INVITED REVIEW

The Significance of Rhizobacteria for Strawberry Cultivation in Tropical Area: A Review

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Highlights

- Rhizobacteria enhance strawberry growth, yield and quality – The presence of beneficial rhizobacteria (e.g., *Bacillus* sp., *Azospirillum* sp., *Azotobacter* sp., *Pantoea* sp., and *Pseudomonas* sp.) has been demonstrated to enhance nutrient availability and promote plant growth by nitrogen fixing, solubilizing phosphorus and potassium, and producing phytohormones and exopolysaccharides (EPS).

- Rhizobacteria enhance plant resilience –The rhizobacteria play a pivotal role in mitigating abiotic stresses and against pathogens as biocontrol agents that are prevalent in tropical climates.

- Potential for Sustainable Strawberry Cultivation in Tropical Regions – The rhizobacteria-based biofertilizers offers a sustainable alternative to chemical fertilizers, thereby reducing environmental impact while maintaining high agricultural productivity, emphasizing their role in sustainable tropical agriculture.

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The Significance of Rhizobacteria for Strawberry Cultivation in Tropical Area: A Review

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Abstract: In tropical regions, high temperatures and low Nitrogen (N) and phosphorus (P) in soil limit plant performance and fruit production. The soil-beneficial microbes, including rhizobacteria, have the potency to overcome the nutrient problems in the soil. Rhizobacteria fix the dinitrogen, solubilize the P and potassium (K), and produce hormones and other metabolites to stimulate plant development and resistance against environmental challenges like inadequate soil fertility, heavy metal concentrations, or drought. Bacterial genera that occur for promoting growth is *Bacillus* sp., *Azospirillum* sp., *Azotobacter* sp, *Pantoea* sp., and *Pseudomonas* sp. Despite the prominent role of rhizobacteria in agriculture and the economic value of strawberries, the potential use of rhizobacteria as a biofertilizer in strawberry cultivation in tropical areas is rarely discussed and reviewed. The information obtained from publications from 2014–2023 by using the keywords of Plant Growth Promoting Rhizobacteria, tropics, biofertilizer, N fixation, P and K solubilization, P mineralization, phytohormones and strawberry is organized according to the rhizobacteria, mechanisms by which they boost plant growth, and research location in tropical area. This review focuses on evaluating 1) the mechanism of rhizobacteria to increase plant growth, 2) the role of rhizobacteria on strawberry

growth, yield, and quality, and 3) the impact of rhizobacteria on biotic and abiotic stress alleviation.

Keywords: Biofertilizer, Rhizobacteria, Review, Strawberry, Tropical

INTRODUCTION

Strawberry (*Fragaria* x *ananassa,* Duch.) is a hybrid of Rosaceae family plants, *Fragaria chiloensis* and *Fragaria virginian* (de Moura et al. 2022). It holds substantial economic value across various industries (Simpson 2018). Major producers such as China, the United States, and Mexico collectively contribute half of the global supply, which exceeded 9 million tons in 2019 (FAO). Cultivation spans tropical, subtropical, and temperate zones, with tropical cultivation typically at high altitudes in mountainous areas (de Andrade et al. 2019).

Due to high drought, temperature, and soil-borne diseases, challenges persist in tropical cultivation (Khammayom, Maruyama, and Chaichana 2022). Intensive weathering processes in tropical regions result in low soil acidity, organic carbon, and limited nitrogen and phosphorus availability (Piamonte, Asio, and Lina 2014). High precipitation can lead to nutrient leaching due to organic matter degradation, which further compounds these challenges (Quan, Nissom, and Tung 2022).

Open-field cultivation is commonly practiced, but soil-borne diseases pose a significant threat. Chemical fertilizers are extensively used to augment nutrient deficiencies, increasing yield (Maurya et al. 2017). *Phytophthora* and *Verticillium* are essential pathogens that cause rotting and wilting diseases in strawberries (Fan et al. 2018). Inoculating with plant growth-promoting rhizobacteria (PGPR) has shown promise in enhancing growth and stress tolerance, offering eco-friendly and cost-effective solutions to increase strawberry yield (Naamala and Smith 2020).

Rhizobacteria application as biostimulants, biofertilizers, or biocontrol agents has surged, recognized for their economic benefits, enhanced yields, and environmental sustainability (Koskey et al. 2021). The bacteria directly influence plant growth by providing nutrients through nitrogen fixation and phosphate and potassium solubilization, phytohormones, and disease protection alongside indirect mechanisms involving the production of volatile compounds, siderophores, exopolysaccharides, and antibiotics (Figure 1). Rhizobacteria are crucial in inducing systemic resistance, reducing disease intensity, and increasing plant development against stressful conditions, significantly contributing to plant resilience (Naamala and Smith 2020).

Widely used genera of rhizobacteria are Nitrogen Fixer bacteria (NFB) such as *Azotobacter, Azospirillum, Bradyrhizobium,* and *Rhizobium*; Phosphate solubilizing bacteria

(PSB) such as *Bacillus* sp. and *Pseudomonas* sp.; and Potassium solubilizing bacteria (KSB), *Bacillus mucilaginous* (Azizoglu 2019). Numerous other genera have been shown to promote plant growth and produce phytohormones, such as auxin, gibberellin, and cytokinin (Chebotar et al. 2022). Certain *Bacillus* species have been reported to enhance the percentage of significant macroaggregates, improving the soil structure and root development through exopolysaccharides (EPS) production (Vikram et al. 2022; Costa, Raaijmakers, and Kuramae 2018).

Balanced nutrient management, incorporating chemical, organic, and microbial-based fertilizers, is advocated for sustainable growth (He and Dijkstra 2014). Rhizobacteria play a crucial role in improving soil and fruit quality while enhancing plant resilience to various stressors (Hindersah et al. 2019; Redondo-Gómez et al. 2022). This review reported the potential role of rhizobacteria in promoting strawberry growth and productivity in tropical regions, emphasizing their role in the soil and plant health.

RHIZOBACTERIA MECHANISM FOR INCREASING PLANT GROWTH

In tropical soils, where nitrogen, phosphorus, and potassium availability is low, rhizobacteria enhance the efficient use of chemical fertilizers by reducing fertilizer doses (de Andrade et al. 2019). According to Le et al. (2019), they contribute to nitrogen fixation, phosphate and potassium solubilization, and stress tolerance promotion. Rhizobacteria synthesize organic acids and enzymes, which solubilize and mineralize P, aiding in heavy metal stress tolerance (Ducousso-Détrez et al. 2022). Additionally, they enhance plant K availability by gluconic and oxalic acid, which solubilize insoluble K in soil (Olaniyan et al. 2022).

Figure 1. Rhizobacteria mechanism as direct and indirect to increase plant development

The rhizosphere is inhabited by NFB that stimulate plant development by converting molecular N_2 to ammonia gas (NH_3), catalyzed by nitrogenase, an oxygen-sensitive enzyme complex (Le, Jun, and Kim 2019). The N fixation reaction is stated elsewhere as the N reduction process:

$$N_2 + 8\,H^+ + 8\,e^- \rightarrow 2NH_3 + H_2 \qquad (1)$$

The N fixation requires 16 adenosine triphosphate molecules to convert one molecule of N_2 to NH. Under nitrogen fixation, PII signal transduction protein interacts with the RnfC gene, which controls electron flow to control electron transfer to nitrogenase (Batista and Dixon 2019).

The available form of N readily uptake by roots are NH_4^+ and NO_3^-. In the non-symbiotic NFB, NH_3 is released from the bacteria into the soil by diffusion (Haskett et al. 2022). Dissolved NH_3 in soil solution exists in chemical equilibrium with ammonium cations, the NH_4^+ (Preez and du T. Burger 1988). The NH_4^+ in soil solution will be converted to NO_3^- by 2-step enzymatic nitrification involving ammonia oxidation to nitrite by chemolithotrophic ammonia-oxidizers and nitrite oxidation to nitrate by nitrite-oxidizers (Levy-Booth, Prescott, and Grayston 2014):

$$2NH_4^+ + 3O_2 \rightarrow 2NO_2^- + 4H^+ + 2H_2O \quad \text{.......2)}$$

$$2NO_2^- + O_2 \rightarrow 2NO_3^- + \text{energy} \quad \text{.......(3)}$$

in contrast, another research ensures that fixed N in nonsymbiotic NFB is assimilated into bacterial biomass and not excreted into the soil (Batista and Dixon 2019). Meanwhile, symbiotic NFB provides plants with asparagine, an amino acid synthesized in the plant cell by using glutamate released by rhizobia living in the nodule (Schwember et al. 2019). Specific mechanisms to increase the availability of N in the soil by nonsymbiotic NFB have not been explicitly stated. However, many studies have shown the impact of this bacteria on the available N increment in soil (dos Santos Cordeiro and Echer 2019; Haerani et al. 2021; Mendes-Santos, Kandasamy, and Cid-Rigobelo 2017).

The rhizobacteria are involved in the P and K cycle in soil. They produce the organic acid to release phosphate from inorganic P (Pi) of Ca, Fe, and Al to become available for plants. (Ducousso-Détrez et al. 2022). The organic acid also solubilizes K minerals, including micas, muscovite, feldspar, biotite, illite, and orthoclase (Olaniyan et al. 2022). The well-known short-chain organic acids (C2 - C6 acids) synthesized by rhizobacteria to solubilize the P and K are lactic, citric, acetic, and succinic acids (Naraian and Kumari 2017; Zhao et al. 2024). They are essential intermediate metabolites in bacterial cells and are commonly produced from sugar via the microbial Tricarboxylic acid cycle and fermentation (Sun et al. 2020).

The low-molecular-weight organic acids solubilize the fixed inorganic P (Pi) by lowering the soil pH, chelating cations, and competing with ortophosphate (PO_4^-) for adsorption sites in the soil (Saeed et al. 2021). The organic acid can solubilize the Pi on soil colloids as chelators of cations such as Fe, Al^{3+}, and Ca^{2+} and compete for P adsorption sites in soil (Menezes-Blackburn et al. 2016). They also form a complex metal cation chelation with base cations on soil such as K^+, Mg^{2+}, and Ca^{2+} as readily for plant uptakes (Vega, Delgado, and Handford 2022). During the process, organic acid has a mechanism for soil acidification as the metal becomes soluble and is released into the soil solution (Achor et al. 2020).

Organic P (OP) in soil accounts for 42% of the P pool (Menezes-Blackburn et al. 2018). OPs contain phosphate groups or P bonded to carbon (C) groups, including orthophosphate monoesters, orthophosphate diesters, and phosphonates (Cade-Menun 2017) originating from microbial cells and plant and animal debris. Bacterial phosphatases catalyze the OP mineralization to available inorganic P (Pi) based on the type of OP substrates (Park et al. 2022). The Pi enters the bacterial cytoplasm via a transporter for cell metabolism, and part of the Pi is adsorbed by roots. Major (N, P, and K) elements available for plants are essential in reducing the impact of stress conditions. Many studies have demonstrated that essential nutrients such as N and P are related to the mitigation of abiotic stress in plants and the reduction of the effect of drought stress (He & Dijkstra, 2014).

The detailed biosynthesis pathway of various phytohormones by individual bacteria is limited. Generally, the rhizobacteria, including *Azospirillum, Bacillus, Pseudomonas, and Rhizobium,* synthesize the indole acetic acid (auxin) via the tryptophan-dependent pathways (Tang et al. 2023). Naturally occurring CKs are adenine derivatives; the microbes synthesize the CK via De novo CK and tRNA-dependent CK biosynthesis pathway (Frébortová and Frébort 2021). Gibberellins (GA) are phytohormones characterized by a complex diterpenoid structure. The biosynthetic pathways of GA in plants and fungi have been elucidated, although knowledge on GA biosynthesis in bacteria remains limited. Symbiotic nitrogen-fixing *Bradyrhizobium japonicum* and *Sinorhizobium fredii* have a putative GA biosynthetic operon/gene cluster for encoding the enzymes to produce GA9 (Nett et al. 2017).

The challenge of growing strawberries in the field is the soil's physical quality. Tropical soil generally has poor physical properties due to low organic C and high clay content, which causes restrained structure and poor infiltration (Zhong et al., 2018). EPS produced by rhizobacteria can adhering soil particles by forming aggregates around the roots (Costa, Raaijmakers, and Kuramae 2018; Sivapriya, S.L. 2018). They also can improve water holding capacity and reduce proline accumulation and antioxidant enzyme activity as tolerant mechanism for drought stress conditions (Sandhya and Ali 2015; Naseem et al. 2024). EPS of Rhizobacteria such as *Pseudomonas bathysetes* secrete EPS to improve porosity, bulk density, and soil aggregate stability to improve micro aggregation (Dar et al. 2021; Olagoke et al. 2022). Application of some Bacillus species increases the percentage of large macro aggregates of >2mm (Vikram et al., 2022). This improves the soil structure by increasing infiltration and providing better porosity for root development (Sharma et al., 2018).

EPS produced by rhizobacteria enables soil particles to form aggregates around the roots, enhances water-holding capacity, and facilitates the plant's uptake of nutrients and minerals. Rhizobacteria produce EPS as a protective mechanism to shield themselves from abiotic stressors like extreme temperatures, metal concentration, drought, and biotic threats (Carezzano et al. 2023). The mechanism of EPS is to protect bacteria and plant hosts from abiotic stress by maintaining and regulation nutrient uptakes and absorption as chelator ions (Paul et al., 2024). Moreover, EPS as a biopolymer is involved in metal-binding to facilitate heavy metal biosorption (Dhanya, Athmika, and Rekha 2021). The EPS acts as a chelator by forming COO^- (carboxyl group) and OH^- (hydroxyl ion) to bind cations, including metals, on soils. The EPS of *Azotobacter* sp. binds Cd and Cr in the contaminated soil (Rasulov, Yili, and Aisa 2015) to reduce their availability. However, the excretion of EPS is also a mechanism for maintaining the balance of C/N ratio when the nitrogen in environment is sufficient (Qian et al. 2022). Therefore, EPS as sorption and retention mechanism may thus affect the mobility and fate of microbially-derived carbon (C), nitrogen (N) and phosphorus (P) in soils (Zhang et al. 2021).

Role of Rhizobacteria Strawberry Growth, Yield and Quality

In tropical soils, where nitrogen, phosphorus, and potassium are often limited, rhizobacteria are vital in fixing nitrogen and solubilizing phosphorus and potassium (Hanyabui et al. 2020). However, soil-borne pathogens pose a challenge, leading to damping-off, root rot, and vascular wilts exacerbated by continuous cropping (Arora et al., 2022). Soilless substrates, typically composed of organic matter and inorganic materials, offer a pathogen-free alternative but lack sufficient nutrients, necessitating fertilizer applications (Hindersah et al. 2022). Rhizobacteria application is feasible in soil-based and soilless cultivation systems (Table 1).

Table 1. Responses of strawberries on rhizobacteria inoculation in soil-based substrates and field soil.

Rhizobacteria function as biofertilizers, providing essential nutrients through nutrient-solubilizing mechanisms (Hindersah et al. 2022). They enhance strawberry development and yield by improving the nutrient supply and phytohormone production (Meena 2018; Liu et al. 2022). These microorganisms, including *Azotobacter* sp. and *Burkholderia* sp, positively impact strawberry development and yield by increasing nutrient content (Kumar et al., 2020b). Various rhizobacteria, such as *Azospirillum brasilense* and *Bacillus megaterium*, stimulate plant growth by solubilizing phosphorus and potassium while synthesizing indole-3-acetic acid (Silva et al., 2022). They can significantly reduce inorganic fertilizer consumption, with studies reporting biomass increases and root parameter enhancements following their application (Hindersah et al. 2021).

Table 2. The impact of rhizobacteria on strawberry development and productivity in soilless substrates.

Table 3. The impact of rhizobacteria on strawberry quality

Rhizobacteria boost growth and yield and enhance fruit quality through increased nutrient availability and ripening regulation (Negi et al. 2021). Potassium, crucial for fruit quality and stress responses, influences pathogen resistance and fruit ripening (Singh et al. 2020). Reduced nitrogen, phosphorus, potassium, and biofertilizer applications have significantly improved fruit quality and yield (Nisarga et al. 2020). Various bacteria strains from *Bacillus* sp. and *Pseudomonas* sp. are employed as biofertilizers to enhance fruit quality (Nam et al. 2023).

IMPACT OF RHIZOBACTERIA ON BIOTIC AND ABIOTIC STRESS

Drought Stress Alleviation

Strawberries are highly vulnerable to drought, causing physiological stress and reducing fruit production and quality (Murthy and Pramanick 2014). In tropical open field areas, drought can lead to yield loss of up to 17% (Kumar et al., 2022). Nitrogen, phosphorus, and potassium are essential nutrients that help plants adapt to abiotic stress, improve soil fertility, and increase plant tolerance to environmental stresses (He and Dijkstra 2014). The shape and physiological functions of strawberry fruits are affected by water deficiency because of their depthless root systems, broad leaf areas, and high fruit water content (Adak, Gubbuk, and Tetik 2018; Mozafari, Havas, and Ghaderi 2018). Induced systemic resistance (ISR) and acquired systemic resistance (ASR) play crucial roles in biotic and abiotic resistance, respectively (Figure 2). ISR enhances defense against pathogens, while ASR helps plants withstand environmental stresses vital for survival and productivity in challenging conditions.

Jasmonic acid (JA) is synthesized to respond to plant damage caused by pest attacks or pathogen colonization. JA also induces a signaling pathway that leads to the production of ethylene hormones (Ma et al. 2020). The interaction between JA and ethylene activates defense-related genes, which express plant resistance and induce systemic resistance (Ravanbakhsh et al. 2018). When a pathogen invades the plant, it also recognizes the signaling of salicylic acid (SA) biosynthesis (Mishra et al. 2024). The accumulation of SA leads to the expression of pathogen-related genes, which secrete metabolites to enhance resistance to pathogens, resulting in systemic acquired resistance (Kim and Lim 2023).

Figure 2. Mechanisms of rhizobacteria on biotic and abiotic stress through induced systemic resistance and acquired systemic resistance.

In response to drought stress, organisms accumulate osmolytes, including betaines, sugars, polyols, polyamines, and proline (Ashraf and Foolad 2007; Giri 2011). In strawberries, drought reduces chlorophyll and carotenoid pigments and relative water content while enhancing antioxidant enzyme activity, osmolyte accumulation, and oxidative markers. (Zahedi et al. 2023). Several genera of bacteria elevate osmolyte concentration, mitigate oxidative damage, and bolster drought tolerance (Kour et al. 2022). These bacteria can break down ethylene precursors by secreting 1-aminocyclopropane-1-carboxylate (ACC) deaminase, thus enhancing plant resilience (Brunetti et al. 2021).

For instance, *Azospirillum* sp. enhances root development in tomatoes and xylem development in *Brassica competes* under drought conditions (Molina-Favero et al. 2008; Timmusk et al. 2014). Inoculation of several strains of *Bacillus* sp. and *Pantoea* sp. strains increases ACC deaminase production, auxin synthesis, and phosphate-solubilizing ability in strawberries (Paliwoda et al. 2022). However, comprehensive studies on rhizobacteria's role in alleviating 'strawberries' drought stress are ongoing.

Rhizobacterias as Biocontrol Agents

Wet tropical climates are marked by abundant rainfall and high humidity, and fungal and bacterial pathogens thrive, presenting substantial risks to strawberry plants (Morkeliūnė, Rasiukevičiūtė, and Valiuškaitė 2021). Disease in such conditions includes black root rot, stem rot, crown rot, and powdery mildew with key pathogens including *Verticillium* sp., *Botrytis cinerea*, *Colletotrichum* sp. and *Phytophthora* sp. (Drobek et al. 2021; Abdel-Gaied et al. 2022). Chemical pesticides can be effective but raise environmental and health concerns. Therefore, non-pathogenic rhizobacteria show promise as a substitute for chemical pesticides.

Many rhizobacteria are effective biocontrol agents (BCAs) for crop protection. Despite colonizing the rhizosphere, they alleviate the detrimental effects by controlling plant disease and triggering immune responses (Abd-El-Kareem, Elshahawy, and Abd-Elgawad 2021). Directly, rhizobacteria combat soil-borne pathogens by synthesizing antimicrobial compounds such as antibiotics, siderophores, bacteriocin, and volatile compounds (Raaijmakers, Vlami, and de Souza 2002; Subramanian and Smith 2015; Ryu et al. 2005; Vlassi et al. 2020). Rhizobacteria such as *B. Amyloliquefaciens* inhibit the mycelial growth of *F. solani* through the secretion of lipopeptide substances (Yang et al. 2024). Rhizobacteria also enhance plant health by providing nutrients and promoting better root growth via bacterial exopolysaccharide (EPS) and phytohormone production. Additionally, they produce antimicrobial substances, competing for nutrients and space (Grover et al. 2021). Indirectly, rhizobacteria can synthesize microbes-to-plant signals such as Lipo-chitooligosaccharides (LCOs) and microbes-to-pathogen signals as volatile organic compounds (VOCs) to provoke and induce systemic resistance (Jiao et al. 2021). *Azotobacter chroococcum, Azospirillum brasilense,* and *Pseudomonas brassicacearum* induces phytohormonal signaling (jasmonic acid and ethylene) of plants due to population of *Tetranychus urticae* by regulating the content of phenolics, flavonoids and anthocyanins (Hosseini, Hosseini, and Schausberger 2022). Some studies have investigated the biocontrol mechanisms of rhizobacteria, encompassing direct and indirect approaches (Table 4).

Table 4. Biocontrol mechanisms of rhizobacteria on the pathogen of strawberry plants.

CONCLUSION

Beneficial rhizobacteria are essential for enhancing strawberry growth and production, especially in soilless-substrate cultivation in tropical regions. They directly contribute to plant growth by fixing nitrogen, solubilizing phosphorus and potassium, producing phytohormones, and synthesizing EPS. They also indirectly alleviate harsh conditions like drought and diseases, improving strawberry yield and quality. With low nutrient availability in tropical soil, N_2-fixing, phosphate-solubilizing, and potassium-solubilizing bacteria become crucial for promoting plant development.

Rhizobacteria function as biocontrol agents, managing pathogen growth in tropical regions with high disease intensity. Their diverse roles contribute to improving strawberry cultivation practices while decreasing dependence on chemical fertilizers, thus fostering environmental sustainability.

This literature review highlights the potential of various rhizobacteria to increase strawberry production and minimize chemical fertilizer usage in tropical climates. Their application proves significant in field-based and soilless cultivation, aiding strawberries to thrive despite drought and abiotic factors. Rhizobacteria offer promising prospects for sustainable strawberry cultivation in tropical regions.

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AUTHOR CONTRIBUTIONS

FF and RH conceptualized the review theme, conducted the literature search and wrote the initial draft; RH, FF, EP, and MA composed the outline of review article and collect the article research for various resources; SM reviewed and edited the manuscript for clarity and coherence. All author contributed in writing, reviewing and editing the article. The authors have made a final review of manuscript and agreed for submission.

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