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Review

Role of rhizospheric microbial enzymes in plant growth promotion, antagonism, and sustainable agriculture: A review

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Abstract: Plant growth-promoting rhizobacteria (PGPR) offer eco-friendly alternatives to chemical fertilizers, promoting sustainable agriculture by enhancing soil fertility, reducing pathogens, and aiding in stress resistance. In agriculture, they play a crucial role in plant growth promotion through the production of agroactive compounds and extracellular enzymes to promote plant health and protection against phytopathogens. In the rhizosphere, diverse microbial interactions, including those with bacteria and fungi, influence plant health by production of antimicrobial compounds. The antagonism displayed by rhizobacteria plays a crucial role in shaping microbial communities and has potential applications in developing a natural and environmentally friendly approach to pest control. The rhizospheric microbes showcase their ecological importance and potential for biotechnological applications in the context of plant-microbe interactions. The extracellular enzymes produced by rhizospheric microbes like amylases, chitinases, glucanases, cellulases, proteases, and ACC deaminase contribute to plant processes and stress response emphasizing their importance in sustainable agriculture. Moreover, this review highlights the new paradigm including artificial intelligence (AI) in sustainable horticulture and agriculture as a harmonious interaction between ecological networks for promoting soil health and microbial diversity that leads to a more robust and self-regulating agricultural system for protecting the environment in the future. Overall, this review emphasizes microbial interactions and the role of rhizospheric microbial extracellular enzymes which is crucial for developing eco-friendly approaches to enhance crop production and soil health.

Keywords: rhizospheric microbes; plant growth promotion; extracellular enzymes; phytopathogens; sustainable agriculture

1. Introduction

In recent times, to reduce the effect of chemical fertilizers on the environment, the concern is increasing on a worldwide scale to shift food production by a sustainable path through the usage of biofertilizers. Bacteria and fungi are plant growth-promoting microbes that increase plant tolerance to stressful environments like drought, salinity, high concentrations of heavy metals, and nutrient deficiency, through various mechanisms in an environmentally friendly manner to improve yields of crops as efficiently as the practice of agrochemicals [1–5].

The potent antimicrobial capabilities and dominance of rhizospheric microbes in soil as saprophytes make them noteworthy for promoting plant growth which is gaining recent attention [6,7]. Various studies propose alternatives to excessive chemical use in agriculture. Microorganisms with diverse functions offer solutions by producing bioactive compounds, enzymes, antimicrobials, and biocontrol substances. These multifunctional traits reduce reliance on chemical fertilizers and pesticides.

Plant growth-promoting rhizobacteria (PGPR) are a good alternative that shows a mutualistic relationship with plants [8–13]. Plant growth-promoting actinobacteria naturally inhabit the rhizosphere, fostering plant growth, increasing yield, improving soil fertility, reducing pathogens, and aiding in stress resistance. They possess multifunctional traits beneficial to plants [14,15]. Modern needs emphasize eco-friendly approaches for increased yields, improved crop production, and enhanced soil fertility [16]. Actinobacteria serve as eco-friendly alternatives to chemical fertilizers, functioning as bio-inoculants and bio-pesticides, enhancing crop production amid diverse stress factors like temperature, pH, salinity, and drought [17]. A prevalent soil actinobacterial genera *Streptomyces* dominates due to rapid growth, efficiently colonizing plant roots, and enduring adverse conditions through spore formation. Its enzymatic potential and organic compound production capacity benefit plant growth [18–20].

Microorganisms are beneficial for plant crops as their natural habitat is soil [21]. To ensure the effectiveness of microbial inoculants and their positive influence on soil health, considerable research has focused on understanding the indigenous soil microbial diversity, studying their distribution, and examining their behaviour in various soil habitats [22]. PGPR enhances soil health through diverse mechanisms such as nitrogen fixation, phosphate solubilization, heavy metal sequestration, and phytohormone production (e.g., indole acetic acid, gibberellins, cytokinins) [23]. They contribute to soil mineralization, decompose crop residues, and suppress phytopathogens. These capabilities make them valuable for promoting plant growth, particularly in nutrient-deficient soils [24,25]. Enzymes play a crucial role in waste management and biofuel production from biomass. PGPR produces hydrolytic enzymes like cellulases, pectinases, proteases, catalases, and chitinases [26,27]. These enzymes exhibit defence-related activities, effectively countering diverse phytopathogens, and showcasing their function in enhancing plant protection and health [28].

Amylases are the enzymes found in plants, animals, bacteria, and fungi that break down starch and play a vital role in plant growth promotion by degrading organic matter (starch) in soil. They inhibit pathogens through protease and carboxylase [29]. Furthermore, cellulase-producing rhizobacteria efficiently break down cellulose into glucose through synergistic actions of glucanases, hydrolases, and glucosidases, facilitating nutrient availability for plants [30]. Cellulases and cellulase-producing bacteria are considered antagonistic agents for fungal diseases [31]. Cellulose-degrading bacteria enrich the soil rhizosphere, enhancing soil health by providing a carbon source and maintaining nutrient balance through cellulosic residue decomposition [30,32].

Chitin, a crucial component of fungal cell walls, becomes a target for PGPR through chitinase secretion, leading to chitin degradation. Chitinolytic bacteria indirectly enhance plant growth and effectively inhibit fungal pathogens like *Botrytis cinerea*, responsible for grey mold affecting over 200 plant species [33,34]. Additionally, ACC deaminase activity is prevalent in the plant microbiome, underscoring its significance in fostering interaction and communication between plants and PGPR, facilitating mutualistic relationships [35]. Microenvironments like the rhizosphere are favoured for isolating and characterizing beneficial rhizobacteria.

Beyond ACC deaminase, this approach allows the exploration of diverse mechanisms promoting plant growth and enhancing agricultural sustainability [36,37].

Proteases are abundantly present in eukaryotes and plants which play diverse roles in processes such as seed germination and plant senescence [38]. Predominantly located in lytic vacuoles, these proteases respond to environmental cues, enabling plants to adapt to stimuli, such as biotic and abiotic stresses. Their presence in lytic vacuoles highlights their involvement in cellular degradation processes, showcasing their significance in maintaining plant homeostasis and responding to external challenges for optimal survival and growth [39]. Thus, the present review focuses on extracellular enzymes from plant growth-promoting microbes that play a crucial role in modern agroecosystems by promoting plant growth and inhibiting fungal and bacterial pathogens, highlighting their significance in modern agroecosystems.

2. Extracellular enzymes produced by PGPR

Plant roots in the rhizosphere engage with diverse microbes including bacteria, fungi, and viruses fostering dynamic ecological interactions for growth [40]. Balancing interactions between beneficial microbes and pathogens is of great significance for plant health, attracting considerable focus for sustainable growth strategies [41]. Diverse PGPR benefits plants by promoting growth and alleviating stress, establishing symbiotic relationships for resilience [42]. PGPR exhibits hyperparasitic activity by releasing enzymes such as chitinases, glucanases, cellulases, and proteases, targeting the cell wall of the pathogen for defense mechanism [43,44].

2.1. Amylase

Starch, a prevalent carbon compound in plant tissues, rises during photosynthesis and decreases when converted to sugars (glucose) by the catalytic activity of amylase. Microbial amylase production is vital for litter degradation in mangroves [45]. Additionally, amylase has a role in seed germination. Seed germination is a multifaceted process encompassing water absorption, reactivation of stored macromolecules, cell division, seed coat rupture, and emergence of radicle and plumule, marking the initiation of new seedling growth [46,47]. It is a pivotal and sensitive stage in seedling establishment, particularly vulnerable to drought stress. Adequate water is crucial for the enzymatic breakdown of stored seed metabolites, including carbohydrates [48,49]. During seed germination, amylases break down endospermic carbohydrates into sugars, fueling the energy needed for embryonic root and shoot growth [50].

Water stress diminishes amylase activity, impairing carbohydrate metabolism and wheat seed germination, and thus, amylase activity serves as a metabolic indicator of stress [51]. In horticulture, drought-tolerant lentil varieties maintain higher amylase activity under stress compared to drought-sensitive types, relative to amylase levels in non-stressed conditions, crucial for efficient seed germination in adverse environments [52]. Moreover, several best amylase-producing PGPR has been isolated from the mangrove ecosystem and identified as *Aspergillus niger*, *Trichoderma viride*, *Penicillium citrinum*, *Paecilomyces variotii*, and *Eurotium amstelodmi* [53].

2.2. Protease

Soil microorganisms produce proteases to recycle organic matter, ensuring microbial nutrition. Proteases hydrolyze proteins into polypeptides and amino acids, facilitating nutrient uptake. They also contribute to microbial interactions by cleaving cell wall proteins, including anti-fungal proteases and alkaline serine proteases from hematophagous bacteria and fungi. Keratinolytic serine proteases in soil bacteria and fungi are crucial for recycling keratinous residues, demonstrating their diverse roles in soil ecosystems [54,55]. Similarly, a rhizospheric strain TSm39 isolated from the Rann of Tiker showed protease activity which could help the plant for nutrient uptake from soil and promote plant growth [56].

2.3. Cellulase

Microbial growth and survival in soils rely on cellulose as a crucial carbon source. Soil cellulases are primarily derived from stem parts of plant debris, with some contribution from fungi and bacteria. This enzymatic activity is vital for decomposing cellulose and sustaining microbial ecosystems in soils [57]. Cellulase plays a key role by breaking down cellulose, a structured homopolymer of cellobiose with β1,4-glycosidic linkages, disrupting its highly ordered structural organization. Cellulase promotes plant growth by killing pathogens in agriculture. It acts on pathogens by hydrolyzing their cell wall's cellulose, breaking glycan chains, and providing cellobiohydrolases (CBH or exoglucanase). Cellobiohydrolases then cleave the ends, producing cellobiose as the major product. β-Glucosidase further hydrolyzes cellobiose into glucose, releasing glucose from cello oligosaccharides [58]. This enzymatic process disrupts pathogen cell walls and indirectly promotes plant growth.

2.4. ACC deaminase

Climate-induced ethylene overproduction disrupts plant physiology, causing stunted growth and potential death if uncontrolled, threatening plant development [59,60]. PGPR alleviates stress by using ACC deaminase to hydrolyze 1-aminocyclopropane-1-carboxylic acid (ACC), the immediate precursor of ethylene. This enzymatic action lowers ethylene levels, thus benefiting plant health and enhancing plant resistance against adverse conditions [61–63]. Plants inoculated with such PGPR exhibit increased resistance to diverse stresses, including salinity, drought, flooding, and pathogens, showcasing the broad protective impact of ACC deaminase [64–67].

The ability to utilize plant 1-aminocyclopropane-1-carboxylate (ACC) enhances the plant growth-promoting (PGP) capabilities of various bacterial strains, notably *Pseudomonas* sp. Previous studies indicated the widespread prevalence and positive selection of the acdS gene, responsible for ACC deaminase production, in plant-associated bacteria, particularly rhizobia symbionts from alpha and beta proteobacteria classes. This highlights the significance of ACC deaminase in bacterial-plant interactions [68–71].

ACC deaminase genes are identified in Actinobacteria such as *Actinoplanes*, *Agreia*, *Arthrobacter*, *Austwickia*, *Brevibacterium*, *Streptomyces*, *Amycolatopsis*, *Mycobacterium*, *Nocardia*, *Rhodococcus*, and others [69]. Halotolerant Actinobacteria such as *Corynebacterium variabile*, *Micrococcus yunnanensis*, and *Arthrobacter nicotianae* exhibited ACC deaminase activities, contributing to enhanced canola plant growth, particularly in saline environments, mitigating salt-induced stress effects [72].

2.5. Chitinase

Chitinase belongs to the glycosyl hydrolase family that hydrolyzes the glycosidic bond of chitin and has different molecular sizes that vary in a wide range of living systems such as fungi, bacteria, yeasts, plants, actinomycetes, arthropods, and humans [73,74]. Plant chitinases are crucial for embryo development, ethylene production, and resilience against cold, drought, and high salt stress, ensuring survival [75]. Plants produce chitinase in response to phytopathogen attack. Recently, a review disclosed the importance of chitinases in diverse horticultural crops like beans, barley, cabbage, carrot, corn, cucumber, garlic, oat, onion, pea, peanut, potato, rice, and tomato, contributing to plant defense and adaptation and it possesses potential antifungal activity [76].

Chitinase from *Trichosanthes dioica* seed showed antifungal activity against *Aspergillus niger* and *Trichoderma* sp. which are phytopathogens. Similarly, chitinase isolated from *Diospyros kaki* fruits showed antifungal activity against *T. Viride* [77]. Recombinant chitinase was also observed to inhibit the growth of *Alternaria solani*, *Fusarium* sp., *Rhizoctonia solani*, and *Verticillium dahlia* [78]. Chitinase derived from *Hippophae rhamnoides* remarkably tolerated cold stress [79], whereas chitinase derived from soya bean tolerated arsenic and cadmium stress [80]. Crop yield reduction is influenced by plant diseases caused by pathogens. To combat them, various methods like chemicals and biological agents are employed for breaking down chitin in fungal pathogens. They not only boost immunity but also contribute to overall plant growth and development [81].

2.6. Pectinase

Pectinases are pectin-degrading enzymes produced by bacteria and fungi and hold multifaceted roles in cell physiology, growth, ripening, and intracellular adhesion. Their increasing demand underscores their significance in biotechnology [82]. Pectinase breaks down pectin through hydrolysis, trans-elimination, and de-esterification reactions, facilitating pectin substance degradation [83]. Pectinase plays a crucial role in plant pathology, plant-microbe symbiosis, and the decomposition of decaying plant matter. Microbial pectinase is vital for natural carbon recycling, contributing to environmental balance [84,85].

2.7. Xylanase

Xylanase, an endo-β-1,4-xylanase, exhibits hydrolytic action on β-1,4-xylan, a key polysaccharide in monocot plant cell walls. Its enzymatic and necrotizing activity can activate plant immunity. Additionally, it acts as an antagonist against pathogens, impeding plant growth and contributing to defense mechanisms [86]. As per the study, the xylanase protected the *Viciafabae* L. plant from the adverse effects of phytopathogenic fungi *Fusarium* and *Rhizoctoniasolani* [87]. The different extracellular enzymes produced by rhizospheric plant growth-promoting microbes are depicted in **Table 1**.

Table 1. Different extracellular enzymes produced by PGP microbes associated with different plants.

Sr. no.	Enzymes produced by PGPR	Name of PGPR	Isolation plant	Mechanism	Reference
1.	Chitinase	*Bacillus subtilis* CRB20	Tomato (*Solanum lycopersicum* L.)	Promotes plant growth and protects tomato seedlings from *Fusarium oxysporum*	[88]
2.	ACC deaminase	*Achromobacter*, *Azospirillum*, *Bacillus*, *Enterobacter*, *Pseudomonas*, *Rhizobium*	Peas (*Pisum sativum* L.)	Cut the level of ethylene in roots under severe stress	[89,90]
3.	ACC deaminase	*Aneurinibacillus Aneurinilyticus* strains ACC02 and ACC06 *Paenibacillus* sp. strain SG-AlOA2	Garlic (*Allium sativum* L.)	ACC deaminase activity	[91]
4.	Cellulase and β-1,3-glucanase	*Streptomyces* sp., *Paenibacillus* strains	Basmati rice (*Oryza sativa* L.)	Causes degradation of pathogenic fungi cell wall	[92,93]
5.	Cellulase and Pectinase	*Pseudomonas*, *Bacillus cereus*, *Azorhizobium* st. BR5401	Sea buckthorn (*Hippophae rhamnoides* L.)	Documented for cellulolytic and pectinolytic activities and provided host plant with antifungal properties against pathogenic fungi	[94]
6.	Cellulase	*Achromobacter xylosoxidans* AKDJ1, AKDJ2, AKDJ3	Physic nut (*Jatropha curcas* L.)	Cellulose degradation	[95]
7.	Pectinase	*B. subtilis, B. velezensis*	Apple (*Malus domestica*L.)	Play a role in cell physiology, growth, and ripening, as well as in intracellular adhesion and separation	[96]
8.	Amylase, Cellulase, Lipase, Protease	*Bacillus aerius* strain BKOU-1	-	Inhibit the growth of plant pathogenic fungi (*Fusarium oxysporum* and *Macrophomina phaseolina*)	[97]

3. Impact of climate change on agriculture

Currently, growing concern over drastic climate changes and their impact on ecosystems affects both living and non-living components. Instances of flooding, droughts, cyclones, and hurricanes highlight the urgent need to reassess our interactions with the biosphere. These events result from both human activities and natural phenomena. Greenhouse gas accumulation significantly contributes to climate fluctuations, leading to a global temperature increase. Research about enhancing plants' tolerance to abiotic stress has notably increased in recent decades. This focus is due to plants being highly vulnerable to climate change impacts, given their immobility and dependence on environmental conditions [98]. Bacteria play a crucial role in mitigating environmental issues caused by natural and human-related challenges, such as heavy metal and pesticide pollution, as well as salinity and drought. They aid plants in coping with these challenges through various plant growth-promoting properties. These include nitrogen (N_2) fixation, phosphate and potassium solubilization through organic acid production, siderophore production, auxin (indole acetic acid) production, and ACC deaminase activity. These properties collectively support plant growth and health, demonstrating the versatility of bacteria in addressing environmental stresses and promoting sustainable agriculture [99,100]. Recently, extensive research has explored the role of plant growth-promoting rhizobacteria (PGPR) in aiding plants under various abiotic stresses. Examples include *Bacillus* species aiding salt tolerance in tall fescue, *Bacillus* and *Enterobacter* alleviating drought stress in maize and wheat, *Bacillus subtilis* mitigating drought stress in potatoes by suppressing oxidative stress and enhancing antioxidative enzymes, and *Pseudomonas fluorescens* enhancing essential oil production in rosemary under salinity stress. Bacterial species, due to their metabolic adaptability and plasticity, offer dynamic applicability. PGPR are beneficial across various plant types, including forest trees, grassland, crops, and important medicinal or ornamental plants. This versatility makes them valuable for cultivating stress-resilient plants in the face of climate change [101–104].

4. Artificial intelligence in sustainable agriculture

Sustainable grain production practices in agriculture are characterized by long-term viability and ecological compatibility. Moreover, "sustainable agriculture" is characterized by its ability to maintain nature without compromising food security for future generations to meet their basic needs, while also enhancing farming efficiency. In recent times, the agricultural sector has mainly focused on smart farming using AI tools to reduce the use of pesticides and increase the production of food for the growing population [105]. However, fragmented agricultural processes lead to operational challenges such as managing smart machines and data [106,107]. Furthermore, AI's capacity to analyze extensive datasets and optimize resource utilization, such as water, fertilizers, and pesticides, can result in substantial cost savings for farmers in resource management while also reducing environmental impact. Moreover, AI-driven monitoring enables early detection of diseases and pests, facilitating targeted interventions to minimize crop damage and enhance overall yield [108]. The potential positive transformation of traditional agriculture through the Internet of Things (IoT) and Artificial Intelligence (AI) technologies by optimizing data from smart sensors, enhancing internal processes (like crop harvesting and storage), reducing waste and costs, automating tasks for greater efficiency, and improving product quality and quantity would provide a holistic approach to sustainable agriculture while protecting our planet [109].

5. Importance of climate change in agriculture

Climate change refers to shifts in a region's climate caused by both human activities (like ozone layer depletion and greenhouse gas emissions) and natural factors [110]. Agricultural yield depends on climate, management practices, pests, pathogens, and extreme weather events impacting crop growth. Climate change is severely impacting agricultural yield in food-insecure regions of Asia. In Sri Lanka, the increasing population resulted in growing pollution through agricultural waste which produces greenhouse gases that lead to climate change that ultimately affect the quality of the water resources. Thus, water management would be an alarming condition for the agriculture sector because it is an economically important sector for Sri Lanka

[111,112]. Similarly, in Uzbekistan, the water irrigation systems are optimized in agricultural practices for water management and decrease the loss of water by up to 20%–30% which can be used in the future for an increased population [113]. Consequently, it is important to manage the natural resources including water and soil to enhance the production of food and save our environment from the adverse effects of the chemicals. Projections indicate significant temperature rises by mid-century, with maximum temperatures expected to increase by 2.8 ℃ and minimum temperatures by 2.2 ℃. This includes adopting technologies and techniques that optimize water use, enhance soil health, promote crop diversification, and integrate climate forecasting into decision-making processes [114].

6. Conclusion

The emphasis of this study is to promote plant development, especially in unfavourable circumstances like heat and drought stress, which are becoming more common as climate change advances. The extracellular enzymes produced by rhizobacteria affect the multifunctional traits of plants, particularly in extreme environments, and protect against phytopathogens. Thus, the rhizospheric microbes are promising sources for novel natural product discovery. Their capacity to enhance soil fertility, reduce pathogens, and improve stress resistance in plants aligns with the modern emphasis on eco-friendly agricultural practices. The understanding of these microbial interactions and enzyme-mediated processes offers eco-friendly solutions for developing strategies that promote plant growth while minimizing environmental impact.

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