Rhizobacteria on the Plant	Reference
Arabidopsis thaliana	Combined mixture of rhizosphere soil or soil-like substrates and *Bacillus* mixtures resulted in a significant increase in plant root fresh weight, shoot fresh weight, nutrient uptake, chlorophyll content, and plant diameter. In addition, the transcript levels of ammonium and nitrate uptake genes in the plant were increased	[41]
Helianthus annuus	*Pseudomonas fluorescens* A506, *P. gessardii* strain BLP141, and *P. fluorescens* strain LMG 2189 improved plant growth, yield, physiology, proline, antioxidant activities, and reduced the malondialdehyde content in inoculated soil	[42]
Ocimum basilicum L.	Rhizobacteria consortium (*Bacillus lentus*, *Pseudomonas* sp. and *Azospirillum brasilens*) had positive effects on the antioxidant activity and chlorophyll pigment content under water-induced and salinity stress	[43]
Festuca rubra	Bacterial consortium immobilized in a mixture of perlite and sawdust (ratio 1:1:1 v/v) led to a substantial improvement of plant roots, stem length, and stem biomass, as well as influencing the elongation of the plants in all soil treated. Soil additives (phosphate fertilizer and sewage sludge) and an immobilized consortium of microorganism had a positive effect on plant growth (longer root, stem length, and stem biomass) compared to the control	[44]
Eucalyptus globulus	Co-application of biochar (20 t hm^{-2}) and PGPB (5 × 10^{10} CFU mL^{-1}) amendments significantly decreased the concentrations of soil total P and NH_4^+-N, whereas they advanced total K, NO_3-N, and soil water content, and hence maintained soil sustainability in eucalyptus plantation	[45]
Curcuma longa	The *Curcuma longa* soil amended with *B. subtilis* MML2490 and *P. aeruginosa* MML2424 enhanced plant growth promotion and management of turmeric rhizome rot disease, and thus appeared promising for commercialization	[46]

A major challenge with applying and using biofertilizers on the field is their inconsistency and unreliability, which calls for innovative solutions. This could be as a result of the diverse growth habitat and community structure of plant roots. This can create a stressful environment for the proliferation of the product [47]. Another limiting factor for their use is their selectivity, resulting in variable quality and efficiency on the field. Innovative solutions that direct the product to the desired location and target crop and an understanding of the root microbiome dynamics and flux in plant metabolic networks can increase the chances of product effectiveness and reproducibility [48].

3. The Role of Rhizosphere Soil and Its Bacteria for Bioremediation and Biofiltration

Recently, researchers have given in-depth attention to bioremediation, which is a process that mainly stimulates and uses microorganisms such as bacteria, plant enzymes, or plants to degrade and treat target pollutants in soil and other environments by manipulating the environmental conditions [42]. Phytoremediation, a combination strategy used by plants and microorganisms to remove pollutants from the environment, has proven to be effective in decontaminating soil polluted with heavy metals and hydrocarbons. Some bacterial species have synergistic interactions (direct or indirect) with environmental factors capable of removing hydrocarbon and heavy metal pollutants from soils, which consequently successfully increases the movement of these pollutants to the above-ground plants' biomass. Rhizoremediation, a phytoremediation approach, is plant–microbe cooperation with the potential to remove soil pollutants through the action of microorganisms and plant enzymes in the rhizosphere [49].

Many PGPR strains capable of removing pollutants from environmental media are found in the rhizosphere soils [50]. dos Santos and Maranho [23] reported the efficiency of *Bacillus*, *Alcaligenes*, *Microbacterium*, and *Curtobacterium* isolated from rhizosphere soil in heavy metal transformation. *Pseudomonas fluorescens* isolated from rhizosphere soil was inoculated into maize soil polluted with cadmium in research conducted by Asilian, et al. [51]. Their discovery revealed that maize soil amended with 2 mmol kg^{-1} Tween 80 had a better Cd uptake than the control (soil uninoculated). Moreover, they reported that soil samples inoculated with 4 mmol kg^{-1} Tween 80 increased translocation efficiencies and phytoextraction (a subprocess of phytoremediation in which plants remove heavy metals from soil or water even at relatively low concentrations) than soil uninoculated with *P. fluorescens.* Therefore, they proposed that phytoextraction of heavy metals can be achieved by *P. fluorescens.* The properties and mineral compositions of rhizosphere soil place them as an excellent accumulator (adsorbent) of heavy metals and a promising technique for soil remediation capable of purifying soil from contaminants [35].

This is evident in research where Mourato, et al. [52] used lead (Pb) metal phytoextraction to reveal that *Brassica nigra* and *Brassica juncea* rhizosphere soils have higher heavy metal-bioaccumulating ability than those that are uninoculated. Other salient findings showed that cultivar of *B. juncea* rhizosphere soil was the most adsorbent of Pb (up to 3.5% on a dry weight basis) compared to the uninoculated soil [53]. Hence, the tight binding of Pb to plant and soil

materials explains the low movements in soil and plants. In another experiment, the researchers reported using grass species (*Cenchrus ciliaris*) irhizosphere soil as a tool for removing Pb and Cu from aqueous solutions [54]. The result from this investigation revealed that the rhizosphere soil absorbed Pb up to 97.31 ppm and 188.3 ppm Cu. They concluded that the rhizosphere remediation using *C. ciliaris* rhizosphere is a compelling and effective green innovation for remediation of heavy metals from soil. Xu, et al. [55] used cadmium (Cd^{2+}) resistant *Pseudomonas* sp. strain 375 from heavy metal polluted rhizosphere soil as an adsorbent to remediate water body polluted with Cd^{2+}. *Pseudomonas* sp. was used as an inexpensive and potential bioadsorbent for bioremediation of Cd^{2+} from wastewater. Other rhizobacteria and pollutants they removed are listed in Table 5.

Table 5. Rhizobacteria and pollutants removed from the environment.

Rhizobacteria	Isolation Source	Pollutant	Reference
Bacillus thurigiensis, B. pumilus and *Rhodococcus hoagii*	*Panicum aquaticum*	Petroluem	[56]
Lysinbacilus fusiformis L8, *Bacillus weihenstephanensis* UT11, *Paenibacillus* sp. M10-6,	*Hosta undulata*	Alkylphenol	[57]
Ensifer, Novosphingobium, Norcardioides, Streptomyces, Rhizobium	*Coronilla varia, Vigna unguiculata*	Phenantrene	[58]
Mycobacterium gilvum	*Phragmites australis*	Pyrene, benzo[a]pyrene	[59]
Bacillus subtilis, Bacillus amyloliquefaciens	*Lactuca sativa* L.	Cadmium	[60]
Microbacterium hydrocarbonoxydans, Achromobacter xylosoxidans, Bacillus subtili, B. megaterium, Alcaligens faecalis, Pseudomonas migulae	*Phragmites australis*	Colored distillery effluent	[61]
Alcaligenes, Bacillus, Curtobacterium, Microbacterium	*Prosopis laevigata, Spharealce aangustifolia*	As(V), Pb(II), Cu(II), Zn(II)	[62]
Bacillussp. CIK-512	*Zea mays*	Pb	[63]

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