

INVITED REVIEW

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

Authors:

Febby Fitriyani, Etty Pratiwi, Masako Akutsu, Reginawanti Hindersah* and Syariful Mubarok

*Correspondence: reginawanti@unpad.ac.id

Submitted: 18 April 2024; Accepted: 21 March 2025; Published: 31 July 2025

To cite this article: Febby Fitriyani, Etty Pratiwi, Masako Akutsu, Reginawanti Hindersah and Syariful Mubarok. (2025). The significance of rhizobacteria for strawberry cultivation in tropical area: A review. *Tropical Life Sciences Research* 36(2): 317–337. https://doi.org/10.21315/tlsr2025.36.2.15

To link to this article: https://doi.org/10.21315/tlsr2025.36.2.15

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, solubilising 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 rhizobacteriabased biofertilisers offers a sustainable alternative to chemical fertilisers, thereby reducing environmental impact while maintaining high agricultural productivity, emphasising their role in sustainable tropical agriculture.

INVITED REVIEW

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

¹Febby Fitriyani, ²Etty Pratiwi, ³Masako Akutsu, ⁴Reginawanti Hindersah and ⁵Syariful Mubarok

¹Masters student of Soil Science, Faculty of Agriculture, Universitas Padjadjaran, Jalan Raya Bandung Sumedang KM 21, Jatinangor 45363, Indonesia

²Research Center for Food Crops, National Research and Innovation Agency, Indonesia ³Faculty of Agriculture, Shinshu University, 8304, Minami-minowa, Kami-ina, Nagano 399-4598, Japan

⁴Department of Soil Science and Land Resources, Faculty of Agriculture, Universitas Padjadjaran, Jalan Raya Bandung Sumedang KM 21, Jatinangor 45363, Indonesia ⁵Department of Agronomy, Faculty of Agriculture, Universitas Padjadjaran, Jalan Raya Bandung Sumedang KM 21, Jatinangor 45363, Indonesia

Submitted: 18 April 2024; **Accepted:** 21 March 2025; **Published:** 31 July 2025 **To cite this article:** Febby Fitriyani, Etty Pratiwi, Masako Akutsu, Reginawanti Hindersah, and Syariful Mubarok. (2025). The significance of rhizobacteria for strawberry cultivation in tropical area: A review. *Tropical Life Sciences Research* 36(2): 317–337. https://doi.org/10.21315/tlsr2025.36.2.15

To link to this article: https://doi.org/10.21315/tlsr2025.36.2.15

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 potential to overcome the nutrient problems in the soil. Rhizobacteria fix the dinitrogen, solubilise 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 biofertiliser 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 (PGPR), tropics, biofertiliser, N fixation, P and K solubilisation, P mineralisation, phytohormones and strawberry is organised according to the rhizobacteria, mechanisms by which they boost plant growth, and research location in tropical area. This review focuses on evaluating (i) the mechanism of rhizobacteria to increase plant growth, (ii) the role of rhizobacteria on strawberry growth, yield and quality and (iii) the impact of rhizobacteria on biotic and abiotic stress alleviation.

Keywords: Biofertiliser, Rhizobacteria, Review, Strawberry, Tropical

[©] Penerbit Universiti Sains Malaysia, 2025. This work is licensed under the terms of the Creative Commons Attribution (CC BY) (http://creativecommons.org/licenses/by/4.0/).

INTRODUCTION

Strawberry (*Fragaria* × *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 *et al.* 2022). Intensive weathering processes in tropical regions result in low soil acidity, organic carbon and limited nitrogen and phosphorus availability (Piamonte *et al.* 2014). High precipitation can lead to nutrient leaching due to organic matter degradation, which further compounds these challenges (Quan *et al.* 2022).

Open-field cultivation is commonly practiced, but soil-borne diseases pose a significant threat. Chemical fertilisers 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 & Smith 2020).

Rhizobacteria application as biostimulants, biofertilisers or biocontrol agents has surged, recognised 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 solubilisation, phytohormones and disease protection alongside indirect mechanisms involving the production of volatile compounds, siderophores, exopolysaccharides and antibiotics (Fig. 1). Rhizobacteria are crucial in inducing systemic resistance, reducing disease intensity and increasing plant development against stressful conditions, significantly contributing to plant resilience (Naamala & Smith 2020).

Widely used genera of rhizobacteria are Nitrogen fixer bacteria (NFB) such as *Azotobacter, Azospirillum, Bradyrhizobium* and *Rhizobium*; Phosphate solubilising bacteria (PSB) such as *Bacillus* sp. and *Pseudomonas* sp. and Potassium solubilising 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 *et al.* 2018).

Balanced nutrient management, incorporating chemical, organic and microbial-based fertilisers, is advocated for sustainable growth (He & 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, emphasising their role in the soil and plant health.

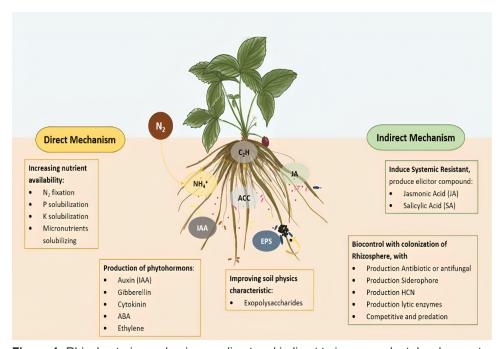


Figure 1: Rhizobacteria mechanism as direct and indirect to increase plant development.

RHIZOBACTERIA MECHANISM FOR INCREASING PLANT GROWTH

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

The rhizosphere is inhabited by NFB that stimulate plant development by converting molecular N_2 to ammonia gas (NH₃), catalysed by nitrogenase, an oxygen-sensitive enzyme complex (Le *et al.* 2019). The N fixation reaction is stated elsewhere as the N reduction process:

$$N_2 + 8 H^+ + 8 e^- \rightarrow 2NH_3 + H_2$$
 (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 & 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^+ (du Preez & 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 *et al.* 2014):

$$2NH_4^+ + 3O_2 \rightarrow 2NO_2^- + 4H^+ + 2H_2O$$
 (2)

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

In contrast, another research ensures that fixed N in nonsymbiotic NFB is assimilated into bacterial biomass and not excreted into the soil (Batista & Dixon 2019). Meanwhile, symbiotic NFB provides plants with asparagine, an amino acid synthesised 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 & Echer 2019; Haerani *et al.* 2021; Mendes-Santos *et al.* 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 solubilises K minerals, including micas, muscovite, feldspar, biotite, illite and orthoclase (Olaniyan *et al.* 2022). The well-known short-chain organic acids (C2–C6 acids) synthesised by rhizobacteria to solubilise the P and K are lactic, citric, acetic and succinic acids (Naraian & 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 solubilise the fixed inorganic P (Pi) by lowering the soil pH, chelating cations and competing with ortophosphate (PO₄⁻) for adsorption sites in the soil (Saeed *et al.* 2021). The organic acid can solubilise the Pi on soil colloids as chelators of cations such as Fe, Al³+, and Ca²+ 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⁺, Mg²+, and Ca²+ as readily for plant uptakes (Vega *et al.* 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 catalyse the OP mineralisation 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,* synthesise the indole acetic acid (auxin) via the tryptophan-dependent pathways (Tang *et al.* 2023). Naturally occurring CKs are adenine derivatives; the microbes synthesise the CK via De novo CK and tRNA-dependent CK biosynthesis pathway (Frébortová & Frébort 2021). Gibberellins (GA) are phytohormones characterised 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 nitrogenfixing *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 et al. 2018; Sivapriya 2018). They also can improve water holding capacity and reduce proline accumulation and antioxidant enzyme activity as tolerant mechanism for drought stress conditions (Sandhya & 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 > 2 mm (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 *et al.* 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 *et al.* 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 solubilising 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 fertiliser 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.

Mechanisms	Impact	Species of rhizobacteria	References
Increase in nutrient availability	Improve plant development, productivity and nutritional content under saline stress.	Alcaligenes 637Ca and Pseudomonas 53/6	(Arikan <i>et al.</i> 2020)
	Increase the number of roots, root activity and improve nutrient uptake.	Piriformospora indica	(Liu <i>et al.</i> 2022)
	Induce earliness in flowering, fruiting and increase yield, quality fruits by substitute 25% of chemical fertiliser.	Azotobacter sp., Azospirillum sp.	(Kumar <i>et al.</i> 2019)
	Increase plant growth, yield and total antioxidant content.	B. amylolequifaciens BChi1 and Paraburkholderia fungorum BRRh	(Rahman <i>et al.</i> 2018)
Phytohormone production	Increase proline and protein levels in the leaves and improve chlorophyll content and leaf area.	Alcaligenes 637Ca and Pseudomonas 53/6	(Arikan <i>et al.</i> 2020)
Cell growth promotion	Increase strawberry fruit yield and fruit weight.	B. amyloliquefaciens IT45	(Mikiciuk <i>et al.</i> 2019)
	Increase percentage of strawberry germination.	B. amyloliquefaciens and Trichoderma harzianum	(Es-Soufi <i>et al.</i> 2020)

Rhizobacteria function as biofertilisers, providing essential nutrients through nutrient-solubilising 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.* 2020). Various rhizobacteria, such as *Azospirillum brasilense* and *Bacillus megaterium*, stimulate plant growth by solubilising phosphorus and potassium while synthesising indole-3-acetic acid (da Silva *et al.* 2022). They can significantly reduce inorganic fertiliser consumption, with studies reporting biomass increases and root parameter enhancements following their application (Hindersah *et al.* 2021).

Table 2 shows the impact of rhizobacteria on strawberry development and productivity in soilless substrates and Table 3 shows the impact of rhizobacteria on the quality of strawberries.

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

Impact	Species of rhizobacteria	References
Increase root length, stomatal conductance, leaf transpiration, CO_2 concentration and nutrient content, fertiliser dose.	Azospirillum brasilense and Bacillus fluminis	(da Silva <i>et al.</i> 2022)
Increase the biomass, growth, flowering and yield under saline treatment.	Bacillus methylotrophicus SMT38, Bacillus aryabhattai SMT48 and Bacillus licheniformis SMT51	(Redondo-Gómez et al. 2022)
Accelerate fruiting time and affected fruit dimensions.	Pedobacter sp. CC1	(Morais <i>et al.</i> 2019)
Produce more flower, enhance stomatal conductivity and decrease spider mite abundant .	Azotobacter chroococcum, Azospirillum brasilense and Pseudomonas brassicacearum	(Hosseini <i>et al.</i> 2022)
Increase the following growth parameters: Plant height, chlorophyll content, fresh and dry root weight.	Azospirillum sp. and Azotobacter sp.	(Rueda et al. 2016)
Increase growth and produce bioactive compound against pathogen <i>in vitro</i> .	Bacillus methylotrophicus	(Vicente-Hernández et al. 2019)
Increase fruit yield and inhibit pathogen growth.	Bacillus velezensis IALR619	(Mei et al. 2021)

Febby Fitriyani et al.

Table 3: The impact of rhizobacteria on strawberry quality.

Mechanism	Impact	Rhizobacteria	References
Humic acid and biofertiliser increase nutrient availability	Increase sweetness	Mixed biofertiliser: N ₂ -fixing and P-solubilising bacteria	(Hindersah <i>et al.</i> 2023)
Vermicompost and biofertiliser increase micronutrients (Mg, Fe, Co)	Increase total soluble solids (TSS)	Bacillus subtilis, Bacillus megaterium and Pseudomonas fluorescens	(Kilic et al. 2023)
Fulvic acid with biofertiliser as biostimulants	Increase TSS and vitamin C	Pseudomonas fluorescens	(Martínez-De La Cruz <i>et al. 2022</i>)
Rhizobacteria decrease population soil pathogen and increase phosphate availability	Maximize juice pH, increase TSS and total sugar, and decrease acidity	Pseudomonas florescence, Bacillus subtilis and Azotobacter chroococcum	(Kumar <i>et al.</i> 2020)
Rhizobacteria as biocontrol disease	Increase ascorbic acid and anthocyanin content	Bacillus sp. RCA3 and Bacillus sp. SYB101 or combination with Pseudomonas sp. MHA75	(Anuradha <i>et al.</i> 2019)
Production IAA phytohormones for improve fruit size and phenolic compounds	Increase fruit length, thickness, total phenolic, content and flavonoid	Pedobacter sp.	(Morais <i>et al.</i> 2019)
Increase micronutrient uptakes	Increase fruit size, sweetness and flavonoid compounds	Azospirillum brasilense	(Pii et al. 2018)

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 biofertiliser applications have significantly improved fruit quality and yield (Nisarga *et al.* 2020). Various bacteria strains from *Bacillus* sp. and *Pseudomonas* sp. are employed as biofertilisers 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 & 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 & 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 *et al.* 2018; Mozafari *et al.* 2018). Induced systemic resistance (ISR) and acquired systemic resistance (ASR) play crucial roles in biotic and abiotic resistance, respectively (Fig. 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 synthesised to respond to plant damage caused by pest attacks or pathogen colonisation. JA also induces a signalling 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 ISR (Ravanbakhsh *et al.* 2018). When a pathogen invades the plant, it also recognises the signalling 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 & Lim 2023).

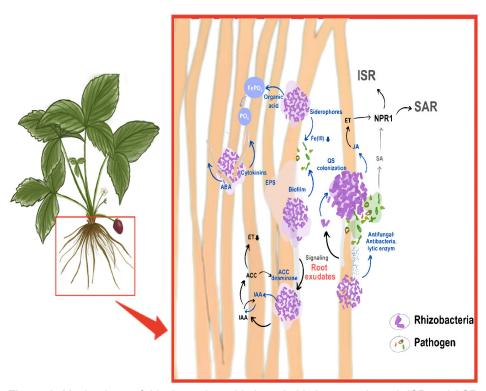


Figure 2: Mechanisms of rhizobacteria on biotic and abiotic stress through ISR and ASR.

Febby Fitriyani et al.

In response to drought stress, organisms accumulate osmolytes, including betaines, sugars, polyols, polyamines and proline (Ashraf & 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-solubilising 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 et al. 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 colonising the rhizosphere, they alleviate the detrimental effects by controlling plant disease and triggering immune responses (Abd-El-Kareem et al. 2021). Directly, rhizobacteria combat soil-borne pathogens by synthesising antimicrobial compounds such as antibiotics, siderophores, bacteriocin and volatile compounds (Raaijmakers et al. 2002; Subramanian & 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 synthesise 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 signalling (jasmonic acid and ethylene) of plants due to population of Tetranychus urticae by regulating the content of phenolics, flavonoids and

anthocyanins (Hosseini *et al.* 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.

Pathogen/ Diseases	Mechanisms	Species of rhizobacteria	References
Botrytis cinereal Gray mold	Indirect mechanism by induction of systemic resistance.	Bacillus methylotrophicus	(Vicente-Hernández et al. 2019)
Botrytis cinerea/Gray mold	Producing fungal antibiotic compounds.	Bacillus sp. and Pantoea sp.	(de Moura <i>et al.</i> 2021)
Colletotrichum gloeosporioides Cg58/ Colletotrichum crown rot	Antibiotic production.	Bacillus velezensis IALR619	(Mei <i>et al.</i> 2021)
Fusarium solani, Rhizoctonia solani and Macrophomina phaseolina/ Black rot	In vitro test: Antagonistic with unknown mechanisms. In field experiment: Increase peroxidase and chitinase activities in the leaves.	P. polymyxa and B. brevis	(Abd-El-Kareem et al. 2021)
Botrytis cinerea/Gray mold	Actinomycin production.	Streptomyces sp. sdu1201	(Yong et al. 2022)

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, solubilising phosphorus and potassium, producing phytohormones, and synthesising EPS. They also indirectly alleviate harsh conditions like drought and diseases, improving strawberry yield and quality. With low nutrient availability in tropical soil, N₂-fixing, phosphate-solubilising and potassium-solubilising 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 fertilisers, thus fostering environmental sustainability.

This literature review highlights the potential of various rhizobacteria to increase strawberry production and minimise chemical fertiliser 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.

ACKNOWLEDGEMENTS

The research was supported by the Padjadjaran Graduate Scholarship Programme of Universitas Padjadjaran, Indonesia, under grant number 1549/UN6.3.1/PT.00/2023.

AUTHORS' CONTRIBUTIONS

Febby Fitriyani: Conceptualised the review theme, conducted the literature search, wrote the initial draft, composed the outline of review article and collect the article research for various resources.

Reginawanti Hindersah: Conceptualised the review theme, conducted the literature search, wrote the initial draft, composed the outline of review article and collect the article research for various resources.

Etty Pratiwi: Composed the outline of review article and collect the article research for various resources.

Masako Akutsu: Composed the outline of review article and collect the article research for various resources.

Syariful Mubarok: 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.

REFERENCES

- Abd-El-Kareem F, Elshahawy I E and Abd-Elgawad M M M. (2021). Application of *Bacillus pumilus* isolates for management of black rot disease in strawberry. *Egyptian Journal of Biological Pest Control* 31(1): 25. https://doi.org/10.1186/s41938-021-00371-z
- Abdel-Gaied T G, Abd-El-Khair H, Youssef M M, El-Maaty S A and Mikhail M S. (2022). First report of strawberry bacterial leaf blight caused by *Pantoea ananatis* in Egypt. *Journal of Plant Protection Research* 62(2): 207–214. https://doi.org/10.24425/jppr.2022.141359
- Achor S, Aravis C, Heaney N, Odion E and Lin C. (2020). Response of organic acid-mobilized heavy metals in soils to biochar application. *Geoderma* 378: 114628. https://doi.org/10.1016/j.geoderma.2020.114628
- Adak N, Gubbuk H and Tetik N. (2018). Yield, quality and biochemical properties of various strawberry cultivars under water stress. *Journal of the Science of Food and Agriculture* 98(1): 304–311. https://doi.org/10.1002/jsfa.8471
- Anuradha, Goyal R K, Sindhu S S and Godara A K. (2019). Effect of PGPR on strawberry cultivation under greenhouse conditions. *Indian Journal of Horticulture* 76(3): 400–404. https://doi.org/10.5958/0974-0112.2019.00064.1

- Arikan Ş, İpek M, Eşitken A, Pırlak L, Dönmez M F and Turan M. (2020). Plant growth promoting rhizobacteria mitigate deleterious combined effects of salinity and lime in soil in strawberry plants. *Journal of Plant Nutrition* 43(13): 2028–2039. https:// doi.org/10.1080/01904167.2020.1766073
- Arora H, Sharma A, Poczai P, Sharma S, Haron F F, Gafur A and Sayyed R Z. (2022). Plant-Derived protectants in combating soil-borne fungal infections in tomato and chilli. *Journal of Fungi* 8(2): 213. https://doi.org/10.3390/jof8020213
- Ashraf M and Foolad M R. (2007). Roles of glycine betaine and proline in improving plant abiotic stress resistance. *Environmental and Experimental Botany* 59(2): 206–216. https://doi.org/10.1016/j.envexpbot.2005.12.006
- Azizoglu U. (2019). *Bacillus thuringiensis* as a biofertilizer and biostimulator: A mini-review of the little-known plant growth-promoting properties of Bt. *Current Microbiology* 76(11): 1379–1385. https://doi.org/10.1007/s00284-019-01705-9
- Batista M B and Dixon R. (2019). Manipulating nitrogen regulation in diazotrophic bacteria for agronomic benefit. *Biochemical Society Transactions* 47(2): 603–614. https://doi.org/10.1042/BST20180342
- Brunetti C, Saleem A R, Rocca G D, Emiliani G, De Carlo A, Balestrini R, Khalid A, Mahmood T and Centritto M. (2021). Effects of plant growth-promoting rhizobacteria strains producing ACC deaminase on photosynthesis, isoprene emission, ethylene formation and growth of *Mucuna pruriens* (L.) DC. in response to water deficit. *Journal of Biotechnology* 331(April): 53–62. https://doi.org/10.1016/j. ibiotec.2021.03.008
- Cade-Menun B J. (2017). Characterizing phosphorus forms in cropland soils with solution 31P-NMR: Past studies and future research needs. *Chemical and Biological Technologies in Agriculture* 4(1): 1–12. https://doi.org/10.1186/s40538-017-0098-4
- Carezzano M E, Strazzi F B A, Pérez V, Bogino P and Giordano W. (2023). Exopolysaccharides synthesized by rhizospheric bacteria: A review focused on their roles in protecting plants against stress. *Applied Microbiology* 3(4): 1249–1261. https://doi.org/10.3390/applmicrobiol3040086
- Chebotar V K, Chizhevskaya E P, Vorobyov N I, Bobkova V V, Pomyaksheva L V, Khomyakov Y V and Konovalov S N. (2022). The quality and productivity of strawberry (*Fragaria* × *Ananassa* Duch.) improved by the inoculation of PGPR *Bacillus velezensis* BS89 in field experiments. *Agronomy* 12(11): 2600. https://doi.org/10.3390/agronomy12112600
- Costa O Y A, Raaijmakers J M and Kuramae E E. (2018). Microbial extracellular polymeric substances: Ecological function and impact on soil aggregation. *Frontiers in Microbiology* 9: 1–14. https://doi.org/10.3389/fmicb.2018.01636
- da Silva L I, Oliveira I P D, Jesus E D C, Pereira M C, Pasqual M, Araújo R C D and Dória J. (2022). Fertilizer of the future: Beneficial bacteria promote strawberry growth and yield and may reduce the need for chemical fertilizer. *Agronomy* 12(10): 2465. https://doi.org/10.3390/agronomy12102465
- Dar A, Zahir Z A, Iqbal M, Mehmood A, Javed A, Hussain A, Bushra and Ahmad M. (2021). Efficacy of rhizobacterial exopolysaccharides in improving plant growth, physiology, and soil properties. *Environmental Monitoring and Assessment* 193(8): 515. https://doi.org/10.1007/s10661-021-09286-6
- de Andrade F M, de Assis Pereira T, Souza T P, Guimarães P H S, Martins A D, Schwan R F, Pasqual M and Dória J. (2019). Beneficial effects of inoculation of growth-promoting bacteria in strawberry. *Microbiological Research* 223–225(April): 120–128. https://doi.org/10.1016/j.micres.2019.04.005

- de Moura G G D, de Barros A V, Machado F, Martins A D, da Silva C M, Durango L G C, Forim M, Alves E, Pasqual M and Doria J. (2021). Endophytic bacteria from strawberry plants control gray mold in fruits via production of antifungal compounds against *Botrytis cinerea* L. *Microbiological Research* 251(May): 126793. https://doi.org/10.1016/j.micres.2021.126793
- de Moura G G D, de Barros A V, Machado F, da Silva Dambroz C M, Glienke C, Petters-Vandresen D A L, Alves E, Schwan R F, Pasqual M and Dória J. (2022). The friend within: Endophytic bacteria as a tool for sustainability in strawberry crops. *Microorganisms* 10(12): 2341. https://doi.org/10.3390/microorganisms10122341
- Dhanya B E, Athmika and Rekha P D. (2021). Characterization of an exopolysaccharide produced by *Enterobacter* sp. YU16-RN5 and its potential to alleviate cadmium induced cytotoxicity *in vitro*. *3 Biotech* 11(12): 1–11. https://doi.org/10.1007/s13205-021-03034-w
- dos Santos C F C and Echer F R. (2019). Interactive effects of nitrogen-fixing bacteria inoculation and nitrogen fertilization on soybean yield in unfavorable edaphoclimatic environments. *Scientific Reports* 9(1): 1–11. https://doi.org/10.1038/s41598-019-52131-7
- Drobek M, Cybulska J, Gałązka A, Feledyn-Szewczyk B, Marzec-Grządziel A, Sas-Paszt L, Gryta A, Trzciński P, Zdunek A and Frąc M. (2021). The use of interactions between microorganisms in strawberry cultivation (*Fragaria × Ananassa* Duch.). *Frontiers in Plant Science* 12(November): 780099. https://doi.org/10.3389/fpls.2021.780099
- du Preez C C and Burger R du T. (1988). Movement of ammonia plus ammonium from nitrogen fertilizers band placed in alkaline soils. *The South African Journal of Plant and Soil* 5: 51–56. https://doi.org/10.1080/02571862.1988.10634252
- Ducousso-Détrez A, Fontaine J, Sahraoui A L H and Hijri M. (2022). Diversity of phosphate chemical forms in soils and their contributions on soil microbial community structure changes. *Microorganisms* 10(3): 609. https://doi.org/10.3390/microorganisms10030609
- Es-Soufi R, Tahiri H, El Oualkadi A,Azaroual L, Martin P, Badoc A and Lamarti A. (2020). Evaluation of plant growth promoting ability of *Bacillus amyloliquefaciens* Bc2 and trichoderma harzianum TR in vivo. *Agricultural Sciences* 11(03): 247–259. https://doi.org/10.4236/as.2020.113016
- Fan R, Cockerton H M, Armitage A D, Bates H, Cascant-Lopez E, Antanaviciute L, Xu X, Hu X and Harrison R J. (2018). Vegetative compatibility groups partition variation in the virulence of *Verticillium dahliae* on strawberry. *PLoS ONE* 13(2): 1–21. https://doi.org/10.1371/journal.pone.0191824
- Frébortová J and Frébort I. (2021). Biochemical and structural aspects of cytokinin biosynthesis and degradation in bacteria. *Microorganisms* 9(6): 1314. https://doi.org/10.3390/microorganisms9061314
- Giri J. (2011). Glycinebetaine and abiotic stress tolerance in plants. *Plant Signaling & Behavior* 6(11): 1746–1751. https://doi.org/10.4161/psb.6.11.17801
- Grover M, Bodhankar S, Sharma A, Sharma P, Singh J and Nain L. (2021). PGPR mediated alterations in root traits: Way toward sustainable crop production. *Frontiers in Sustainable Food Systems* 4(January): 618230. https://doi.org/10.3389/fsufs.2020.618230
- Haerani N, Syam'un E, Rasyid B and Haring F. (2021). Isolation and characterization of N-fixing and IAA producing rhizobacteria from two rice field agro-ecosystems in South Sulawesi, Indonesia. *Biodiversitas* 22(5): 2497–2503. https://doi. org/10.13057/biodiv/d220506

- Hanyabui E, Apori S O, Frimpong K A, Atiah K, Abindaw T, Ali M, Asiamah J Y and Byalebeka J. (2020). Phosphorus sorption in tropical soils. *AIMS Agriculture and Food* 5(4): 599–616. https://doi.org/10.3934/agrfood.2020.4.599
- Haskett T L, Karunakaran R, Batista M B, Dixon R and Poole P S. (2022). Control of nitrogen fixation and ammonia excretion in *Azorhizobium caulinodans*. *PLoS Genetics* 18(6): 1–20. https://doi.org/10.1371/journal.pgen.1010276
- He M and Dijkstra F A. (2014). Drought effect on plant nitrogen and phosphorus a metaanalysis. *New Phytologist* 204: 924–931. https://doi.org/10.1111/nph.12952
- Hindersah R, Ayu R, Aini P, Setiawati M R, Simarmata T, Indrawibawa D and Akutsu M. (2023). Boosting strawberry yield and fruit sweetness with humic substances and biofertilizer in soiless cocopeat-based culture. *Jurnal Ilmiah Pertanian* 20(3): 1–11. https://doi.org/10.31849/jip.v20i3.13242
- Hindersah R, Purba P S J, Cahyaningrum D N, Nurbaity A, Kamaluddin N N and Akutsu M. (2022). Evaluation of strawberry seedling growth in various planting media amended with biofertilizer. KnE Life Sciences 2022: 358–367. https://doi.org/10.18502/kls.v7i3.11144
- Hindersah R, Rahmadina I, Fitriatin B N, Setiawati M R and Indrawibawa D. (2021). Microbescoated urea for reducing urea dose of strawberry early growth in soilless media. *Jordan Journal of Biological Sciences* 14(3): 593–599. https://doi.org/10.54319/ijbs/140328
- Hindersah R, Suryatmana P, Setiawati M R, Fitriatin B N, Nurbaity A and Simarmata T. (2019). Salinity resistance of azotobacter isolated from saline soil in West Java. In R Sayyed, M Reddy and S Antonius. (eds.), *Plant Growth Promoting Rhizobacteria* (*PGPR*): Prospects for sustainable agriculture. Singapore: Springer, 323–334. https://doi.org/10.1007/978-981-13-6790-8_25
- Hosseini A, Hosseini M and Schausberger P. (2022). Plant growth-promoting rhizobacteria enhance defense of strawberry plants against spider mites. *Frontiers in Plant Science* 12(January): 783578. https://doi.org/10.3389/fpls.2021.783578
- Jiao X, Takishita Y, Zhou G and Smith D L. (2021). Plant associated rhizobacteria for biocontrol and plant growth enhancement. Frontiers in Plant Science 12(March): 634796. https://doi.org/10.3389/fpls.2021.634796
- Khammayom N, Maruyama N and Chaichana C. (2022). The effect of climatic parameters on strawberry production in a small walk-in greenhouse. *AgriEngineering* 4(1): 104–121. https://doi.org/10.3390/agriengineering4010007
- Kilic N, Dasgan H Y and Gruda N S. (2023). A novel approach for organic strawberry cultivation: Vermicompost-based fertilization and microbial complementary nutrition. *Horticulturae* 9(6): 1–16. https://doi.org/10.3390/horticulturae9060642
- Kim T -J and Lim G -H. (2023). Salicylic acid and mobile regulators of systemic immunity in plants: Transport and metabolism. *Plants (Basel, Switzerland)* 12(5): 1013. https://doi.org/10.3390/plants12051013
- Koskey G, Mburu S W, Awino R, Njeru E M and Maingi J M. (2021). Potential use of beneficial microorganisms for soil amelioration, phytopathogen biocontrol, and sustainable crop production in smallholder agroecosystems. *Frontiers in Sustainable Food Systems* 5(April): 1–20. https://doi.org/10.3389/fsufs.2021.606308
- Kour D, Khan S S, Kaur T, Kour H, Singh G, Yadav A and Yadav A N. (2022). Drought adaptive microbes as bioinoculants for the horticultural crops. *Heliyon* 8(5): e09493. https://doi.org/10.1016/j.heliyon.2022.e09493

- Kumar P, Rakesh K, Hansra B S, Dubey N and Kumar A. (2022). Potting substrate effect on yield and quality of strawberry (*Fragaria × Ananassa*) in terrace gardening. *The Indian Journal of Agricultural Sciences* 92(5): 667–669. https://doi.org/10.56093/ ijas.v92i5.124805
- Kumar P, Sharma N, Sharma S and Gupta R. (2020). Rhizosphere stochiometry, fruit yield, quality attributes and growth response to PGPR transplant amendments in strawberry (*Fragaria × Ananassa* Duch.) growing on solarized soils. Scientia Horticulturae 265: 109215. https://doi.org/https://doi.org/10.1016/j.scienta.2020.109215
- Kumar S, Kundu M, Das A, Rakshit R, Siddiqui M W and Rani R. (2019). Substitution of mineral fertilizers with biofertilizer: An alternate to improve the growth, yield and functional biochemical properties of strawberry (*Fragaria* × *Ananassa* Duch.) cv. Camarosa. *Journal of Plant Nutrition* 42(15): 1818–1837. https://doi.org/10.1080/ 01904167.2019.1643363
- Le T T H, Jun S E and Kim G-T. (2019). Current perspectives on the effects of plant growth-promoting rhizobacteria. *Journal of Life Science* 29(11): 1281–1293.
- Levy-Booth D J, Prescott C E and Grayston S J. (2014). Microbial functional genes involved in nitrogen fixation, nitrification and denitrification in forest ecosystems. Soil Biology and Biochemistry 75: 11–25. https://doi.org/10.1016/j. soilbio.2014.03.021
- Liu W, Tan M, Qu P, Huo C, Liang W, Li R, Jia Y, Fan X and Cheng C. (2022). Use of *Piriformospora indica* to promote growth of strawberry daughter plants. *Horticulturae* 8(5): 1–11. https://doi.org/10.3390/horticulturae8050370
- Ma F, Yang X, Shi Z and Miao X. (2020). Novel crosstalk between ethylene- and jasmonic acid-pathway responses to a piercing–sucking insect in rice. *New Phytologist* 225(1): 474–487. https://doi.org/10.1111/nph.16111
- Martínez-De La Cruz S, González-Fuentes J A, Robledo-Olivo A, Mendoza-Villarreal R, Hernández-Pérez A, Dávila-Medina M D and Alvarado-Camarillo D. (2022). Humic substances and rhizobacteria enhance the yield, physiology and quality of strawberries. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca* 50(1): 12578. https://doi.org/10.15835/nbha50112578
- Maurya J K, Singh J P, Tomar S and Kumar R. (2017). Optimization of NPK fertilizers for higher yield and quality of strawberry (Gragaria x Ananassa Duch.) fruits. *International Journal of Current Microbiology and Applied Sciences* 6(8): 1534–1538. https://doi.org/10.20546/ijcmas.2017.609.188
- Meena V S. (ed.) (2018). Role of rhizospheric microbes in soil: Volume 1: Stress management and agricultural sustainability. Singapore: Springer Nature Singapore Pte. Ltd. https://doi.org/10.1007/978-981-10-8402-7
- Mei C, Amaradasa B S, Chretien R L, Liu D, Snead G, Samtani J B and Lowman S. (2021). A potential application of endophytic bacteria in strawberry production. *Horticulturae* 7(11): 1–11. https://doi.org/10.3390/horticulturae7110504
- Mendes-Santos R, Kandasamy S and Cid-Rigobelo E. (2017). Ammonium and nitrate levels of soil inoculated with *Azospirillum brasilense* in maize. *African Journal of Agricultural Research* 12(11): 863–870. https://doi.org/10.5897/ajar2016.11800
- Menezes-Blackburn D, Giles C, Darch T, George T S, Blackwell M, Stutter M, Shand C, Lumsdon D, Cooper P, Wendler R, Brown L, Almeida D S, Wearing C, Zhang H and Haygarth P M. (2018). Opportunities for mobilizing recalcitrant phosphorus from agricultural soils: A review. *Plant and Soil* 427(1): 5–16. https://doi.org/10.1007/s11104-017-3362-2

- Menezes-Blackburn D, Paredes C, Zhang H, Giles C D, Darch T, Stutter M, George T S, Shand C, Lumsdon D, Cooper P, Wendler R, Brown L, Blackwell M, Wearing C and Haygarth P M. (2016). Organic acids regulation of chemical–microbial phosphorus transformations in soils. *Environmental Science & Technology* 50(21): 11521–11531. https://doi.org/10.1021/acs.est.6b03017
- Mikiciuk G, Sas-Paszt L, Mikiciuk M, Derkowska E, Trzciński P, Głuszek S, Lisek A, Wera-Bryl S and Rudnicka J. (2019). Mycorrhizal frequency, physiological parameters, and yield of strawberry plants inoculated with endomycorrhizal fungi and rhizosphere bacteria. Mycorrhiza 29(5): 489–501. https://doi.org/10.1007/s00572-019-00905-2
- Mishra S, Roychowdhury R, Ray S, Hada A, Kumar A, Sarker U, Aftab T and Das R. (2024). Salicylic acid (SA)-mediated plant immunity against biotic stresses: An insight on molecular components and signaling mechanism. *Plant Stress* 11: 100427. https://doi.org/10.1016/j.stress.2024.100427
- Molina-Favero C, Creus C M, Simontacchi M, Puntarulo S and Lamattina L. (2008). Aerobic nitric oxide production by *Azospirillum brasilense* Sp245 and its influence on root architecture in tomato. *Molecular Plant-Microbe Interactions : MPMI* 21(7): 1001–1009. https://doi.org/10.1094/MPMI-21-7-1001
- Morais M C, Mucha A, Ferreira H, Gonçalves B, Bacelar E and Marques G. (2019). Comparative study of plant growth-promoting bacteria on the physiology, growth and fruit quality of strawberry. *Journal of the Science of Food and Agriculture* 99(12): 5341–5349. https://doi.org/10.1002/jsfa.9773
- Morkeliūnė A, Rasiukevičiūtė N and Valiuškaitė A. (2021). Meteorological conditions in a temperate climate for *Colletotrichum acutatum*, strawberry pathogen distribution and susceptibility of different cultivars to anthracnose. *Agriculture* 11(1): 80. https://doi.org/10.3390/agriculture11010080
- Mozafari A, Havas F and Ghaderi N. (2018). Application of iron nanoparticles and salicylic acid in *in vitro* culture of strawberries (*Fragaria* × *Ananassa* Duch.) to cope with drought stress. *Plant Cell, Tissue and Organ Culture (PCTOC)* 132: 511–523. https://doi.org/10.1007/s11240-017-1347-8
- Murthy B N S and Pramanick K K. (2014). Strawberry cultivation in mild-tropics: Prospects and challenges from diseases' perspective. *Acta Horticulturae* 1049: 151–159. https://doi.org/10.17660/ActaHortic.2014.1049.13
- Naamala J and Smith D L. (2020). Relevance of plant growth promoting microorganisms and their derived compounds, in the face of climate change. *Agronomy* 10(8): 1179. https://doi.org/10.3390/agronomy10081179
- Nam J H, Thibodeau A, Qian Y L, Qian M C and Park S H. (2023). Multidisciplinary evaluation of plant growth promoting rhizobacteria on soil microbiome and strawberry quality. *AMB Express* 13(1): 18. https://doi.org/10.1186/s13568-023-01524-z
- Naraian R and Kumari S. (2017). Microbial production of organic acids. In V K Gupta, H Treichel, V O Shapaval, L A de Oliveira and M G Tuohy (eds.), *Microbial functional foods and nutraceuticals*. Hoboken, NJ: John Wiley and Sons Ltd., 93–121. https://doi.org/10.1002/9781119048961.ch5
- Naseem M, Chaudhry A N, Jilani G, Alam T, Naz F, Ullah R, Zahoor M, Zaman S and Sohail. (2024). Exopolysaccharide-producing bacterial cultures of *Bacillus cereus* and *Pseudomonas aeruginosa* in soil augment water retention and maize growth. *Heliyon* 10(4): e26104. https://doi.org/10.1016/j.heliyon.2024.e26104
- Negi Y K, Sajwan P, Uniyal S and Mishra A C. (2021). Enhancement in yield and nutritive qualities of strawberry fruits by the application of organic manures and biofertilizers. *Scientia Horticulturae* 283: 110038. https://doi.org/10.1016/j.scienta.2021.110038

- Nett R S, Montanares M, Marcassa A, Lu X, Nagel R, Charles T C, Hedden P, Rojas M C and Peters R J. (2017). Elucidation of gibberellin biosynthesis in bacteria reveals convergent evolution. *Nature Chemical Biology* 13(1): 69–74. https://doi.org/10.1038/nchembio.2232
- Nisarga G, Madaiah D, Dinesh Kumar M and Yogananda H S. (2020). Influence of fertigation and liquid plant growth promoting rhizo microbial consortia on yield of strawberry (Fragaria x Ananassa Duch.) under naturally ventilated polyhouse. *International Journal of Current Microbiology and Applied Sciences* 9(8): 256–262. https://doi.org/10.20546/ijcmas.2020.908.030
- Olagoke F K, Bettermann A, Nguyen P T B, Redmile-Gordon M, Babin D, Smalla K, Nesme J, Sørensen S J, Kalbitz K and Vogel C. (2022). Importance of substrate quality and clay content on microbial extracellular polymeric substances production and aggregate stability in soils. *Biology and Fertility of Soils* 58(4): 435–457. https://doi.org/10.1007/s00374-022-01632-1
- Olaniyan F T, Alori E T, Adekiya A O, Ayorinde B B, Daramola F Y, Osemwegie O O and Babalola O O. (2022). The use of soil microbial potassium solubilizers in potassium nutrient availability in soil and its dynamics. *Annals of Microbiology* 72(1): 45. https://doi.org/10.1186/s13213-022-01701-8
- Paliwoda D, Mikiciuk G, Mikiciuk M, Kisiel A, Sas-Paszt L and Miller T. (2022). Effects of rhizosphere bacteria on strawberry plants (*Fragaria* × *Ananassa* Duch.) under water deficit. *International Journal of Molecular Sciences* 23(18): 10449. https://doi.org/10.3390/ijms231810449
- Park Y, Solhtalab M, Thongsomboon W and Aristilde L. (2022). Strategies of organic phosphorus recycling by soil bacteria: Acquisition, metabolism, and regulation. *Environmental Microbiology Reports* 14(1): 3–24. https://doi.org/10.1111/1758-2229.13040
- Paul S, Parvez S S, Goswami A and Banik A. (2024). Exopolysaccharides from agriculturally important microorganisms: Conferring soil nutrient status and plant health. *International Journal of Biological Macromolecules* 262: 129954. https://doi. org/10.1016/j.ijbiomac.2024.129954
- Piamonte M K, Asio V and Lina S. (2014). Morpho-physical and chemical characteristics of strongly weathered soils in Silago, Southern Leyte, Philippines. *Annals of Tropical Research* 36(2): 115–147. https://doi.org/10.32945/atr3627.2014
- Pii Y, Graf H, Valentinuzzi F, Cesco S and Mimmo T. (2018). The effects of plant growth-promoting rhizobacteria (PGPR) on the growth and quality of strawberries. *Acta Horticulturae* 1217: 231–238. https://doi.org/10.17660/ActaHortic.2018.1217.29
- Qian L, Ye X, Xiao J, Lin S, Wang H, Liu Z, Ma Y, Yang L, Zhang Z and Wu L. (2022). Nitrogen concentration acting as an environmental signal regulates cyanobacterial EPS excretion. *Chemosphere* 291: 132878. https://doi.org/10.1016/j. chemosphere.2021.132878
- Quan A C Y, Nissom P M and Tung T L. (2022). A review on potential of plant growth promoting microorganisms in silviculture of neolamarckia cadamba to Industrial Timber Production Areas (ITPAs) in Malaysia. *Chiang Mai University Journal of Natural Sciences* 21(2): 1–12. https://doi.org/10.12982/CMUJNS.2022.027
- Raaijmakers J M, Vlami M and de Souza J T. (2002). Antibiotic production by bacterial biocontrol agents. *Antonie van Leeuwenhoek* 81(1–4): 537–547. https://doi.org/10.1023/a:1020501420831

- Rahman M, Rahman M, As Sabir A, Mukta J A, Khan M M A, Mohi-Ud-Din M, Miah M G and Islam M T. (2018). Plant probiotic bacteria bacillus and paraburkholderia improve growth, yield and content of antioxidants in strawberry fruit. *Scientific Reports* 8(1): 1–11. https://doi.org/10.1038/s41598-018-20235-1
- Rasulov B A, Yili A and Aisa H A. (2015). Removal of silver from aqueous solution by *Azotobacter chroococcum*; XU1 biomass and exopolysaccharide. *Advances in Microbiology* 05(03): 198–203. https://doi.org/10.4236/aim.2015.53019
- Ravanbakhsh M, Sasidharan R, Voesenek L A C J, Kowalchuk G A and Jousset A. (2018). Microbial modulation of plant ethylene signaling: Ecological and evolutionary consequences. *Microbiome* 6(1): 52. https://doi.org/10.1186/s40168-018-0436-1
- Redondo-Gómez S, García-López J V, Mesa-Marín J, Pajuelo E, Rodriguez-Llorente I D and Mateos-Naranjo E. (2022). Synergistic effect of plant-growth-promoting rhizobacteria improves strawberry growth and flowering with soil salinization and increased atmospheric CO₂ levels and temperature conditions. *Agronomy* 12(9): 2082. https://doi.org/10.3390/agronomy12092082
- Rueda D, Valencia G, Soria N, Rueda B B, Manjunatha B, Kundapur R R and Selvanayagam M. (2016). Effect of Azospirillum spp. and Azotobacter spp. on the growth and yield of strawberry (Fragaria vesca) in hydroponic system under different nitrogen levels. Journal of Applied Pharmaceutical Science 6(1): 048– 054. https://doi.org/10.7324/JAPS.2016.600108
- Ryu C M, Farag M A, Pare P W and Kloepper J W. (2005). Invisible signals from the underground: Bacterial volatiles elicit plant growth promotion and induce systemic resistance. *Plant Pathology Journal* 21(1): 7–12. https://doi.org/10.5423/ PPJ.2005.21.1.007
- Saeed Q, Wang X, Haider F U, Kučerik J, Mumtaz M Z, Jiri Holatko, Naseem M, Kintl A, Ejaz M, Naveed M, Brtnicky M and Mustafa A. (2021). Rhizosphere bacteria in plant growth promotion, biocontrol, and bioremediation of contaminated sites: A comprehensive review of effects and mechanisms. *International Journal of Molecular Sciences* 22(19): 10529. https://doi.org/10.3390/ijms221910529
- Sandhya V and Ali S Z. (2015). The production of exopolysaccharide by *Pseudomonas putida* GAP-P45 under various abiotic stress conditions and its role in soil aggregation. *Microbiology (Russian Federation)* 84(4): 512–519. https://doi.org/10.1134/S0026261715040153
- Schwember A R, Schulze J, del Pozo A and Cabeza R A. (2019). Regulation of symbiotic nitrogen fixation in legume root nodules. *Plants* 8(9): 333. https://doi.org/10.3390/plants8090333
- Sharma P, Singh A, Kahlon C S, Brar A S, Grover K K, Dia M and Steiner R L. (2018). The role of cover crops towards sustainable soil health and agriculture: A review paper. *American Journal of Plant Sciences* 9: 1935–1951.
- Simpson D. (2018). The economic importance of strawberry crops. In T Hytönen, J Graham and R Harrison (eds.), *The genomes of rosaceous berries and their wild relatives: Compendium of plant genomes*. Cham: Springer, 1–7. https://doi.org/10.1007/978-3-319-76020-9 1
- Singh R K, Singh P, Li H B, Song Q Q, Guo D J, Solanki M K, Verma K K, Malviya M K, Song X -P, Lakshmanan P, Yang L-T and Li Y-R. (2020). Diversity of nitrogen-fixing rhizobacteria associated with sugarcane: A comprehensive study of plant-microbe interactions for growth enhancement in *Saccharum* spp. *BMC Plant Biology* 20(1): 1–21. https://doi.org/10.1186/s12870-020-02400-9

- Sivapriya S L. (2018). Selection of efficient EPS producing and cyst forming Azotobacter isolates under stress condition. *International Journal of Science and Research* (*IJSR*) 7(6): 59–65. https://doi.org/10.21275/ART20183061
- Subramanian S and Smith D L. (2015). Bacteriocins from the rhizosphere microbiome From an agriculture perspective. *Frontiers in Plant Science* 6: 1–7. https://doi.org/10.3389/fpls.2015.00909
- Sun F, Song C, Wang M, Lai D Y F, Tariq A, Zeng F, Zhong Q, Wang F, Li Z and Peng C. (2020). Long-term increase in rainfall decreases soil organic phosphorus decomposition in tropical forests. Soil Biology and Biochemistry 151(October): 108056. https://doi.org/10.1016/j.soilbio.2020.108056
- Tang J, Li Y, Zhang L, Mu J, Jiang Y, Fu H, Zhang Y, Cui H, Yu X and Ye Z. (2023). Biosynthetic pathways and functions of Indole-3-Acetic acid in microorganisms. *Microorganisms* 11(8): 2077. https://doi.org/10.3390/microorganisms11082077
- Timmusk S, El-Daim I A A, Copolovici L, Tanilas T, Kännaste A, Behers L, Nevo E, Seisenbaeva G, Stenström E and Niinemets U. (2014). Drought-tolerance of wheat improved by rhizosphere bacteria from harsh environments: Enhanced biomass production and reduced emissions of stress volatiles. *PLoS ONE* 9(5): e96086. https://doi.org/10.1371/journal.pone.0096086
- Vega A, Delgado N and Handford M. (2022). Increasing heavy metal tolerance by the exogenous application of organic acids. *International Journal of Molecular Sciences* 23(10): 5438. https://doi.org/10.3390/ijms23105438
- Vicente-Hernández A, Salgado-Garciglia R, Valencia-Cantero E, Ramírez-Ordorica A, Hernández-García A, García-Juárez P and Macías-Rodríguez L. (2019). Bacillus methylotrophicus M4-96 stimulates the growth of strawberry (*Fragaria* × *Ananassa* 'Aromas') plants in vitro and slows Botrytis cinerea infection by two different methods of interaction. *Journal of Plant Growth Regulation* 38(3): 765–777. https://doi.org/10.1007/s00344-018-9888-6
- Vikram K V, Meena S L, Kumar S, Ranjan R, Nivetha N and Paul S. (2022). Influence of medium-term application of rhizobacteria on mustard yield and soil properties under different irrigation systems. *Rhizosphere* 24(October): 100608. https://doi. org/10.1016/j.rhisph.2022.100608
- Vlassi A, Nesler A, Perazzolli M, Lazazzara V, Büschl C, Parich A, Puopolo G and Schuhmacher R. (2020). Volatile Organic compounds from Lysobacter capsici AZ78 as potential candidates for biological control of soilborne plant pathogens. Frontiers in Microbiology 11(August): 1–11. https://doi.org/10.3389/fmicb.2020.01748
- Yang R, Liu P, Ye W, Chen Y, Wei D, Qiao C, Zhou B and Xiao J. (2024). Biological control of root rot of strawberry by *Bacillus amyloliquefaciens* strains CMS5 and CMR12. *Journal of Fungi* 10(6): 1–19. https://doi.org/10.3390/jof10060410
- Yong D, Li Y, Gong K, Yu Y, Zhao S, Duan Q, Ren C, et al. (2022). Biocontrol of strawberry gray mold caused by Botrytis cinerea with the termite associated Streptomyces sp. Sdu1201 and Actinomycin D. Frontiers in Microbiology 13(November): 1–14. https://doi.org/10.3389/fmicb.2022.1051730
- Zahedi S M, Hosseini M S, Hoveizeh N F, Kadkhodaei S and Vaculík M. (2023). Comparative morphological, physiological and molecular analyses of drought-stressed strawberry plants affected by SiO2 and SiO2-NPs foliar spray. *Scientia Horticulturae* 309: 111686. https://doi.org/10.1016/j.scienta.2022.111686
- Zhang M, Peacock C L, Cai P, Xiao K Q, Qu C, Wu Y and Huang Q. (2021). Selective retention of extracellular polymeric substances induced by adsorption to and coprecipitation with ferrihydrite. *Geochimica et Cosmochimica Acta* 299: 15–34. https://doi.org/10.1016/j.gca.2021.02.015

- Zhao Y, Liang H, Zhang J, Chen Y, Dhital Y P, Zhao T and Wang Z. (2024). Isolation and characterization of Potassium-Solubilizing Rhizobacteria (KSR) promoting cotton growth in saline–sodic regions. *Microorganisms* 12: 1474. https://doi.org/10.3390/microorganisms12071474
- Zhong Z, Chen Z, Xu Y, Ren C, Yang G, Han X, Ren G and Feng Y. (2018). Relationship between soil organic carbon stocks and clay content under different climatic conditions in central China. *Forests* 9: 598. https://doi.org/10.3390/f9100598