

Role of plant-associated microbes in plant health and development: the case of the *Serratia* genus

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Abstract

The genus *Serratia*, a member of the family Enterobacteriaceae, is found in diverse ecological environments. Recently, *Serratia* has emerged as a multifaceted contributor to plant growth promotion and defense against plant diseases and insect pests. This review examines the mechanisms by which *Serratia* spp. induce plant growth and alleviate both abiotic and biotic stresses. Their seamless integration within the plant ecosystem allows *Serratia* spp. to produce quorum-sensing molecules, N-acyl homoserine lactones (AHLs), facilitating colonization of plant tissues and capitalizing on nutrition from plant exudates. This intricate web of communication enables *Serratia* to produce phytohormones and break down essential nutrients from the soil for plant uptake. When confronted with ecological competitors, many *Serratia* strains showcase remarkable adaptability by producing a diverse array of hydrolytic enzymes and antibacterial, antifungal, or insecticidal compounds, effectively controlling harmful bacteria, fungi, and insect pests. Furthermore, beneficial *Serratia* strains also use induced systemic resistance (ISR) and tolerance (IST) to alleviate biotic and abiotic stresses, respectively. Various agricultural applications of *Serratia* include the direct use of bacterial cells for seed coating, foliar spraying, and soil inoculation, or the application of their bioactive compounds alone or in combination with other materials on various plant parts. These efforts aim to bolster plant health, curb diseases, and manage pest populations. Despite promising applications, there have been reports of opportunistic pathogenicity in plants and animals. Therefore, several safety approaches and the use of virulence factor mutant strains should be considered. The trend toward the application of *Serratia* in agriculture is expected to continue.

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Introduction

The genus *Serratia* is an intriguing member of the family Enterobacteriaceae. Presently, 23 species with validly published and correct names have been documented (referencing LPSN). Initially described in Italy as the producer of blood-like spots on polenta, *Serratia marcescens* was named by Bizio in 1823 and is considered the type species of this genus in recent studies^[1]. The presence of red spots on food was often attributed to the activity of red-pigmented bacteria, such as *Serratia marcescens*, which were believed to be responsible for food spoilage as 'saprophytes'. The genus *Serratia* occupies a broad range of habitats, being isolated from soil, water, plants, insects, vertebrates, and hospitalized patients. Various studies have demonstrated that multiple species within the *Serratia* genus inhabit the interior or surface of plant tissues, classifying them as either endophytic or epiphytic bacteria^[2-4]. *Serratia* associated with plants exhibit a plethora of traits that promote plant growth, including the production of phytohormones, the augmentation of nutrient availability, and protect plants from the deleterious effect of biotic and abiotic stressors^[5,6]. The red pigment, known as prodigiosin, has been found to effectively combat various phytopathogens in crop plants^[7-9]. Besides, various other secondary metabolites produced *Serratia* spp. have been demonstrated as antimicrobial, which have also been applied for controlling phytopathogens^[10-12]. The increasing demand for sustainable agriculture has highlighted the importance of microbial pesticides and biostimulants in research, drawing

significant attention to *Serratia* spp. However, the communication between plants and *Serratia*, along with their respective metabolites, remains ambiguously defined. On the other hand, several *Serratia* spp. are considered pathogens for plants and humans. This lack of clarity has spurred us to consolidate information on plant-associated *Serratia*, prompting a deeper exploration into the intricate interactions between plants and the *Serratia* genus. The strategy for safe exploitation of potential *Serratia* bacteria in agriculture is also the focus of this review.

An overview of *Serratia*

The genus *Serratia* consists of Gram-negative, catalase-positive, and oxidase-negative rods found in diverse ecological environments^[13]. Many species within this genus are distinguished by their ability to produce the red pigment prodigiosin, a pyrrole alkaloid, which makes them easily identifiable from other members of the family Enterobacteriaceae. However, it is important to note that not all *Serratia* strains produce prodigiosin; these non-pigmented strains are classified as non-pigment *Serratia*^[1].

Regarding *Serratia* from plants, *Serratia proteamaculans* was first isolated in 1919 from a leaf spot disease of the tropical plant *Protea cynaroides* and was later shown to cause a hypersensitivity reaction in detached leaves of the plant. Many other *Serratia* spp. were isolated from plants. A comprehensive survey conducted by Grimont in 1981 revealed that bacteria from eight of the 10 known *Serratia* species of the time (*S.*

marcescens, *S. plymuthica*, *S. liquefaciens*, *S. proteamaculans*, *S. grimesii*, *S. rubidaea*, *S. odorifera*, and *S. ficaria*) were isolated from various plants, including vegetables, mushrooms, mosses, decaying materials, grasses, small plants, and trees. *S. liquefaciens* and *S. proteamaculans* were particularly prevalent, followed by *S. marcescens*^[14]. Pigmented *S. marcescens* biotypes were rarely isolated from plants. Several *S. marcescens* biogroups frequently encountered in nosocomial infections in humans were also isolated from plants. There is a hypothesis that vegetables used in salads might bring *Serratia* strains to hospitals and contaminate the patients' digestive tracts^[1].

To date, 13 additional *Serratia* species have been isolated, including *Serratia oryzae*, an endophyte of rice stem; *Serratia inhibens*, a new antifungal species isolated from potato, and *Serratia rhizosphaerae*, isolated from rhizospheric soil and recognized as a novel plant resistance inducer against soft rot disease in tobacco^[15–17].

Many species within the genus *Serratia*, including *S. plymuthica*, *S. liquefaciens*, *S. proteamaculans*, *S. grimesii*, *S. nematodiphila*, *S. rubidaea*, and *S. marcescens*, have been reported as plant growth-promoting bacteria. Additionally, some less common species, such as *S. ficaria*, *S. fonticola*, *S. odorifera*, *S. entomophila*, and *S. quinivorans*, have been recognized for their roles in stimulating plant growth^[18].

These bacteria promote plant growth through various mechanisms, such as directly enhancing nutrient availability by breaking down high molecular weight organic compounds, converting nitrogen compounds, and solubilizing minerals etc. They also produce phytohormones and help alleviate salinity and drought stress in plants. Furthermore, the production of secondary metabolites such as prodigiosin, pyrrolnitrin, and biosurfactants enable *Serratia* spp. to combat phytopathogens and insect pests, thereby stimulating plant growth even under stressful conditions^[19–21].

Serratia spp. possess mechanisms that enable them to adapt to diverse lifestyles, distinguishing them from other plant growth-promoting bacteria^[22]. For instance, genome analysis of *Serratia grimesii* BXF1, isolated from pinewood nematode (*Bursaphelenchus xylophilus*), revealed the presence of several genes associated with antagonistic traits, plant growth regulation, and nematode development modulation. Moreover, most of the BXF1 genes are involved in environmental and genetic information processing, consistent with its ability to sense and colonize various niches. These findings enhance our understanding of the role and evolution of strain BXF1 as a mediator of interactions in complex disease systems and provide insights into the broader evolution of *Serratia* and Enterobacteriaceae towards multitrophic interactions^[23]. Similarly, *S. nematodiphila*, initially reported as a symbiont of the entomopathogenic nematode *Heterorhabditoides chongmingensis*^[24], has been also found in the rhizosphere, exhibiting plant growth-promoting activities^[25,26]. Unfortunately, eight species (*Serratia liquefaciens*, *Serratia ficaria*, *Serratia fonticola*, *Serratia grimesii*, *Serratia odorifera*, *Serratia plymuthica*, *Serratia quinivorans*, and *Serratia rubidaea*) were reported to be associated with human infection, among which *S. marcescens*, *S. liquefaciens*, and *S. odorifera* are best known^[27]. Of all *Serratia* species, *S. marcescens* is not only the most common nosocomial pathogen, but also considered the causal agent of plant diseases^[22]. Some *S. marcescens* strains are known to cause leaf spot disease on industrial hemp (*Cannabis sativa*)^[28]. Additionally, *S. marcescens* strain HFP01

has been identified as the causal agent of cucurbit yellow vine disease, a devastating disease for cucurbit production^[22,29].

Recent advancements in whole genome sequencing and comparative genomic studies have significantly contributed to distinguishing clinical strains from other strains of *Serratia* spp., particularly through the identification of antibiotic resistance genes and the presence of plasmids. Genomic analysis has been pivotal in determining the virulence factors of *Serratia* spp.^[30,31]. Comparative genomic studies of plant pathogenic and nonpathogenic *Serratia marcescens* strains have revealed genetic markers specific to phytopathogenic strains^[32]. This approach has further elucidated the mechanisms by which plant-associated *Serratia* spp. colonize plant tissues, uncovered various genes responsible for plant growth-promoting traits, biosynthesis of quorum sensing (QS) signals, production of secondary metabolites effective against phytopathogens and insect pests, and elicitors of induced systemic resistance (ISR)^[33,34].

Plant-associated *Serratia*

Plant-associated bacteria are recognized as indigenous members of the plant microbiome, residing in high densities on the plant and influencing plant development^[35]. Recent research has revealed that bacterial populations in the rhizosphere can range between 10^7 and 10^9 CFU/g of rhizosphere soil, while populations on the rhizoplane range from 10^5 to 10^7 CFU/g fresh weight (fw). After establishing themselves in the rhizosphere and rhizoplane, bacterial endophytes can enter plant roots and colonize with sub-populations ranging from 10^5 to 10^7 CFU/gfw. Once inside the roots, these endophytic bacteria can spread systemically to colonize above-ground tissues, establishing population densities in stems and leaves between 10^3 and 10^4 CFU/gfw under natural conditions^[35]. In a study involving various rice varieties, endophytic bacteria were isolated from surface-sterilized roots and stems. The bacterial population in the roots ranged from approx. 10^5 to 10^6 CFU/gfw, whereas the bacterial population in the stems ranged from approx. 10^2 to 10^4 CFU/gfw. One strain, *Serratia marcescens* IRBG500, was identified as a diazotrophic bacterium capable of systemic spread. It colonized the roots (approx. 10^7 CFU/gfw on the surface and internal areas), stems (approx. 10^1 CFU/gfw on the surface and 10^5 CFU/gfw in the internal area), and leaves (approx. 10^2 CFU/gfw on both the surface and internal areas), positively influencing plant growth^[2]. Several studies have indicated that biofilm formation is critical for the colonization process of plant-associated *Serratia* species, generally regulated by QS signal molecules^[36,37]. Indeed, the biofilm-forming *Serratia glossinae* GS2 (a later synonym of *Serratia fonticola*), isolated from the rhizosphere of a sesame plant, as a producer of two quorum-sensing signal molecules: N-hexanoyl-L-homoserine lactone and N-octanoyl-L-homoserine lactone, boosts plant biomass and chlorophyll content^[38]. An interesting assay revealed that the population density of root-associated bacterial communities varies on the roots of transgenic plants engineered with either AHL or acylhomoserine lactonase (AiiA) genes. The density of Gram-negative bacterial increased in AHL-expressing plants, whereas it significantly decreased in AiiA-expressing plants^[39]. These findings suggest that plant colonization by Gram-negative bacteria like *Serratia* may rely on quorum sensing (QS) signal molecules, specifically AHLs,

Plant-associated *Serratia* spp.

which also regulates other potential cell surface adhesins, including exopolysaccharide and outer membrane proteins^[40]. Additionally, swarming motility, regulated by the *flhD* gene, enhances biofilm formation by promoting cell surface attachment. Major fimbriae subunits encoded by *fimA* and *fimC* are essential for adhesion and colonization. Genes *bsmA* and *bsmB* also regulate biofilm formation, with mutations impairing this process. The gene *swrR* acts as an AHL-dependent regulator. Downregulation of *fimA*, *fimC*, *bsmA*, *bsmB*, *flhD*, and *swrR* reduces attachment capacity, biofilm formation, and swarming motility^[41,42].

Biofilm-forming bacteria aid plants cope with biotic and abiotic stressors by upregulating induced systemic resistance, balancing cytotoxicity, and inhibiting pathogens with substances like exopolysaccharide (EPS) matrix, antibiotics, and enzymes. They also trigger the production of defense hormones, antioxidants, and osmolytes, enhancing plant growth through mechanisms such as indole-3-acetic acid (IAA) production, mineral solubilization, nitrogen compound production, and ACC deaminase production^[43]. Specifically, *Serratia* species form an EPS matrix that serves as a scaffold for biofilm structure, facilitating intercellular communication and surface adhesion. They also produce the red pigment prodigiosin and several extracellular virulence factors, including DNase, lipase, hemolysin, proteases, chitinase, and biosurfactants. These factors primarily contribute to biofilm formation through quorum sensing (QS) mechanisms^[41].

In this intricate communication, plant exudates play a key role in attracting and stimulating the colonization and biofilm formation of beneficial *Serratia* to address the challenges that the plant faces^[44,45]. One study demonstrated that seedlings treated with high red/far red (R/FR) light maintained high populations of *S. plymuthica* A21-4 in the roots, while populations of *S. plymuthica* A21-4 markedly reduced in seedlings treated with low R/FR light. The authors suggested that the composition of plant exudates changed with different light ratios. They also reported that plants secrete 10%–40% of their photosynthetically fixed carbon into the rhizosphere as root exudates, potentially affecting plant growth-promoting rhizobacteria (PGPR). In their experiment, high R/FR ratio exposure induced the secretion of certain tomato root exudates such as L-Leucine, L-Methionine, L-Glutamine, 6-Aminocaproic acid, and D-melezitose, which promoted the chemotaxis response, biofilm formation, and root colonization of *S. plymuthica* A21-4 on tomato seedlings^[46]. Additionally, the growth of plants and the population of inhabitant *Serratia* influence each other. The authors of a previous study have indicated that the density of *S. plymuthica* HRO-C48 on plants influences both plant growth and its ability to compete with phytopathogens^[47]. During the plant colonization process, *S. plymuthica* G3 and *S. plymuthica* HRO-C48 positively regulate antifungal activity and exoenzyme production but negatively regulate indole-3-acetic acid (IAA) production during plant-microbe interactions^[36,48]. Plant-associated *Serratia* are known to produce phytohormones, particularly IAA, which promotes plant growth. When the bacterial population is low, higher amounts of IAA are released, supporting plant growth and supplying additional nutrients to the bacteria. Conversely, at high population densities, IAA production decreases to prevent damage and disease promotion^[48]. In the presence of indigenous *Serratia* species as plant inhabitants, a plethora of plant growth-promoting traits and features

for reducing plant pests are expressed, as depicted in Fig. 1. However, QS-deletion mutants in *S. fonticola* GS2 showed considerably fewer PGP activities compared to the wild type^[49]. Interestingly, AHL-producing *Serratia* can inhabit both host and non-host plants, expressing various PGP traits and protecting plants from pathogens^[50]. Therefore, plant colonization by *Serratia* focuses on chemotaxis response and biofilm formation, influenced by plant exudates under normal or environmentally changing conditions.

Intriguingly, the presence of an appropriate amount of plant cell wall-degrading enzymes, such as cellulase, xylanases, and peptinase activity establishes pathways for bacteria to access the root endosphere through the colonization process, enabling them to exhibit growth-promoting activities^[51,52]. Notably, the cell wall-degrading enzymes of endophytic *Serratia* sp. S119 are influenced by root exudates from three plants: peanuts, soybeans, and maize^[53]. These observations have led to the hypothesis that root exudates function as rewards, attracting beneficial microbes to collaborate in supporting plant growth.

Plant-growth promoting *Serratia*

In the intricate web of communication between plants and microbes, beneficial microorganisms, particularly bacteria, play a pivotal role. These bacteria, identified as plant growth-promoting bacteria (PGPBs), play a crucial role in fostering plant health. PGPBs exhibit traits that contribute significantly to plant well-being, including the production of substances vital for plant vitality and the breakdown of organic compounds in the soil into more accessible nutrients for enhanced plant uptake. Additionally, they serve as formidable defenders, shielding plants against both abiotic and biotic stressors^[18,20]. A synthetic review further underscores the advantages of specific bacteria, such as *Serratia*, as elucidated in Table 1. This comprehensive overview highlights the numerous benefits these microorganisms provide in plant-microbe interactions, emphasizing their mechanisms in promoting plant growth.

IAA production

In plant-microbe interactions, bacterial auxin from rhizospheric bacteria is crucial for colonization^[54]. Researchers have revealed that 80% of rhizosphere bacteria produce IAA, which enhances biofilm formation, aiding bacterial adherence and stress resilience^[55]. Bacterial IAA biosynthesis can be tryptophan-dependent or independent. While the tryptophan-independent pathway is not yet understood, the tryptophan-dependent pathway involves several known genes and enzymes, with plants providing tryptophan through exudates as a precursor for bacterial IAA synthesis^[55]. To illustrate, a study revealed that root-associated *S. marcescens* RSC-14 contains the *trpEGDCBA* gene cluster, encoding key enzymes in the tryptophan biosynthesis pathway, linked to various biological processes, including IAA biosynthesis^[5]. The RSC-14 genome includes *ipdC* for indolepyruvate decarboxylase and *dhaS* for indole-3-acetaldehyde dehydrogenase, essential for converting tryptophan to IAA. The pathway involves tryptophan-2-monooxygenase (*iaaM*) and indoleacetamide hydrolase (*iaaH*), though RSC-14 only has a putative *iaaH* gene and lacks *iaaM*. Similarly, *S. fonticola* strain GS2 from the rhizosphere contains many of the same genes as *S. marcescens* RSC-14^[56]. Additionally, *Serratia* species isolated from various plants, such as

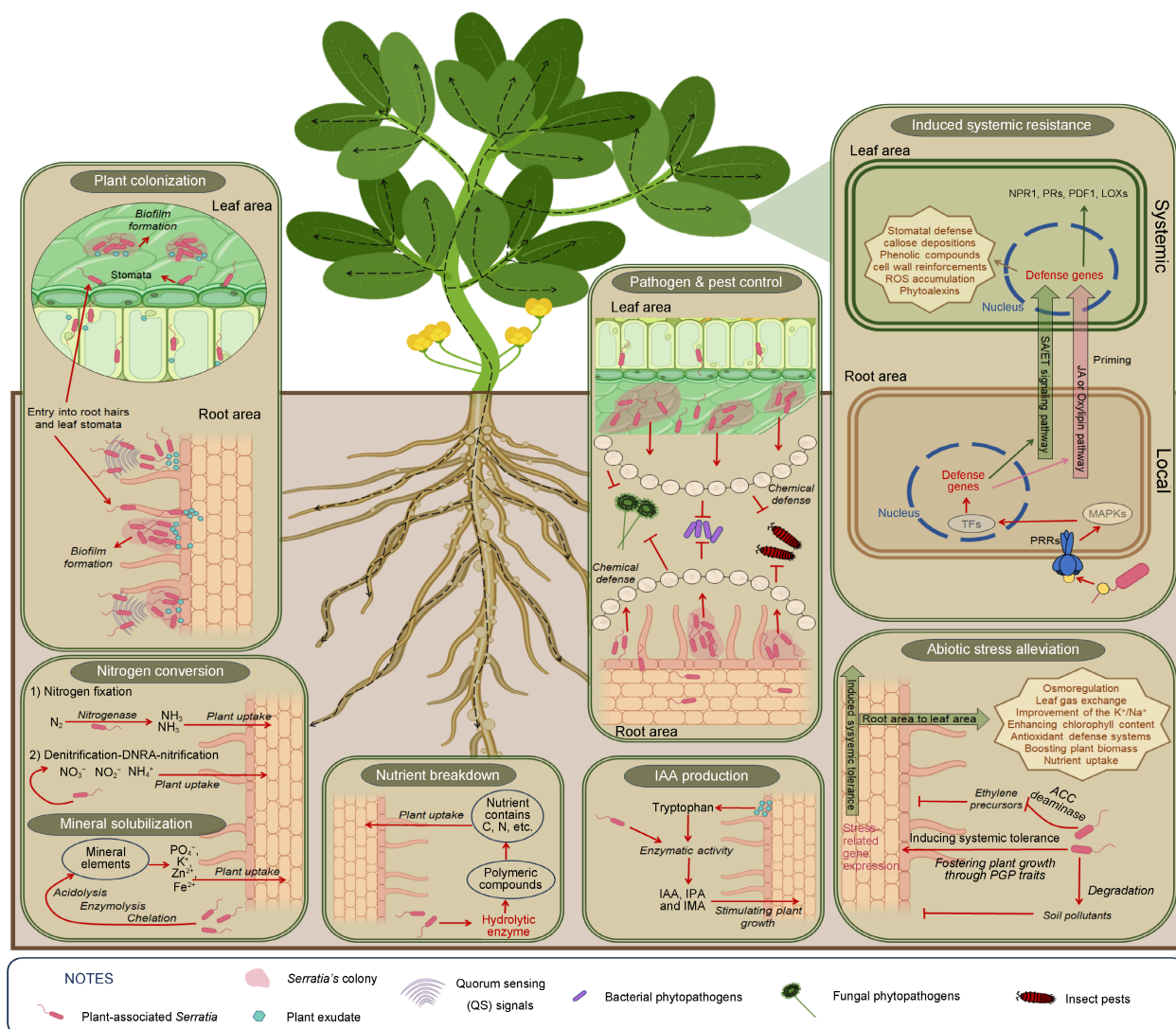


Fig. 1 Benefits of *Serratia* species to host-plants.

common wheat, soybean, turmeric, and nepenthes, have been identified as IAA producers^[8,26,36,48,57,58]. Interestingly, after colonizing the rhizosphere, *S. marcescens* PLR synthesizes IAA using tryptophan provided by root exudates, exporting it back to the roots along with its precursor's indole-3-pyruvate (IPA) and indole-3-acetamide (IAM). This up-regulates the expression of multiple auxin biosynthesis genes and nutrient transporter genes in plants, accelerating root development^[59]. Thus, plant-associated *Serratia* may produce IAA to colonize and stimulate plant growth through tryptophan provided by plant exudates in the plant-bacteria communication.

Nitrogen conversion

Nitrogen is essential for proteins, nucleic acids (DNA and RNA), ATP, and NAD in all living cells. It is a key component of chlorophyll, necessary for photosynthesis, thus critical for plant growth. Dinitrogen (N_2) is the most abundant atmospheric gas, but plants can only assimilate reactive forms like oxidized (NOx) and reduced (NH_3 and amines) nitrogen. N_2 is converted to usable nitrogen (NH_3) by biological nitrogen fixation by certain bacteria and archaea (diazotrophic prokaryotes)^[60]. Additionally, root development through IAA produced by beneficial

plant-microbe interaction can facilitate plant access to available nitrogen compounds fixed by microbes^[61]. For instance, certain diazotrophic bacteria like *Serratia*, when present as endophytes in plants like rice and soybean, exhibit significant nitrogen fixation activity through the enzyme nitrogenase. These bacteria not only fix nitrogen efficiently but also colonize plant tissues effectively, contributing to sustained nitrogen availability. In particular, studies have shown that *Serratia* localize densely around plant root tips shortly after inoculation^[2,58], a critical area where plants release plant exudates. Moreover, other bacteria like *S. nematodiphila* RGK have been found to produce ammonia, further supporting plant growth^[26]. Nitrogenase is a bacterial enzyme that reduces dinitrogen (N_2) to ammonia (NH_3) using ATP. It consists of two proteins: the catalytic molybdenum-iron protein (MoFeP) and the iron protein (FeP). The enzyme's activity involves synchronized electron and proton transfers, driven by ATP-dependent interactions between FeP and MoFeP^[62]. Interestingly, a study has revealed that Biological Nitrogen Fixation (BNF) fueled by As(III) oxidation is a novel biogeochemical process. Over 20 *Serratia* genomes from NCBI contained essential genes for As(III) oxidation and BNF (*aioA* and *nifH*), indicating that

Table 1. Plant growth promoting traits of *Serratia* species.

No.	Plant growth-promoting traits	Mechanisms	<i>Serratia</i> species	Ref.
1	Colonization	Biofilm formation Chemotaxis Entry into root hairs and leaf stomata	<i>S. marcescens</i> <i>S. plymuthica</i> <i>S. fonticola</i> <i>S. oryzae</i> <i>Serratia</i> spp.	[2,36–39,44,46–50,53]
2	IAA production	Trp-dependent pathway	<i>S. marcescens</i> <i>S. liquefaciens</i> , <i>S. plymuthica</i> <i>S. Rubidaea</i> <i>S. glossinae</i> <i>S. nematodiphila</i> <i>Serratia</i> spp.	[5,8,26,38,48,57–59,90]
3	Nitrogen conversion	Nitrogen fixation Denitrification-DNRA-nitrification	<i>S. marcescens</i> <i>S. nematodiphila</i> <i>Serratia</i> spp.	[2,26,58,63,64]
4	Mineral solubilization	Organic acid production H ⁺ extrusion Exopolysaccharide production Siderophores production Solubilizing enzyme production	<i>S. marcescens</i> <i>S. nematodiphila</i> <i>S. plymuthica</i> <i>Serratia</i> spp.	[26,44,58,65,67–69,71,74,123]
5	Nutrient breakdown	Extracellular hydrolytic enzyme production	<i>S. marcescens</i> <i>Serratia</i> spp.	[53,64]
6	Abiotic stress alleviation	ACC deaminase production Induced systemic tolerance PGP traits stimulation Cadmium (Cd) detoxification Pyrene degradation	<i>S. marcescens</i> <i>S. liquefaciens</i> <i>S. proteamaculans</i> <i>Serratia</i> spp.	[5,6,44,58]
7	Induced systemic resistance	Elicited by AHLs, bacterial flagellin (flg22), translation elongation factor Tu (elf18), and 2,3-butanediol	<i>S. marcescens</i> <i>S. liquefaciens</i> <i>S. rhizosphaerae</i> <i>Serratia</i> spp.	[17,39,82,83]

As-dependent BNF may be common in *Serratia* species^[63]. Moreover, the isolated *S. marcescens* (OK482790) from the lupin rhizosphere, possesses genes involved in denitrification-DNRA-nitrification pathways. This strain plays a crucial role in converting nitrate to nitrite and other nitrogen compounds, thereby enhancing plant growth and nutrient availability^[64]. It can be seen that *Serratia* may provide usable nitrogen to plants through several microbiological processes.

Mineral solubilization

Interestingly, under phosphorus deficiency, plants secrete exudates to attract phosphorus-solubilizing *Serratia*, which aids in nutrient acquisition^[44]. Plant-associated *Serratia* produces organic acid, gluconic acid through its phosphate solubilization mechanisms^[65]. Organic acids form soluble complexes with metal ions in insoluble phosphates, releasing the phosphate. Gram-negative bacteria like *Serratia* are more efficient at dissolving mineral phosphates than Gram-positive bacteria due to their secretion of organic acids from glucose metabolism. This metabolism can occur *via* phosphorylation to glucose-6-phosphate or direct oxidation to gluconate, leading to the Entner–Doudoroff pathway. Phosphate solubilization results from acidification of the periplasmic space by acids produced during glucose oxidation by quinoprotein glucose dehydrogenase (PQQGDH), which converts glucose to gluconic acid^[66]. In *Serratia*, phosphorus (P)-limitation, and root exudates from P-limited peanut plants enhance *pqqE* gene expression and *pqq* promoter activity. Under P-limitation, both *pqqE* expression and promoter activity increase, varying with root exudate concentration and bacterial growth phase^[67]. Further studies have shown that organic acids such as malic acid, lactic acid, and acetic acid are produced during the phosphate solubilization process in *Serratia* sp. PSB-37^[68]. Additionally, High

Performance Liquid Chromatography (HPLC) analysis of culture supernatants revealed that gluconic acid is secreted through the direct oxidation pathway of glucose in *S. marcescens* CTM 50650 when grown on National Botanical Research Institute's phosphate (NBRIP) medium containing glucose as the sole carbon source^[69]. Various organic acids, particularly 2-ketogluconic acid, and gluconic acid, play key roles in the phosphate solubilization process *via* excretion by Phosphate Solubilizing Microorganisms (PSMs)^[70]. Moreover, H⁺ extrusion aids in the mineral solubilization process of beneficial microorganisms. Ammonium (NH₄⁺) in soil is assimilated by PSMs for amino acid synthesis and converted to ammonia (NH₃), releasing excess H⁺ into the cytoplasm. This acidifies the surrounding medium, aiding in the dissolution of insoluble phosphates^[70]. In addition to phosphate solubilization, *Serratia* species can also solubilize compounds containing zinc (Zn) and potassium (K), transforming them into minerals available for direct plant uptake^[26,71]. The mechanisms for K- and Zn-solubilization similarly involve organic acid production and H⁺ release by beneficial bacteria^[72,73].

In organic phosphate solubilization, enzymes such as acid and alkaline phosphatases and phytase, phosphonates/carbon–phosphorus (C–P) lyases produced by microorganisms facilitate the dissolution of organic phosphates through mineralization^[70]. One study has shown the effect of low phosphate concentration and acidic pH on the alkaline phosphatase (APase) activities of *S. marcescens*. Under low phosphate conditions, some strains of *S. marcescens* synthesize two different types of APases: constitutive (CAPase) and inducible (IAPase)^[74]. Conversely, another study found that *Serratia* sp. PSB-37 significantly produces acid phosphatase under high pH conditions to decrease pH, enhancing soil fertility and contributing to sustainable agriculture^[68].

Nutrient breakdown

Extracellular enzymes in soils degrade organic matter through hydrolytic reactions. These enzymes cleave specific bonds in complex organic materials like plant debris, requiring microbial cells to transform organic matter into smaller molecules for cellular uptake, exemplified by the decay of cellulose and lignin, and contributing to the carbon-cycling process. Hydrolytic extracellular enzymes produced by microbes can break down polymers into monomers derived from deceased organisms (including plants and other living entities), serving as valuable sources of carbon, nitrogen, and other nutrients for plant uptake and proliferation^[75]. Numerous studies indicate that plant-associated *Serratia* species produce various degrading enzymes, including protease, lipase, cellulase, and chitinase effectively promoting plant growth^[64,76].

Serratia in the alleviation of abiotic stress

Plant abiotic stresses can be alleviated by chemical substances synthesized by beneficial microbes. For example, under salt stress, ethylene production in plants increases, exacerbating stress. The rhizobacterial strain *S. proteamaculans* M35 produces 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which reduces ethylene levels, alleviates stress, and enhances wheat productivity^[77]. ACC deaminase production is a key trait for promoting plant growth in *Serratia*^[44]. During abiotic stress alleviation, *Serratia* also fosters plant growth through phosphate solubilization, siderophore and IAA production, nitrogen fixation, and ammonia production^[6,20]. Besides that, using *Serratia* can induce plant tolerance to abiotic stresses. For example, when plants face salinity stress, *S. marcescens* CDP-13 modulates osmoprotectants and enhances antioxidant enzyme activities in wheat under salinity stress, minimizing oxidative damage^[6]. Plants primed with AHLs (quorum-sensing molecules in *Serratia*, as described above) or AHL-producing rhizobacteria can better cope with abiotic stresses through induced systemic tolerance. AHLs activate Mitogen-activated protein kinases (MAPKs) and upregulate transcription factors, glutathione-S-transferase *GST6*, and heat shock protein *Hsp60* genes, priming plants *via* the salicylic acid (SA) and oxylipin pathways. This modulates osmoprotectants, improves gas exchange, reduces the Na⁺/K⁺ ratio, enhances antioxidant enzymes, and boosts plant biomass and chlorophyll content. Specifically, inoculation with *S. liquefaciens* KM4 significantly reduces oxidative stress markers (hydrogen peroxide (H₂O₂), malondialdehyde (MDA), and electrolyte leakage (EL)), enhancing leaf gas exchange, osmoregulation (proline, soluble sugars, soluble protein, total free amino acids, phenols, and flavonoids), antioxidant defense systems (antioxidant enzymes: ascorbate peroxidase (APX), superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD)); and levels of non-enzymatic antioxidants: ascorbic acid (AA) and glutathione (GSH)), and nutrient uptake under salt stress. These benefits are accompanied by the upregulation of stress-related genes, antioxidant genes (APX, CAT, SOD), Rubisco and photosynthesis-encoding genes (RBCS and RBCL), and genes mediating ion balance (H⁺-PPase, HKT1, NHX1), and the downregulation of the key gene in abscisic acid (ABA) biosynthesis (NCED)^[78]. In soils containing pollutants like heavy chemicals, *Serratia* can help plants cope with these stressors. For example, introducing *Serratia* CP-13 to maize cultivars grown in cadmium (Cd)-stressed soil enhances

Cd detoxification by modulating phytohormones and gas exchange^[79]. Similarly, *Serratia* sp. Wed4 degrades pyrene and promotes plant growth through its PGP traits^[58].

The positive effects of *Serratia* in alleviating abiotic stress bring various benefits to plant growth and health. According to the researchers, the potential strain *S. proteamaculans* demonstrated promising performance under abiotic stress conditions, significantly increasing plant height, root length, grain yield, and straw yield by up to 60%^[77]. Introducing *Serratia* under abiotic stress conditions leads to substantial increases in plant biomass, seed germination, photosynthetic pigments, plant physiology, and nutrient uptake^[58,79]. Overall, *Serratia* spp. make a significant contribution to plant growth and development across various environmental conditions.

Triggering plant immunity *via* induced systemic resistance (ISR) by *Serratia*

Beneficial bacteria within plant tissues can activate the plant immune system to defend against phytopathogens and insect pests through Induced Systemic Resistance (ISR)^[80]. Microbe-Associated Molecular Patterns (MAMPs) activate Pattern Recognition Receptors (PRRs), leading to hormonal defenses against pathogens and various plant immune responses. Elicitors from beneficial bacteria such as flagella, lipopolysaccharides, siderophores and quorum-sensing molecules act as MAMPs, recognized by PRRs, priming plant immunity^[80,81].

To induce plant systemic resistance, numerous reports indicate that AHLs produced by *Serratia* act as elicitors, perceived by plants, leading to the activation of SA/ET and oxylipin signaling pathways in the ISR process^[82]. For instance, a study showed that AHL produced by *S. liquefaciens* MG44 induces systemic resistance in plants through SA- and ET-dependent pathways^[83]. Additionally, AHLs prime plants for controlling phytopathogens *via* SA-dependent and oxylipin pathways^[84]. Phyto-oxylipins, including JA and its metabolites like cis-OPDA, methyl jasmonate, and JA-Ile, are unsaturated fatty acids produced by lipoxygenases (LOX) that oxidize lipid chains. Specifically, root treatment with *S. marcescens* B2 elevates lipoxygenase levels after pathogen inoculation, leading to induced systemic resistance to rice blast disease^[85]. Plant roots primed with oxo-C14-HSL lead to the accumulation of SA and cis-OPDA in plant leaves^[84]. Additionally, oxo-C14-HSL-treated *Arabidopsis* plants exhibit increased resistance to the hemibiotrophic bacterial pathogen *Pseudomonas syringae* pv. tomato DC3000. Oxo-C14-HSL promotes stronger activation of mitogen-activated protein kinases (MAPKs) AtMPK3 and AtMPK6 when challenged with flg22, followed by higher expression of defense-related transcription factors (TFs) WRKY22 and WRKY29, and the *PATHOGENESIS-RELATED1* (*PR1*) gene^[86]. Elicitors like flg22 and elf18 peptides in *S. rhizosphaerae* strain KUDC3025 also induces plant systemic resistance *via* SA and ET pathways^[17]. Research on plant ISR elicited by 2,3-butanediol produced by *S. marcescens* 90-166, regulated by their AHLs, suggests that this strain may trigger plant ISR through both JA- and SA-dependent pathways^[39]. Similarly, another study has shown that the intermediate response of plants was produced by metabolic elicitors from *S. rubidaea* strain N 12.34, which induced a strong differential expression of marker genes in the SA pathway and a marker in the JA/ET pathway^[87]. However,

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these elicitors remain unexplored. Thus, further exploration of *Serratia*-induced plant immunity is needed in future studies.

Following hormonal signaling pathways, numerous defense genes are expressed in response to plant disease. For instance, the activation of defense genes like PR1a, 26 kDa acidic chitinase, and 30 kDa basic chitinase occurs when plant roots are treated with AHL-producing *S. liquefaciens* in the rhizosphere^[83]. The induction of the SA/cis-OPDA pathway enhances stomatal defense by activating MPK3 and MPK6, which induce the guard cell lipoxygenase 1 (LOX1), leading to the peroxidation of polyunsaturated fatty acids into oxylipins and the subsequent accumulation of SA. Similarly, rice primed with *S. plymuthica* IC1270 accumulates reactive oxygen species (ROS) and phenolic compounds^[88]. A study has shown that seedlings inoculated with *S. rubidaea* strain N 12.34 exhibit a significant increase in the differential expression of gene coding for defense-related proteins, including *Nonexpressor of pathogenesis-related protein 1 (NPR1)* (149.74-fold), *PR2* (57.09-fold), *Plant defensin 1 (PDF1)* (675.98-fold), *PR3* (41.37-fold), and *LOX2* (32.79-fold), compared to negative controls^[87]. Various actions induced by ISR elicited by *Serratia* include cell wall reinforcement, phenolic compound deposition, and callose formation. Other pathogenesis-related (PR) proteins involved in these defenses include chitinase, glucanase, phenylalanine ammonia-lyase (PAL), polyphenol oxidase (PPO), and peroxidases (POX). Additionally, secondary metabolites like phytoalexins play a crucial role in these defense mechanisms^[18].

***Serratia* in the direct suppression of plant diseases and insect pests**

In the interaction between plant growth-promoting bacteria (PGPB) and plants, many *Serratia* spp. effectively trigger the plant immune system through induced systemic resistance (ISR) as previously discussed. Additionally, *Serratia* employs direct antagonism to overcome ecological competitors. *Serratia* species are renowned producers of a diverse array of bioactive compounds, encompassing hydrolytic enzymes and secondary metabolites (Table 2). These compounds exhibit direct inhibitory effects on the growth of plant pathogens. When confronted with ecological competitors such as harmful fungi, plant bacteria employ a diverse array of cell wall-degrading enzymes, including protease, chitinase, and β -1,3 glucanase. These enzymes can break down peptidic and glycosidic linkages present in the protein and various polysaccharides of the cell wall of phytopathogens, thereby reducing the density of plant pathogenic cells. Although various studies have extensively explored genes encoding protease and chitinase^[22,89], genes coding for β -1,3 glucanase remain less explored. However, numerous studies have indicated that various *Serratia* species can produce β -1,3 glucanase (Table 2). This suggests that future studies need to explore the genes coding for β -1,3 glucanase in *Serratia* more thoroughly. The hydrolytic enzymes synthesized by *Serratia* species are recognized as crucial anti-

Table 2. Common compounds produced by *Serratia* for the control of plant diseases and insect pests.

No.	Compounds produced by <i>Serratia</i> spp.	Analyzed biosynthetic genes	Mechanisms of action	Ref.
1	Protease	<i>yfgC</i>	Degrading the cell walls of most of fungi and the insect's midgut	[8,22,47,48,76,89,90,111]
2	Chitinase	<i>chiA,B,C</i>	Degrading the cell walls of most of fungi	
3	β -1,3 glucanase	Gene encoding β -1,3-glucanase in glycoside hydrolase family	Degrading the insect exoskeletons	
4	Lipase	<i>lipA,B,C,D</i>	Degrading the cell walls of most of fungi	[140]
5	Phospholipase	<i>phlA</i>	Degrading the insect's midgut	[109]
6	Serralyisin (alkaline metalloprotease)	<i>prtA1-prtA4</i>	Degrading the peritrophic membrane lining the midgut	[22,114–116]
7	Prodigiosin Tripyrrole alkaloid	<i>pig</i> gene cluster (<i>pig A-N</i>)	Promoting hemolymph bleeding in insect pests	[7–9,57,91,117–121]
8	Pyrrolnitrin - tryptophan-derived secondary metabolite	<i>prnABCD</i>	Inhibiting spore germination and growth of hyphae	[8,37,48,90,93–95]
9	Oocydin A - chlorinated macrocyclic lactone	<i>ooc</i> gene cluster	Inhibiting immune system enzymes: protease phosphatase, acid phosphatase, and acetylcholine esterase	[4,141]
10	Biosurfactants Serrawettin W1, Serrawettin W2	<i>swrW, swrA</i>	Reducing pH in the insect's midgut	[21,96,97]
11	Serratiochelin A, B, C, D	<i>sch</i> gene cluster	Damaging the cell membrane in combination with phospholipids	[48,90,139,142]
12	Bis catecholate siderophores Volatile organic compounds (VOCs) Sodorifen DMDS acetic acid, methylthiolacetate	Terpene synthase gene (Q5A_011535) <i>mdeA</i> Methyltransferase gene (Q5A_011540)	Inhibiting fungal growth by inhibiting the respiratory electron transport system	[99–101]
			Anti-oomycete activity	
			Swarming activity of <i>Serratia</i> spp.	
			Biosurfactant activity disturbing the cell membrane of phytopathogenic cells	
			Iron competition with phytopathogenic cells	
			Inhibition of fungal growth	

fungal compounds in various studies focused on reducing plant fungal diseases^[47,48,64,76,90].

The most prominent secondary metabolite of several *Serratia* spp. is prodigiosin. This tripyrrol alkaloid, synthesized under the instruction of the *pig* gene cluster (*pigA-N*) has been suggested to be associated with surface adherence and enhancing bacterial dispersal in addition to its antibacterial, and antifungal activities. Moreover, the biosynthesis of prodigiosin might function as a 'metabolic sink' by consuming the overflow of NAD(P)H or proline from primary metabolism^[91]. Multiple studies underscore the pivotal role of prodigiosin in conferring *Serratia*'s proficiency in controlling plant diseases induced by deleterious bacteria or fungi^[8,9,57]. The wide spectrum of activity against phytopathogenic bacteria or fungi has been substantiated across various plant diseases. Prodigiosin induces bactericidal activity indicative of programmed cell death (PCD), involving DNA fragmentation, ROS generation, and proteins with caspase-like activity. Prodigiosin localizes in the membrane and nuclear fractions of bacterial cells, facilitating its binding to bacterial DNA. Regarding its fungicidal activity, prodigiosin has been reported to inhibit spore germination and hyphal growth. These findings suggest that the red-pigmented *S. marcescens* holds promise as a biocontrol agent for combating diverse plant diseases in crop cultivation^[7,92].

Another noteworthy compound is pyrrolnitrin, which exhibits targeted efficacy against a broad range of plant diseases. The pyrrolnitrin biosynthesis with the *prn* gene cluster by rhizobacteria presumably has a key role in their life strategies and in the biocontrol of plant diseases^[93]. The biosynthetic operon that encodes the pathway that converts tryptophan to pyrrolnitrin is composed of four genes, *prnA* through *D*^[93]. The impact of pyrrolnitrin, produced by *Serratia* species has been observed across various crop diseases such as oilseed rapes, wheat, and cucumbers^[8,37,48,90]. Pyrrolnitrin's mechanism of action is believed to involve damaging the cell membrane in combination with phospholipids^[94] and inhibiting fungal growth by suppressing the respiratory electron transport system^[95].

To combat fungal diseases caused by oomycetes such as *Pythium* or *Phytophthora*, plant-associated *Serratia* strains produce oocydin A and other haterumalides, which are chlorinated macrocyclic lactones. These compounds hold potential as antimycotics in agricultural applications, particularly for crop protection^[4,10].

Lipopeptide biosurfactants, such as serrawettin W1 and W2 produced by *S. marcescens* strains, are responsible for the swarming activity of *Serratia* spp. These biosurfactants are synthesized by nonribosomal peptide synthetase genes, *swrW* and *swrA*, respectively. Their amphiphilic structures enable them to act as chemical defenders by disrupting the cell membranes of phytopathogenic cells^[96,97]. Additionally, a new hybrid non-ribosomal peptide–polyketide antibiotic (serramid) produced by *S. plymuthica* C1 can control 15 bacterial phytopathogens. It displays strong antibacterial activity against *Ralstonia solanacearum* and four *Xanthomonas* spp. The mode of action of this compound is expected to inhibit the carboxyltransferase step of the bacterial acetyl-CoA carboxylase-catalyzed reactions^[98].

Another strategy involves limiting ions like available Fe³⁺ in the environment to impede the growth of plant pathogens. Iron-chelating siderophores serratiochelin A, B, C, D produced by *Serratia* spp. competitively acquire ferric iron in plant environments from phytopathogenic cells^[48,90].

Crucially, the antagonistic compounds produced by *Serratia* are regulated by quorum sensing (QS) signals, such as AHLs. The AHL-negative mutants in *S. plymuthica* HRO-C48 significantly reduced the production of antifungal compounds^[48]. This phenomenon is believed to be influenced by mechanisms involved in microorganism–plant interactions^[90], and the *Serratia* population increases in the presence of rich plant nutrients until it reaches a critical bacterial size, triggering the QS system^[48]. Thus, the establishment of the plant-associated *Serratia* cell with the host plant is deemed a key process, influencing the expression of its capabilities in controlling plant diseases.

Recently, the study of microbial interspecies communication and the mode of action of various antagonistic interactions, particularly those mediated by volatile organic compounds (VOCs), has garnered significant research interest. Bacteria respond to fungal VOCs by altering gene and protein expression related to motility, signal transduction, energy metabolism, cell envelope biogenesis, and secondary metabolite production. For instance, in response to VOCs emitted by the phytopathogen *Fusarium culmorum*, *S. plymuthica* PRI-2C, isolated from the maize rhizosphere, produces sodorifen, an unusual antifungal terpene^[99]. Similarly, *S. ureilytica* strain ILBB 145 emits significant amounts of dimethyl disulfide (DMDS) when challenged by fungal phytopathogens, which inhibit the growth of *Pythium cryptoirregularare*^[100]. Exposure to the fungal volatilome shifts the metabolism of *S. plymuthica* HRO-C48 into a defense mode by downregulating genes involved in cellular functioning while upregulating defense mechanisms at the volatile level. The activation of acetic acid and methylthiolacetate production in response to volatiles from fungal pathogens *Rhizoctonia solani*, *Leptosphaeria maculans*, and *Verticillium longisporum* suggests a common defense mechanism in *S. plymuthica* HRO-C48 against volatile-mediated fungal attacks. Notably, three-quarters of the VOCs produced by *S. plymuthica* HRO-C48 are antimicrobial substances, underscoring the significant contribution of VOCs to the biocontrol efficacy of *S. plymuthica*^[101].

In the struggle for ecological niches and nutrients, microorganisms employ several mechanisms simultaneously. For instance, among 18 strains of *S. plymuthica*, *S. rubidae*, and *S. liquefaciens* isolated from the rhizosphere of oilseed rape, many exhibited strong antifungal activities against three phytopathogens: *Verticillium dahliae*, *Rhizoctonia solani*, and *Sclerotinia sclerotiorum*. Their mechanism of action typically involves a combination of at least two mechanisms, including antibiosis (production of prodigiosin and/or pyrrolnitrin), iron capture, and the production of hydrolytic enzymes (chitinases and/or β -1,3-glucanases)^[8]. The broad-spectrum antimicrobial activity observed for *Serratia* spp. is hypothesized to result from a synergistic effect^[21]. Additionally, *Serratia* produces other potent antimicrobial compounds, such as stephensiolides, glucosamine derivatives^[102,103], and zeamines^[104,105], which are effective against a wide range of Gram-positive and Gram-negative bacteria. Antibiotics such as althiomycin and carbapenem, along with glycolipid biosurfactants such as rubiwettins and rhamnolipids, are also expected to control plant diseases^[106]. These compounds have not been extensively studied for controlling plant diseases and pests, suggesting that future research should explore their potential to mitigate the negative impacts of phytopathogens and protect plant health.

Plant-associated *Serratia* spp.

Serratia is widely recognized for its entomopathogenic properties, with various studies revealing that plant-associated bacteria, including endophytes and epiphytes, also exhibit entomopathogenic activity against insect pests. For instance, the endophytic *S. marcescens* SMR, isolated from summer squash flowers displayed entomopathogenic activity against *Helicoverpa armigera* larvae^[107]. Another study highlighted the entomopathogenic effect of rhizospheric *S. marcescens* NPKC3_2_21 on *Spodoptera litura*, providing valuable insights into the potential of *S. marcescens* for pest control in plants^[108]. These bacteria can persist in insect bodies by inhabiting the gut and hemolymph, overcoming host defenses, and rapidly proliferating throughout the gut and hemocoel. This process results in the reddening of the insect body due to the production of a red pigment called prodigiosin, ultimately leading to the insect's demise^[107]. Research also suggests that *S. marcescens* functions as an insect pathogenic disease, taking residence in the insect's gut and hemolymph. The virulence of *Serratia* disease is associated with various enzymatic activities such as protease, lipase, phospholipase, and chitinase, which have been implicated in the degradation of the insect exoskeletons and gut epithelial tissue^[109]. Notably, motility, demonstrated through swimming and swarming activities, has been identified as a significant factor contributing to *Serratia*'s pathogenicity^[110]. A pangenome analysis of the 73 *S. marcescens*'s genomes indicates a preference for insects as hosts, associated with diverse enzymes such as hydrolases, isochorismatase, and N-acetyltransferase, the latter possibly exerting a neurotoxic effect^[113]. Infections are believed to result from the interaction between insects and plant-associated bacteria, where insects either directly feed on plant materials or *Serratia* infects them through enzymes that hydrolyze and destroy the surface and periplasmic structure of insects^[111–113]. Additionally, serralysin an alkaline metalloprotease (synthesized with *prtA1* to *prtA4*), produced by *Serratia* spp., acts as an insecticidal toxin for reducing insect pests, offering potential applications in insect control^[114,115]. The pathogenesis of serralysin producer *S. marcescens* involves inhibiting wound healing, leading to a substantial loss of hemolymph from silkworm larvae^[116]. Red-pigment prodigiosin has demonstrated insecticidal activity in many studies^[117–119]. It induces a drop in pH in the insect's midgut, leading to reduced nutrient uptake and ultimately resulting in the insect's death^[120]. Furthermore, prodigiosin has been reported to inhibit insect immune system enzymes such as protease phosphatase, acid phosphatase, and acetylcholine esterase when exposed to insects^[121]. However, a separate study suggests that prodigiosin may not be an essential virulence factor in entomopathogenic *Serratia*^[122]. Regarding compounds produced by *Serratia* spp. that induce the plant immune system to respond to insect pests, limited information is available. Therefore, further studies are necessary to gain insights into the beneficial role of *Serratia* in triggering induced systemic resistance in plants.

The application of *Serratia* in agriculture and future trends

To date, several examples illustrate the beneficial effects of using *Serratia* on plant growth (Table 3). For instance, a study on *Serratia marcescens* demonstrated that rice plants inoculated with *S. marcescens* IRBG500 exhibited a significant

increase in both root length and root dry weight compared to uninoculated control plants. Specifically, the root length and dry root weight of plants treated with IRBG500 were 1.32 and 1.39 times higher, respectively, than those of the control plants^[2]. Furthermore, *S. marcescens* OK482790, when applied to soil, effectively promoted wheat growth. Soil inoculation significantly enhanced shoot and root lengths by 30.5% and 109.07%, respectively, over control plants. Additionally, soil inoculation led to the most significant increases in plant biomass, with fresh and dry shoot weights increasing by 295% and 172%, respectively, compared to controls^[64]. In addition to its benefits under normal conditions, *Serratia* shows promise under abiotic stress. *S. nematodiphila* EU-PW75 enhanced barley growth under low-temperature conditions, effectively improving growth and physiological parameters^[123]. Similarly, *S. proteamaculans* M35, as a wheat rhizospheric inhabitant, increased wheat height, root length, and grain yield under various salinity stress conditions compared to controls^[77]. Furthermore, plants grown under low-nutrient conditions, including petunia, impatiens, and pansy, showed significant biomass increases of 24%, 41%, and 51%, respectively, when treated with *S. plymuthica* MBSA-MJ1^[124]. *Serratia* species also demonstrated the ability to reduce soil contaminants and stimulate plant growth. For example, *Serratia* sp. Wed4 increased the dry weight of barley by 18.9%–33.9% and reduced pyrene residues by 46.4% in shoots, and 32.1% in roots^[58]. Additionally, *Serratia* CP-13 showed potential in enhancing cadmium (Cd) detoxification in maize crops, promoting plant biomass and seed germination under soil Cd stress ranging from 0 to 30 μM , suggesting its promise as a biofertilizer for future soil Cd bioremediation efforts^[79]. Overall, *Serratia* is a beneficial species for stimulating plant growth under both normal and abiotic stress conditions, promising a potential approach in agricultural applications.

To control biotic stress, *Serratia* species are used for effective management of plant diseases and pests, with multiple studies highlighting their potential. In the 1990s, various species of the *Serratia* genus, including *S. liquefaciens*, *S. plymuthica*, and *S. rubidaea*, were isolated from the rhizosphere of oilseed rape and screened as potent antifungal agents against *Verticillium* wilt (caused by *V. dahliae* var. *longisporum*), post-emergence damping-off, and brown girdling root rot (caused by *R. solani*), showing promise as potential plant biocontrol agents^[8]. Additionally, *S. liquefaciens* CL80 effectively mitigates post-harvest rot of Dutch white cabbage, reducing fungal growth from 32%–82% to 15%–25% of leaf area covered^[125]. Greenhouse trials demonstrate that bacterial treatment reduces *Verticillium* wilt by 18.5% and *Phytophthora* root rot by 33.4%. In three consecutive field trials on commercial strawberry farms in Germany, pre-planting dipping in *S. plymuthica* suspension decreased *Verticillium* wilt by 0% to 37.7% (average 24.2%) and boosted yield by 156% to 394% (average 296%). *Phytophthora* root rot was reduced by 1.3% to 17.9% (average 9.6%), with a yield increase of 60% compared to untreated controls^[47]. Moreover, *S. plymuthica* HRO-C48 defends cucumbers against *Pythium aphanidermatum*, lowering disease incidence from 93.3% to 44.4% and inducing systemic resistance to *B. cinerea*, reducing lesion areas threefold in beans and tomatoes^[37]. Additionally, the utilization of *S. marcescens* NPKC3_2_2 has significantly reduced damage from rice stem borer attacks (*Scirpophaga innotata*) in rice crops, decreasing incidence from 75% to

Table 3. Application of *Serratia* species for enhancing plant growth and plant protection.

No.	Strains	Hosts	Applications	Ref.
1	<i>S. marcescens</i> IRBG500	Rice (<i>Oryza sativa</i> L.)	Improving plant biomass	[2]
2	<i>S. marcescens</i> OK482790	Wheat (<i>Triticum aestivum</i> L.)	Improving plant biomass	[64]
3	<i>S. nematodiphila</i> EU-PW75	Barley (<i>Hordeum vulgare</i> L.)	Reducing plant abiotic stress Improving plant biomass	[123]
4	<i>S. proteamaculans</i> M35	Wheat (<i>Triticum aestivum</i> L.)	Reducing plant abiotic stress Improving plant biomass	[77]
5	<i>S. plymuthica</i> MBSA-MJ1	Petunia (<i>Petunia × hybrida</i>), impatiens (<i>Impatiens walleriana</i>), and pansy (<i>Viola × wittrockiana</i>)	Reducing plant abiotic stress Improving plant biomass under	[124]
6	<i>Serratia</i> sp. Wed4	Barley (<i>Hordeum vulgare</i> L.)	Reducing plant abiotic stress Improving plant biomass	[58]
7	<i>Serratia</i> CP-13	Maize (<i>Zea mays</i> L.)	Reducing plant abiotic stress Improving plant biomass	[79]
8	<i>S. nematodiphila</i> (code SN01)	Rice (<i>Oryza sativa</i> L.)	Biocontrol of Rice blast caused by <i>Magnaporthe oryzae</i> Improving grain yield	[127]
9	<i>S. nematodiphila</i> RGK	Turmeric rhizome (<i>Curcuma longa</i> L.)	Biocontrol of <i>Pythium aphanidermatum</i> Improving plant biomass and bioactive compounds	[26]
10	<i>Serratia liquefaciens</i> , <i>S. plymuthica</i> and <i>S. rubidaea</i>	Oilseed rape (<i>Brassica napus</i> L.)	Biocontrol of <i>Verticillium dahliae</i> , <i>Rhizoctonia solani</i> and <i>Sclerotinia sclerotiorum</i>	[8]
11	<i>S. liquefaciens</i> CL80	Dutch white cabbage (<i>Brassica oleracea</i> L.)	Biocontrol of <i>B. cinerea</i>	[125]
12	<i>S. plymuthica</i> HRO-C48	(<i>Fragaria × ananassa</i> Duch.)	Biocontrol of <i>Verticillium dahliae</i> and <i>Phytophthora cactorum</i>	[47]
13		Cucumber (<i>Cucumis sativus</i> L.), bean (<i>Phaseolus vulgaris</i> L.), and tomato (<i>Lycopersicon esculentum</i> L.)	Biocontrol of <i>Pythium aphanidermatum</i> and <i>Botrytis cinerea</i>	[37]
14		Oilseed rape (<i>Brassica napus</i> L.)	Biocontrol of <i>Verticillium</i> wilt	[48]
15	<i>S. nematodiphila</i> CT-78	Rice (<i>Oryza sativa</i> L.)	Biocontrol of leaf blight disease	[25]
17	<i>S. marcescens</i>	Dolichos bean (<i>Lablab purpureus</i> L.)	Biocontrol of Anthracnose disease caused by <i>Colletotrichum lindemuthianum</i>	[132]
18	<i>Serratia</i> sp. G3	Wheat (<i>Triticum aestivum</i> L.)	Biocontrol of <i>Botrytis cinerea</i> , <i>Cryphonectria parasitica</i> , <i>Rhizoctonia cerealis</i> and <i>Valsa sordida</i>	[90]
20	<i>S. marcescens</i> NPKC3_2_2	Rice (<i>Oryza sativa</i> L.)	Reducing the damages from rice stem borer attacks (<i>Scirpophaga innotata</i>) in rice crops	[108]
21	<i>S. marcescens</i> HJ-01	The red palm weevil (RPW), <i>Rhynchophorus ferrugineus</i> (Olivier)	Reducing the red palm weevil (RPW), <i>Rhynchophorus ferrugineus</i> (Olivier) larvae	[111]
22	<i>S. marcescens</i> B2	Rice (<i>Oryza sativa</i> L.)	Eliciting plant ISR against rice blast caused by <i>Pyricularia oryzae</i>	[85]
23	<i>S. liquefaciens</i> MG1	Tomato (<i>Lycopersicon esculentum</i> L.)	Inducing systemic resistance against <i>Alternaria alternata</i> infection	[83]
24	<i>S. marcescens</i>	Tomato (<i>Lycopersicon esculentum</i> L.)	Inducing systemic resistance against against root-knot nematode <i>Meloidogyne incognita</i>	[126]
25	<i>S. marcescens</i> 90-166	Tobacco (<i>Nicotiana tabacum</i> L.)	Inducing systemic resistance against <i>Pectobacterium carotovorum</i> subsp. <i>carotovorum</i> and <i>Pseudomonas syringae</i> pv. <i>tabaci</i> and cucumber mosaic virus	[39]
26	<i>S. rhizosphaerae</i> KUDC3025	Tobacco (<i>Nicotiana tabacum</i> L.)	Inducing systemic resistance against soft-rot disease caused by <i>P. carotovorum</i> subsp. <i>carotovorum</i> SCC1	[17]
27	<i>S. marcescens</i> GPS5	Groundnut (<i>Arachis hypogaea</i> L.)	Inducing systemic resistance against late leaf spot disease	[130]
28	<i>S. marcescens</i> N4-5 (extract)	Cucumber (<i>Cucumis sativus</i> L.)	Control of cucumber damping-off caused by <i>Pythium ultimum</i>	[128]
29	<i>S. marcescens</i> SE1 and SE2 (extracts)	Peanut (<i>Arachis hypogaea</i> L.)	Control of yellow mold disease caused by <i>A. flavus</i>	[129]
30	<i>S. plymuthica</i> AED38 (extract)	Avocado (<i>Persea americana</i> L.)	Control of root rot caused by <i>Phytophthora cinnamomi</i>	[139]
31	<i>Serratia</i> sp. ARP5.1 (extract)	Avocado (<i>Persea americana</i> L.)	Control of fruit body rot (<i>Colletotrichum gloeosporioides</i>) and root rot (<i>Phytophthora Cinnamomi</i>)	[138]

below 25% under field conditions^[108]. Another study demonstrated that *S. marcescens* HJ-01 exhibits remarkable pathogenicity against the red palm weevil (RPW), *Rhynchophorus ferrugineus* (Olivier) larvae. At a concentration of 1.0×10^8 CFU/mL, the mortality rate of RPW reached 82.22%, with a half-lethal time (LT50) of 4.72 d^[111]. Various applications of ISR-eliciting *Serratia* have shown promising results for large-scale use. Root treatment with *S. marcescens* B2 enhances resistance against rice blast caused by *Pyricularia oryzae*, reducing disease incidence to 59% in rice plants^[85]. Inoculating tomato plants with

AHL-producing *S. liquefaciens* MG1 triggers ISR, reducing necrotic cell death from *A. alternata* infection by over 70%^[83]. The root-knot nematode *Meloidogyne incognita* is controlled by *S. marcescens*, enhancing plant fitness by 2.25–2.29 times, and reducing egg masses by 3.92–4.17 times and eggs by 7.23–8.45 times^[126]. Applying *S. marcescens* 90–166 to plant roots enhances ISR against bacterial pathogens such as *Pectobacterium carotovorum* subsp. *carotovorum* and *Pseudomonas syringae* pv. *tabaci*, as well as cucumber mosaic virus^[39]. Additionally, a novel species, *S. rhizosphaerae* KUDC3025, has been

Plant-associated *Serratia* spp.

reported to suppress *P. carotovorum* subsp. *carotovorum* SCC1, the causal pathogen of soft-rot disease in tobacco, by priming the plant defense system^[17]. These findings suggest that utilizing ISR-eliciting *Serratia* strains could be a promising approach in sustainable agriculture.

The versatile applications of *Serratia* in enhancing plant growth and protecting against diseases underscore its potential in sustainable agriculture. This review outlines various approaches researchers have used to harness *Serratia* for diverse agricultural purposes. For example, the direct application of *S. marcescens* cells to rice soil increases fresh biomass by 1.21–1.43 times compared to seed coating with a high bacterial density^[64]. To combat bacterial leaf blight in rice, researchers have tested *S. nematodiphila* CT-78 through seed coating, foliar spraying, and soil drenching. Notably, foliar spraying 14 d before inoculation and seed coating proved most effective, reducing infected tillers by up to 83%, infected leaves by up to 88%, and disease severity by 4.5-fold, while also improving grain yield and quality^[25]. Additionally, seed coating with one strain of *S. nematodiphila* provided blast control and grain yield comparable to microbial products applied as transplant dipping and post-transplanting foliar spray, as well as fungicide control^[127]. Furthermore, the ethanol extract of *S. marcescens* N4-5, containing prodigiosin and serratomolides, effectively controls cucumber damping-off caused by *Pythium ultimum*. Seeds treated with a ¼ dilution of the N4-5 extract showed significantly greater plant stand compared to non-treated and ethanol-only controls at pathogen inoculum levels of 30 and 50 sporangia/cm³^[128]. Recent research has focused on enhancing the production of antifungal compounds in *Serratia* by supplementing fungal biomass or chitin in culture broths, aiming to control fungal diseases in plants. For instance, seed treatment with *S. marcescens* strains SE1 and SE2 induced by fungal biomass effectively controlled yellow mold disease caused by *A. flavus* in peanut plants, reducing disease severity index from approximately 70% to 40%^[129]. Additionally, chitin-supplemented foliar application of *S. marcescens* GPS5 significantly enhanced control of late leaf spot disease in groundnut by inducing plant defense-related enzymes, reducing lesion frequency by 64% compared to chitin-treated controls and by 67% compared to phosphate buffer-treated controls^[130]. Research also indicates that combining PGP *Serratia* with other plant-associated bacteria, such as *Microbacterium arborescens* and *Enterobacter* sp., significantly enhances wheat growth parameters in pot and field trials compared to individual strain applications^[131]. To reduce Anthracnose disease caused by *Colletotrichum lindemuthianum*, researchers have combined *S. marcescens* cells with *Allium sativum* extracts in both seed treatment and foliar spray approaches, achieving superior results compared to commercial fungicide^[132]. In another innovative study, alginate beads containing *S. marcescens* cells and chitinolytic enzymes demonstrated promising results, achieving a 60% reduction in bean disease compared to a 10% reduction with free *S. marcescens* in greenhouse experiments^[133]. Commercially, potent species exhibiting robust bioactive activities can be formulated into conventional products suitable for application in bio-agriculture. For instance, liquid or granular formulations generated from *S. entomophila*, following specific procedures, can be effectively utilized in biological pest and disease control^[134]. Overall, this diversity in approaches underscores the vast potential of *Serratia* and its metabolites in agricultural applications.

Despite various studies highlighting the agricultural benefits of *Serratia*, it also presents potential risks to human and plant health. Numerous studies have documented that several *Serratia* species can cause diseases in both humans and plants. In unfavorable conditions, microbial inoculants may behave as parasites or pathogens, escaping their intended use, invading other ecosystems, disrupting native microbiomes and posing threats to human and plant health^[135]. In scenarios involving opportunistic pathogenic *Serratia*, the absence of adequate control measures could lead to adverse consequences in treated lands and surrounding areas. Therefore, research has emphasized the importance of implementing stringent biosafety testing to mitigate these risks. Before the routine field application of bioinoculants, it is essential to establish robust regulations and a comprehensive biosafety assessment framework for plant growth-promoting bacteria (PGPB) strains, encompassing considerations for humans, animals, plants, and the environment^[136,137]. Furthermore, the use of metabolites from *Serratia* spp. is emerging as a rapid alternative approach to curb the proliferation of opportunistic pathogens. For instance, crude extracts from the cell-free supernatant of *S. marcescens* SE1 and *S. marcescens* SE2 have effectively alleviated symptoms of yellow mold disease caused by *Aspergillus flavus* in peanut plants^[129]. Similarly, extracts from *Serratia* sp. ARP5.1 have demonstrated significant efficacy in combating both root rot infections caused by *Phytophthora cinnamomi* and postharvest body rot infections caused by *Colletotrichum gloeosporioides*^[138]. Additionally, siderophore-containing extracts from *Serratia plymuthica* AED38 have proven to be a potent strategy against avocado root rot induced by *Phytophthora cinnamomi*^[139].

Thanks to advancements in genome editing techniques, we can now create non-pathogenic *Serratia* strains with robust plant growth-promoting (PGP) traits and strong biocontrol activities, paving the way for their commercialization. While various studies have explored mutant *Serratia* strains for their antibiotic production capabilities, research on mutants targeting *Serratia*'s virulence factors has been limited. We propose further research on the agricultural application of these mutant *Serratia* strains.

Conclusions

Serratia species are found in diverse environments, including soil, water, plants, and animals, and have developed mechanisms that enable them to adapt to various lifestyles. These bacteria exhibit numerous plant growth-promoting traits and produce bactericidal, fungicidal, or insecticidal compounds. Many *Serratia* strains demonstrate beneficial roles by inducing systemic resistance (ISR) in plants, sparking significant interest in their potential applications for biological control and plant growth stimulation in crop cultivation.

Despite this interest, specific aspects of the interactions between plants and *Serratia*, such as the particular compounds produced by *Serratia* that trigger plant immune responses against insect pests, remain relatively unexplored. Further studies are essential to delve deeper into these interactions and unravel the intricacies of plant-*Serratia* relationships. By investigating these relationships more comprehensively, we can better understand the potential benefits and implications for utilizing *Serratia* species in agriculture and beyond.

While this review primarily focuses on plant-associated *Serratia*, various species residing in different habitats, such as

insects, nematodes, soils, waters, or mammals, may also exhibit plant growth-promoting traits and the ability to protect plants against phytopathogens by producing antimicrobial and insecticidal compounds or by eliciting ISR. Therefore, we recommend considering non-plant-associated *Serratia* for use in bio-agriculture, as their positive effectiveness has been demonstrated in plants.

The application of live *Serratia* cells is the best way to exploit all their plant-growth-promoting and protective activities. To achieve this, it is critical to exclude pathogenic strains that are harmful to plants and animals, including humans. Identifying the genetic markers of pathogenic strains is essential in this regard. Alternatively, cell-free supernatants or their crude solvent extracts could be researched to develop biostimulation and bioprotection agents for sustainable agriculture.

Author contributions

The authors confirm contribution to the paper as follows: study conception and design: Trinh LL, Nguyen HH; data collection: Trinh LL, Nguyen HH; analysis and interpretation of results: Trinh LL, Nguyen HH; draft manuscript preparation: Trinh LL, Nguyen HH. All authors reviewed the results and approved the final version of the manuscript.

Data availability

Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

Conflict of interest

The authors declare that they have no conflict of interest.

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