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Rhizobacteria as a Potential Microbial Agents for Suppression of Emerging Nematode Diseases in Plants

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ABSTRACT

The increasing limitations and risks associated with synthetic nematicides have intensified interest in rhizobacteria as sustainable alternatives for managing plant-parasitic nematodes. This review synthesizes current advances in understanding rhizobacteria-plant-nematode interactions with a specific focus on mechanistic insights rather than descriptive compilation. It highlights key genera such as *Bacillus*, *Pseudomonas*, and *Streptomyces*, which suppress nematodes through multiple mechanisms including production of nematicidal metabolites, modulation of root exudates, competition in the rhizosphere, and induction of systemic resistance via jasmonic acid and salicylic acid signaling pathways. Particular emphasis is placed on emerging concepts such as rhizobacteria-mediated priming, signaling cross-talk, and interference with nematode host recognition. The review also critically examines current limitations, including inconsistent field performance, gaps in mechanistic understanding, and challenges in formulation and large-scale application. By integrating recent findings and identifying key knowledge gaps, this work provides a clearer conceptual framework and outlines future research directions for developing effective rhizobacteria-based strategies for sustainable nematode management.

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1. Introduction

Shrinking agricultural land, rapid population growth, and increasing pest pressure pose major challenges to global food security [1]. Among biotic constraints, plant-parasitic nematodes (PPNs) are particularly damaging due to their wide host range, hidden soil habitat, and ability to interact with other pathogens to form complex disease syndromes [2, 3]. Globally, PPNs are estimated to cause yield losses of about 12.3% across major crops, with higher impacts in developing regions, resulting in substantial economic losses [2, 4]. In India, their economic burden is also significant, with notable damage reported in both field and horticultural crops [5]. Among PPNs, root-knot nematodes (*Meloidogyne* spp.) are the most destructive, contributing a major share of total losses, while species such as *M. graminicola*, *Heterodera avenae*, and *Globodera* spp. further aggravate crop productivity constraints in specific agro-ecosystems [5, 6].

Conventional management of PPNs relies heavily on chemical nematicides; however, their widespread use raises serious concerns regarding environmental safety, human health, and regulatory restrictions [7]. Consequently, there is a growing shift toward sustainable alternatives, particularly biological control strategies that are eco-friendly and compatible with integrated pest management systems [8, 9]. Among these, rhizosphere-associated microorganisms have emerged as key regulators of soil health and nematode populations due to their diverse functional roles [10].

Rhizobacteria, in particular, establish intimate associations with plant roots and influence plant–nematode interactions through multiple direct and indirect mechanisms, including production of bioactive metabolites, competition in the rhizosphere, and induction of plant defense responses [11, 12]. Although numerous studies have documented their potential against nematodes such as *Meloidogyne*, *Heterodera*, and *Rotylenchulus* [10, 13], the underlying mechanisms, signaling pathways, and consistency of field performance remain insufficiently understood.

In this context, the present review aims to provide a focused synthesis of rhizobacterial diversity and their interactions with host plants and nematodes, with particular emphasis on mechanistic insights, signaling cross-talk, and emerging concepts such as induced resistance and disruption of host recognition. Furthermore, it identifies key research gaps and challenges in translating laboratory findings into field applications, thereby offering a clearer framework for developing effective rhizobacteria-based strategies for sustainable nematode management.

2. Rhizobacteria and the Plant Rhizosphere

The rhizosphere denotes the narrow zone of soil directly influenced by plant roots and typically supports diverse microbial communities [12]. Bacteria inhabiting this region are termed rhizobacteria, and their influence on plant development can vary from detrimental or neutral to extremely advantageous [12]. These microorganisms form a highly varied and complex group actively involved in rhizosphere biological processes [14].

Plant roots critically determine the microbial diversity and functional dynamics of this zone [15]. They offer physical support to soil structure and enable water and mineral absorption [16]. The metabolic activity of rhizosphere bacteria is heavily shaped by nutrient-dense root exudates [17]. These exudates contain numerous compounds, including amino acids, organic acids, oligosaccharides, sugars, vitamins, nucleotides, flavonoids, enzymes, hormones, volatile substances, phenolic compounds, mucilage, carbohydrates, and various secondary products. This chemically complex mixture energizes the biological processes occurring within the rhizosphere [17].

3. Interactions Among Rhizobacteria, Plants, and Nematodes

Rhizosphere soil constitutes an exceptionally favorable environment containing rich microbial diversity, including bacteria, fungi, viruses, protozoa, and nematodes [18]. Research indicates that plants release approximately 30% of their fixed carbon into the rhizosphere [19]. This organic carbon serves as the primary energy source fueling microbial activity, resulting in bacterial densities roughly 60 times greater and fungal populations about 12 times higher in rhizosphere soil compared to bulk soil [18]. Due to this abundant microbial community, the rhizosphere attracts large numbers of bacteria-feeding and fungi-feeding nematodes [18].

Root exudate compounds further increase the rhizosphere's attractiveness, drawing plant-parasitic nematodes toward roots and creating conditions for complex microbial-PPN interactions [20]. Although PPNs are obligate parasites requiring host roots for survival, their journey through the rhizosphere exposes them to numerous soil microorganisms, including both plant pathogens and beneficial species [21]. Within this highly dynamic environment, three-way relationships develop among microbes, PPNs, and free-living nematodes [9]. These interactions can produce antagonistic effects on PPNs while benefiting the host plant, thus determining the ecological characteristics of the belowground ecosystem [22].

4. Antagonistic Rhizobacteria

Rhizobacteria contribute significantly to plant growth enhancement through the synthesis of growth regulators, improved nutrient accessibility, and activation of resistance mechanisms against soilborne pathogens [23]. Various rhizobacterial groups have been characterized and recorded from crop rhizospheres using molecular techniques (Table **1**) [24]. Specific nematicidal rhizobacterial strains active against particular nematode species have also been documented (Table **2**) [25]. These microorganisms show strong potential for development as commercial biopesticides [9]. Consequently, rhizobacteria hold considerable importance in plant-parasitic nematode management and represent an essential component of integrated pest management programs [8].

5. Antagonistic Rhizobacteria for Nematode Suppression

Many antagonistic microbial communities include endophytic organisms residing in agricultural crop rhizospheres [9]. The rhizosphere microbial flora functions as an initial protective barrier against various pathogens, including nematodes, giving it substantial value for biological nematode control [12]. These rhizobacterial strains also help preserve ecological equilibrium since they can survive in soil for prolonged periods and generate "suppressive soils" that inhibit plant-parasitic nematodes and other pathogens through their antagonistic properties [22].

Rhizobacterial antagonists typically fall into three main categories: epiphytic bacteria (living on root surfaces), endophytic bacteria (living inside plant tissues), and endoparasitic bacteria (infecting nematodes directly) [8]. These microorganisms operate through various mechanisms including parasitism, resource competition, antibiosis, and the triggering of systemic acquired resistance (SAR) and induced systemic resistance (ISR) against PPNs [8].

6. Mechanisms of Rhizobacterial Action Against Nematodes

Rhizobacteria interact with plant-parasitic nematodes through multiple pathways within the rhizosphere and employ various strategies to reduce pest populations (Table **3**) [26]. Nematode suppression mechanisms fall broadly into two categories: direct antagonism and indirect antagonism [21]. Direct antagonism encompasses antibiosis, production of cell-wall-degrading enzymes, toxins, and other bioactive metabolites [26]. Indirect antagonism involves modification of host root exudates, production of repellent compounds that disrupt host recognition, promotion of plant development through phytohormone synthesis (auxins, cytokinins, ethylene, abscisic acid, and other growth regulators), siderophore production, and improved plant nutrient acquisition [26]. Additionally, these rhizobacteria contribute to nitrogen fixation, phosphate solubilization, and activation of host systemic resistance, thereby boosting plant tolerance to nematode-induced stress [26, 27].

7. Direct Antagonism

7.1. Antibiosis

Antibiosis represents a crucial mechanism microorganisms employ to combat diseases [26]. Antagonistic rhizobacteria play a central role in this process by generating toxins, secondary metabolites, and antibiotic enzymes that suppress plant-parasitic nematodes [26]. These microbial activities can inhibit various nematode life stages, including egg hatching, juvenile development, survival, and reproduction [26]. The secondary metabolite 2,4-diacetylphloroglucinol produced by *Pseudomonas fluorescens* reportedly reduces cyst nematode populations [28]. Furthermore, ammonia generated during nitrogen-rich organic matter decomposition (ammonification) exhibits toxicity to nematodes [28]. Certain rhizobacteria also produce hydrogen cyanamide, which demonstrates antagonistic activity against soilborne plant pathogens and nematodes.

Table 1: Metagenomic analysis of taxonomic composition of rhizobacteria from different host plants (Rhizosphere, Endosphere).

S. No.	Plant/Crop	Rhizosphere	Endosphere	Sequencing Technique Used	Dominant Species	Ref.
1	Para grass (*Urochloa mutica*)	+++	-	16S rRNA	*Bacillus*, *Chloroflexi*, *Microcoleus Clostridium Caldilinea*	[24]
2	Wheat (*Triticum aestivum*)	+++	---	16S rRNA	*Achromobacter, Clostridia, Cellulomonas, Bacillus, Microbacterium*	[62]
3	Maize (*Zea mays* L.)	+++		16S rRNA variable gene (V4–V5)	*Acidobacteria, Gemmatimonas Rhodoferax*	[63]
4	*Taxus cuspidate* var. Nana	+++		16S rRNA	*Actinobacteria, Chloroflexi*	[64]
5	Aloe vera (*Aloe barbadensi*)	+++	+++	16S rRNA variable gene (V3–V4)	*Proteobacteria, Firmicutes, Actinobacteria, Bacteriodetes*	[65]
6	Rice (*Oryzaesativa*)	+++		16S rRNA gene sequencing	*Geodermatophilus Actinokineospora, Actinoplanes, Streptomyces, Kocuria*	[66]
7	*Triticumaestivum* (Wheat)	+++		16S rRNA gene sequencing	*Azoarcus, Balneimonas, Bradyrhizobium, Gemmatimonas, Lysobacter*	[67]
8	Soybean (*Glycine max*)	+++		16S rRNA gene sequencing	*Bacillus, Bradyrhizobium rhizobium, Stenotrophomonas, Streptomyces*	[68]
9	Lettuce (*Lactucasativa*)	+++		16S rRNA gene sequencing	*Alkanindiges, Sphingomonas, Burkholderia, Novosphingobium, Sphingobium*	[69]
10	Salix (Willow)	+++		16S rRNA gene sequencing	*Pseudomonas, Sphingomonasyanoikuyae, Staphylococcus*	[70]
11	*Arabidopsis thaliana* (Thale cress)	+++		16S rRNA gene sequencing	*Arthrobacter, Kineosporiaceae, Flavobacterium, Massilia*	[15]
12	*Arabidopsis thaliana* (Thalecress)	+++	+++	16S rRNA. Variable Gene (V5–V6)	*Acidobacteria, Planctomycetes, Proteobacteria*	[16]
13	*Pennisetum*		+++	BOX-PCR ,16S rRNA and nifH sequences	*Azospirillumbrasilense, Gluconacetobacterdi azotrophicus*	[71]
14	*Oryzasativa* (Cultivated Rice)	+++			*Metaproteogenomic approach* *Actinobacteria, Proteobacteria*	[72]
15	*Populusdeltoides* *(*Poplar*)*	+++	+++		*Acidobacteria, Proteobacteria*	[73]
16	Sugarcane		+++	16S rRNA gene sequencing	*Citrobacter, Enterobacter, Pantoea, Klebsiella, Erwinia, Pseudomonas* sp.	[74]
17	Poplar *(Populus deltoides)*	+++			*Shotgun metagenomics* *P. putida*	[75]
18	*Avenafatua* (wild oat)	+++		16S rRNA Microarray (Phylochip)	*Actinobacteria, Firmicutes, Proteobacteria*	[17]

Table 2: List of rhizobacteria on plant parasitic nematodes control.

S. No.	Rhizobacteria Strains	Crops	Nematodes	Ref.
1	*Bacillus subtilis*	Tomato	*Rotylenchulus reniformis*	[25]
2	*Azotobacterchroococcum*	Tomato	*Meloidogyne incognita*	[76]
3	*Azotobacterchroococcum*	Brinjal	*Meloidogyne javanica*	[77]
4	*Pseudomonads stutzeri*	Turmeric	*Meloidogyne incognita*	[78]
5	*Pseudomonads fluorescens* + oil cakes	Carrot & Okra	*Rotylenchulus reniformis, M. incognita*	[79, 80]
6	*Pseudomonads fluorescens* & *R. leguminosarum*	Bean	*Meloidogyne javanica*	[81]
7	*Pseudomonads putida, Serratiamarcescens, B. amyloliquefaciens, B. subtilis* & *B. cereus*	Tomato	*Meloidogyne incognita*	[82]
9	*Pseudomonads fluorescent*		*Heterodera cruciferae*	[83]
10	*Bacillus* sp.	Tomato & pepper	*Meloidogyne incognita*	[84]
11	*Bacillus velezensis* and *Bacillus mojavensis*	Soybean	*Heterodera glycines*	[58]
12	*Paenibacilluspolymyxa* & *P. lentimorbus*	Tomato	*Meloidogyne incognita*	[85]
13	*Bacillus sp., Azotobacter sp., P. putida & P. fluorescens*	Tomato	*Meloidogyne incognita*	[86]
14	*Bacillus* consortium	Papaya	*Meloidogyne incognita*	[87]
15	*Bacillus firmus*	Corn, cotton, sorghum, soybean, sugar beet	*Heterodera* sp., *Meloidogyne* sp., *Pratylenchus* sp.	[88]
16	*Pasteuria*sp.	Cotton	*Rotylenchusreniformi*	[89]
17	*P. putida* & *P. alcaligenes*	Chickpea	*Meloidogyne incognita*	[90]
18	*Bacillus amyloliquefaciens*	Tomato	*Meloidogyne incognita*	[91]
19	*Rhizobium etli*	Tomato	*Meloidogyne incognita*	[92]
20	*Pseudomonas oryzihabitans*	Potato	*Globoderarostochiensis*	[93]
21	*Rhizobium etli*	Potato	*Globoderapallida*	[42]
22	*Bacillus subtilis*	Carrot	*Meloidogyne incognita*	[59]
23	*Bacillus tequilensis* and *Bacillus flexus*	Basil	*Meloidogyne incognita*	[60]
24	*Streptomyces* sp.	Eggplants	*M. incognita*	[51]
25	*Stenotrophomonas maltophilia, B. mycoides* and *Pseudomonas* sp.	Potato	*Paratrichodoruspachydermus* & *Trichodorusprimitivus*	[32]
26	*Bacillus subtilis*	Banana	*M. incognita*, *P. coffeae, R. similis* & *H. multicinctus*	[94]
27	*P. aeruginosa*	Mungbean	*Meloidogyne* sp.	[30]
28	*P. aeruginosa* and *Bacillus subtilis*	Tomato	*Meloidogyne javanica*	[30]
29	*P. fluorescence*	Mungbean	*H. cajani*	[95]
30	*P. fluorescens*	Tomato	*M. javanica*	[96]
31	*Pseudomonas fluorescens*	Castor and Cotton	*Rotylenchulus reniformis*	[97]
32	*P. fluorescens*	Tomato	*M. incognita*	[98]
33	*Pseudomonas fluorescens*	Banana	*Helicotylenchus Multicinctus*	[99]
34	Consortium: *P. fluorescens* (Pf 128) + *B. subtilis* (Bbv 57)	Tomato	*Meloidogyne incognita*	[100]
35	*B. polymyxa*+VAM	Tomato	*M. incognita*	[101]
36	*Pseudomonas fluorescens*	Okra	*M. incognita*	[102]
37	*P. fluorescens*, and *B. Subtilis*	Rice	*M. graminicola*	[103]

Table 3: Different mode of action rhizobacteria for suppression of plant parasitic nematodes.

S. No.	Rhizobacteria Strains	Target PPNs	Mode of Action	References
1	*Bacillus cereus*	*Heterodera avenae, Meloidogyne incognita*, *M. javanica*	Sphingosine, Protease, Chitinase, Antibiotic production, Secondary metabolites	[104, 105]
2	*Bacillus coagulans*	*M. incognita*	Hydrolytic enzymes	[106]
3	*Bacillus firmus*	*Ditylenchusdipasi, Heterodera* spp., *Meloidogyne incognita*, *Pratylenchus* spp., *Radopholussimilis*	Sep 1 protease, Secondary metabolites	[56, 107, 108]
4	*Bacillus licheniformis*	*B. xylophilus, M. incognita*	Protease, Chitinase	[27, 109]
5	*Bacillus megaterium*	*H. glycines*, *M. incognita*, *M. graminicola*	Protease, Secondary metabolites	[14, 36, 110]
6	*Bacillus pumilus*L1	*H. glycines*, *M. arenaria*	Protease, Chitinase	[53, 111]
7	*Bacillus subtilis*	*Helicotylenchus multicinctus, M. graminicola, M. incognita, M. javanica, Rotylenchulus reniformis*	Lipopeptide antibiotics, Hydrolytic enzymes, Secondary metabolites	[57, 112-114]
8	*Corynebacterium paurometabolum*	*Meloidogyne incognita*	Hydrogen sulphide, Chitinase	[31]
9	*Pseudomonas fluorescens* F113	*Globoderarostochinensis*	2,4,diacetylphloroglucinol (DAPG), ISR and SAR	[115]
10	*Pseudomonas aeruginosa*	*Caenorhabditiselegans, M. incognita, M. javanica*	Hydrogen cyanide (HCN), ISR and SAR	[116,117]
11	*Pseudomonas fluorescens* CHA0	*Meloidogyne incognita, Meloidogyne javanica*	HCN, DAPG, Pyoluteorin, Extracellular protease, ISR and SAR	[28, 45, 118]
12	*Serratia marcescens*	*M. incognita, M. javanica, Radopholussimilis*	Volatile metabolites, Prodigiosin and ISR	[119, 120]
13	*Agrobacterium radiobacter* (G12)	*Globodera* spp.	ISR	[121-123]
14	*Bacillus amyloliquefacies*	*Heterodera glycine, M. incognita*	ISR and SAR	[58, 124]
15	*Bacillus cereus*	*M. javanica, M. incognita*	ISR	[58, 125, 126]
16	*Bacillus mycoides*	*M. incognita*	ISR and SAR	[58]
17	*Bacillus pumilus*	*Heterodera glycine, Meloidogyne incognita*	ISR and SAR	[34, 127]
18	*Rhizobium etli*	*Meloidogyne* spp.	ISR	[42]
19	*Pseudomonas putida*	*Meloidogyne incognita*	ISR	[82]
20	*Bacillus subtilis*	*Heterodera cajani, M. arenaria, M. incognita, M. javanica*	ISR and SAR	[34, 58, 127]
21	*Bacillus sphaericus*	*Globoderapallida, M. incognita*	ISR	[58]

Rose *et al*. documented that active *Pseudomonas fluorescens* in the rhizosphere effectively suppresses nematode development through antibiosis [29]. Particularly promising outcomes emerged when *Pseudomonas* was combined with neem cake and other rhizobacteria such as *Azospirillum*, *Azotobacter*, *Rhizobium*, and the mycorrhizal fungus *Glomus* sp. [30]. This combination substantially reduced root gall formation and suppressed *Meloidogyne javanica* populations in chickpea through antibiosis [30].

7.2. Production of Lytic Enzymes

The production of specific enzymes by rhizobacteria constitutes another important strategy for plant-parasitic nematode suppression [9]. For instance, *Corynebacterium paurometabolum* produces both hydrogen sulphide and chitinase, which effectively inhibit *M. incognita* egg hatching [31]. In a separate study, three rhizobacterial isolates—*Stenotrophomonas maltophilia*, *Bacillus mycoides*, and *Pseudomonas* sp.—achieved 56-74% reduction in trichodorid nematode populations in potato fields [32]. These isolates were characterized by their phenol oxidation capacity, antifungal properties, and production of hydrolytic enzymes and hydrogen cyanide [32].

Additionally, culture filtrates from *Bacillus subtilis*, *Pseudomonas fluorescens*, and *Burkholderia cepacian* effectively inhibited egg hatching and J2-stage juvenile mobility across several root-knot nematode species [33]. Moreover, the antimicrobial metabolites 2,4-diacetylphloroglucinol (2,4-DAPG) and pyoluteorin produced by *P. fluorescens* strain CHA0 suppressed egg hatching and juvenile survival of *M. javanica* [28].

7.3. Competition

Plant-parasitic nematodes and antagonistic bacteria compete intensely for space and essential nutrients since they occupy identical ecological niches [21]. Nutrient competition serves as a fundamental driver of interactions between rhizobacteria like *Pseudomonas fluorescens* and the sugar beet cyst nematode *Heterodera schachtii* [34]. Conversely, Siddiqui and Mahmood reported niche exclusion as the primary inhibitory mechanism employed by *Rhizobium* against *Meloidogyne* spp. [26]. Effective competition consequently requires high bacterial densities in close proximity to nematodes [26]. However, Hallmann *et al*. observed elevated populations of the antagonistic bacterium *Rhizobium etli* G12 within root galls caused by *M. incognita*, highlighting the complexity of these interactions [35].

8. Indirect Effects of Rhizobacteria on Nematode Suppression

8.1. Repellence and Disruption of Nematode-Host Recognition

Antagonistic rhizobacteria not only deter nematodes through direct metabolite production but also actively reprogram rhizosphere signaling processes that govern nematode host-finding behavior. These bacteria can alter root exudate composition-modifying key attractants such as sugars, amino acids, and phenolic compounds-thereby disrupting chemoreception and orientation of infective juveniles [26, 35]. In addition, the production of volatile organic compounds (VOCs), lipopeptides, and other diffusible metabolites by rhizobacteria has been shown to impair nematode chemotaxis and induce avoidance responses, while localized changes in oxygen availability and microbial competition may further reduce host recognition efficiency. For example, Padgham and Sikora demonstrated that *Bacillus megaterium* significantly reduced Meloidogyne graminicola penetration in rice roots by over 55%, suggesting interference with host-location cues rather than solely nematicidal activity [26]. More recent studies have also highlighted the role of rhizobacteria-mediated modulation of plant signaling pathways (e.g., jasmonic acid and salicylic acid) in indirectly altering root exudation patterns and nematode attraction [35-38]. However, despite these advances, the precise molecular mechanisms underlying this tripartite interaction-particularly the identification of specific signaling molecules, nematode sensory receptors, and microbial metabolites involved-remain insufficiently explored. Future research integrating metabolomics, chemical ecology, and functional genomics approaches is therefore essential to elucidate these mechanisms and exploit them for targeted and sustainable nematode management strategies.

8.2. Induced Systemic Resistance (ISR) and Systemic Acquired Resistance (SAR)

Rhizobacterial strains are known to trigger induced systemic resistance against plant-parasitic nematodes in various crops [37]. This process involves activation of plant defense mechanisms by an inducing agent [37]. Hasky-Günther and Sikora first reported ISR, and subsequent studies demonstrated its occurrence in numerous bacteria-nematode interactions [38]. For example, *Bacillus sphaericus* B43 and *Rhizobium etli* G12 induced ISR in tomato against *M. incognita*, resulting in reduced juvenile penetration into root systems [38, 39]. Compared to controls, ISR triggered by strain G12 reduced egg hatching by 36%, while strain B43 achieved a 25% reduction [40].

In split-root experiments, both living and heat-killed cells of *B. sphaericus* B43 and *R. etli* G12 induced ISR in potato against *Globodera pallida* [40]. Interestingly, culture filtrates of *B. sphaericus* B43 produced ISR, whereas *R. etli* G12 filtrates failed to do so [40]. Furthermore, strain G12 was characterized as a heat-stable inducing agent, suggesting that lipopolysaccharides served as the primary elicitor [41].

ISR and SAR activated by rhizobacterial priming produce multiple defense responses, including physical cell wall thickening through callose deposition and lignification, accumulation of phenolic compounds, increased activity of defense-related enzymes such as chitinase and peroxidase, and synthesis of phytoalexins [42]. Anita *et* *al*. reported induction of defense enzymes in tomato against *M. incognita* following *P. fluorescens* inoculation [43]. They observed elevated activities of peroxidase (PO), polyphenol oxidase (PPO), phenylalanine ammonia-lyase, chitinase, and catalase in roots of bacterially treated tomato plants subsequently challenged with nematodes [43]. Isoform analysis further revealed unique PO and PPO isoforms in plants induced by *Pseudomonas fluorescens* treatment [43].

Additionally, Siddiqui and Shaukat described the involvement of salicylic acid production in ISR induced by *P. fluorescens* strain CHA0 against *M. javanica* [44, 45]. Interconnected signaling pathways of SAR and ISR, highlighting the roles of salicylic acid (SA) and jasmonic acid/ethylene (JA/ET). SAR is mainly SA-dependent, involving NPR1 and TGA transcription factors to activate PR genes, whereas rhizobacteria-mediated ISR primarily functions through JA/ET signaling without strong PR induction. Importantly, rhizobacteria (e.g., *Bacillus, Pseudomonas*) modulate cross-talk between SA and JA pathways, often priming plant defenses. Mechanistically, rhizobacteria influence signaling components including transcription factors such as MYC2, WRKYs, NPR1, and JAZ repressors, along with downstream defense genes, while microbial metabolites (e.g., VOCs, lipopeptides) can alter signaling dynamics. Although NPR1 acts as a central node, several aspects—such as root-to-shoot signaling, microbial perception, and epigenetic priming-remain unclear. The figure would benefit from distinguishing solid arrows (established pathways) and dashed arrows (emerging mechanisms), and from highlighting unexplored areas such as small RNA regulation, metabolite signaling, and microbiome-driven immune memory (Fig. **1**) [44, 45].

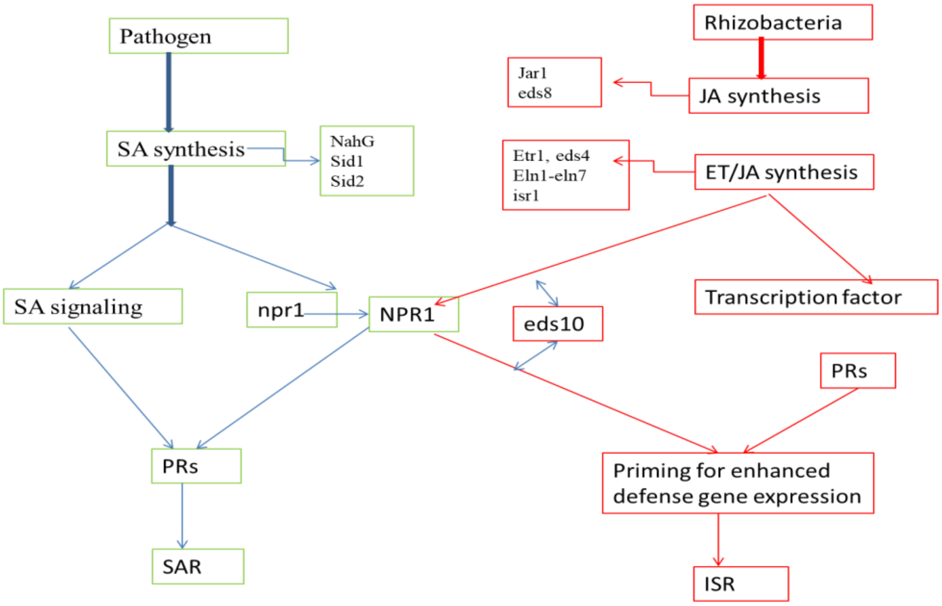

Figure 1: Schematic representation of the pathogen- induced systemic acquired resistance (SAR) and rhizobacteria-mediated induced systemic resistance (ISR) signal transduction in Plants [128].

8.3. Rhizobacteria-Elicited Phytohormone Production

Phytohormones play essential roles in regulating plant growth and development by stimulating cell division, elongation, and tissue expansion [45]. Consequently, they strongly influence plant growth parameters and ultimate crop yield [46, 47]. The phytohormone group, also known as plant growth regulators, includes auxins (indole acetic acid, indole butyric acid, phenylacetic acid), cytokinins (isopentenyl adenosine, isopentenyl adenine riboside, transzeatin ribose, zeatin), gibberellic acid, abscisic acid, ethylene, polyamines, brassinosteroids, jasmonates, salicylic acid, and strigolactones [48]. Among these, indole acetic acid promotes lateral and adventitious root formation, thereby enhancing plant mineral and nutrient uptake [46, 49]. Rashad *et al*. reported that phytohormone-producing Streptomyces strains significantly improved eggplant growth while reducing gall formation and nematode egg masses [50, 51], suggesting that their effects extend beyond growth promotion to modulation of plant defense pathways. Mechanistically, such rhizobacteria are known to influence hormone-mediated signaling networks-particularly auxin, salicylic acid (SA), and jasmonic acid (JA)-which can alter root architecture, strengthen cell walls, and induce systemic resistance, thereby limiting nematode penetration, establishment, and reproduction. For instance, JA- and SA-dependent pathways may enhance defense gene expression, while auxin modulation can disrupt nematode-induced feeding site formation. However, the precise molecular mechanisms linking microbial phytohormone production to nematode suppression remain insufficiently understood. Future research integrating hormone profiling, transcriptomics, and mutant studies could clarify how rhizobacteria reprogram host signaling to interfere with nematode development, representing a promising and largely unexplored area for targeted biocontrol strategies.

9. Commercial Formulations of Rhizobacterial Strains

Developing commercially viable bacterial strains requires extensive research and close collaboration among interdisciplinary scientific organizations, private industries, and various stakeholders [52]. Additionally, successful commercial bio-nematicides must possess several essential characteristics, including broad-spectrum activity against plant-parasitic nematodes, safety for non-target organisms, stability during storage, extended shelf life, low production costs, and ready availability of raw materials [53]. In India and internationally, several commercial products derived from rhizobacterial strains have demonstrated efficacy against specific PPNs (Table **4**) [54]. These products represent promising options for addressing nematode-related agricultural challenges [55].

10. Challenges in Developing Rhizobacterial Bioformulations

Developing rhizobacterial formulations containing effective microbes with prolonged shelf life and rapid rhizosphere colonization ability remains a major commercialization hurdle [56]. In some cases, inoculating these microbes with unsuitable carrier materials or at doses insufficient for effective rhizosphere colonization due to competition with native soil micro- and macro-fauna under field conditions can lead to formulation failure [57]. Furthermore, applying organic pesticides, herbicides, and fertilizers may impede rhizosphere colonization by Rhizobacteria since these inputs can alter soil microbial community structure and consequently affect soil health [58].

Moreover, isolating and evaluating rhizobacterial strains based solely on in vitro growth-promoting traits does not always guarantee successful plant growth promotion under field conditions [14]. Some strains exhibiting limited in vitro growth-promoting ability may still enhance plant growth through alternative mechanisms that remain poorly understood and difficult to assess in laboratory settings [12]. To overcome these limitations, it is necessary to develop rhizobacterial bio-inoculants tailored to specific soil conditions, address environmental constraints, and provide training to farmers and extension personnel on effective application methods for crop plants [21].

11. Future Prospects

Despite these challenges, rhizobacterial strains harboring beneficial microbes possess strong potential for future agricultural applications [9]. Research on rhizobacteria for nematode management has progressed from initial strain isolation and in vitro screening to more advanced stages involving mechanistic elucidation, formulation development, and early field validation. Recent advances include the identification of functionally superior indigenous strains with traits such as lipopeptide production, enzyme secretion, and ISR induction; improved understanding of plant-microbe-nematode interactions through omics approaches; and development of carrier-based and liquid formulations with enhanced shelf life and field stability [46]. Despite these developments, translation to large-scale application remains limited due to variability in field performance, inconsistent colonization under diverse soil conditions, and gaps in understanding strain–host specificity and signaling mechanisms. Therefore, future research should focus on integrating mechanistic insights with formulation technologies, multi-location field validation, and microbiome-based approaches to ensure consistent efficacy and successful commercialization. However, many rural farmers lack formal agricultural education and training, making it essential for experts from universities, state agencies, pesticide manufacturers, and distributors to collaborate with farmers and other stakeholders to enhance awareness and acceptance of rhizobacteria-based biopesticides [8]. Encouragingly, research institutes, agricultural universities, and state extension departments are actively involved in farmer field schools and outreach programs [59]. Demonstrating successful microbial biopesticide technologies among progressive farmers can significantly improve local adoption rates and support sustainable crop production [60].

Table 4: Commercially available rhizobacteria products as biocontrol agents against plant parasitic nematodes.

S. No.	Commercial Products/Type	Rhizobacteria Strains	Applications	References
1	BioNemaGon™	*Bacillus firmus*	Reduce nematode population and root Infestation by nematodes in vegetables and herbs	BioNemaGon™. Available online: http://www.agrilife.in/biopesti_microrigin_nemagon.htm.
2	BioYield™	*Bacillus subtilis* GB03, *Bacillus amyloliquefacien*	Nematodes control in tomato, strawberry, and bell pepper	[52]
3	Clariva® pn	*Pasteurianishizawae* Pn1	Seed treatment; Target *Heterodera glycines* to reduce feeding and reproduction, and increase yields	Clariva®pn. Available online: https://www.syngenta-us.com/seed-treatment/clariva-pn
4	Deny, Blue Circle	*Burlkholderiacepacia*	Inhibit egg hatching and mobility of nematode juveniles	Nematode: Alternative Controls. Available online: www.attra.ncat.org/attrapub/PDF/nematode.pdf.
5	MeloCon®, BioAct and NemOut	*Purpureocilliumlilacinus* 251	Inhibit root knot, burring, cyst, Reniform, Spiral, sting, and root lesion nematodes.	MeloCon® WG. Available online: https://www.certisusa.com/products/bionematicides/melocon-wg
6	Naviva ST	*Pasteuria* sp. Ph3	Seed treatment; Inhibit *Rotylenchulus reniformis* in cotton, soy, vegetables, cucurbits, and floriculture	Mistures Comprising a *Bacillus* Strain and a Pesticide. Available online: https://patentswarm.com/patents/US10251400B2
7	NewPro	*Pasteuriausgae* Bl1 + *Pasteuria* sp. Ph3	Inhibit lance and sting nematodes in turf (Bermudagrass and St. Augustine grass)	US EPA, Pesticide Product Label, New Pro. Available online: https://www3.epa.gov/pesticides/chem_search/ppls/085004-00011-20130422.pdf.
8	Nortica 10 WP	*Bacillus firmus* I-1582	Inhibit cyst, lance, lesion, ring, root knot sheath, spiral, and sting, nematode	Nortica 10 WP. Available online: http://www.tomirwin.com/pdf/labels/Nortica%2010WP.pdf.
9	VOTiVO FS	*Bacillus firmus* I-1582	Seed treatment; inhibit a broad range of nematodes.	VoTIVo FS. Available online: https://agrobaseapp.com/united-states/pesticide/votivo-fs.
10	1% WP, 1% AS	*Pseudomonas fluorescens*	Nematicide	https://www.iihr.res.in
11	1% WP, 1% AS	*Bacillus subtilis*	Nematicide	https://www.iihr.res.in
12	Arka Plant Growth Booster	*Pseudomonas fluorescens*	Plant growth promoter	https://www.iihr.res.in
13	Arka Plant Growth Enhancer and Yield Promoter	*Pseudomonas fluorescens* + *Trichoderma harzianum*	Plant growth and yield promoter	https://www.iihr.res.in

12. Conclusion

One of the major global challenges today is meeting rising food demands while coping with limited land resources and reduced reliance on chemical fertilizers and agrochemicals [1]. The Green Revolution, driven by extensive synthetic agrochemical use, initially enhanced global agricultural production but also raised concerns regarding human health and environmental safety [7]. Consequently, many chemical products have been banned worldwide [61]. Addressing this challenge requires adopting strategies that improve crop productivity and protection while minimizing dependence on harmful agrochemicals [53].

Achieving this goal involves enhancing soil fertility, adopting safer crop protection approaches, and promoting plant growth through application of appropriately selected agro-climatic rhizobacterial strains [11]. With continued advances in genetic engineering, consortium-based applications, and biopesticide development, the stability and productivity of agro-ecosystems can be sustained, leading to more sustainable agricultural production and a better future [46].

Conflict of Interest

The authors declare that, they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author’s Contribution

Devindrappa: Conceived and, collected the data, data analysed and wrote the paper; R. Umamaheswari: Revived and edited the manuscript; Prassana Kumar NR: Revived and edited the manuscript; G Santhosh: Edited the manuscript.

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