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Review

Rhizobacterial Control of Root Diseases and Stimulation of Plant Growth

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Abstract: Plant growth promoting rhizobacteria (PGPR) are a diverse group of microorganisms including genera such as *Pseudomonas*, *Bacillus*, *Serratia*, *Enterobacter* and *Klebsiella*. These bacteria have the ability to colonize roots externally and internally, and to directly enhance plant growth employing various mechanisms like phytohormone production and nutrient mineralization. These microbes can also promote plant growth indirectly by secreting antimicrobial compounds (e.g., siderophores, hydrogen cyanide) to antagonize root pathogens or by inducing defensive responses in the plant. Interestingly, there are also cases where production of antibiotic compounds such as 2,4-Diacetylphloroglucinol have the direct effect of enhancing plant growth and yield, irrespective of their biocontrol effects. The objective of this paper is to review publications showcasing PGPRs that have the capacity to both control root pathogens and stimulate plant growth, and to discuss what mechanisms might be involved.

Keywords: biological control; growth promotion; antagonist; antimicrobial compounds; plant defense; soilborne pathogens

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1. Introduction

Many root pathogens can persist in and be dispersed by soil. Although root diseases are usually hard to diagnose and treat, they are economically important, estimated to cause 26% of the crop losses that are recorded around the world [1]. They are caused by a very broad group of microbes that include viruses, bacteria, fungi, oomycetes, and nematodes that invade and injure root tissues, often leading to a reduction in the plant's ability to absorb water and nutrients [2]. Soil pathogens employ chemotaxis to sense and move towards roots which secrete exudates containing sugars and amino acids in order to attract and feed beneficial microbes [3,4]. Arriving at the plant/soil interface, pathogens attach, penetrate, and invade root tissues including epidermis and vasculature, causing root rotting, shoot wilting, or alterations in the germination and growth of the seedlings [2], [5–7].

Fungi and oomycetes are the most common cause plant pathogens, responsible for some of the most severe plant diseases. One such soil transmitted fungus, *Fusarium oxysporum* enters the plant through the root and invades its vascular system, causing significant economic losses in a wide range of crops, including chickpeas, potatoes, strawberries, and tomatoes; for the latter, yield losses can be as high as 90% or 95% in Tunisian or Canadian farms, respectively [8–12]. Late blight can also be transmitted by soil and is caused by species of *Phytophthora* which can reduce potato plantation yields by up to 75% [13]. Between the years 1845-52, late blight of disease susceptible potatoes grown by Irish potato farmers led to the starvation of 1.5 million people [14]. Another soil transmitted pathogen, *Pythium* infects root tissues of both seedlings and adult plants, causing major economic losses exceeding 50% in soybean, maize and ginger crops in the United States and India [15,16]. *Rhizoctonia solani* has been reported to occur in 50-60% of rice plantations and can create infestations with losses approaching 20% [17,18], while *Meloidogyne incognita* also infects roots and can reduce yields up to 33% [19,20]. A few recent papers review root diseases and methods to manage them including chemical or biological control [21,22].

Given the severity of these diseases and the economic losses they cause, farmers have tried various techniques to control soilborne pathogens. Some techniques include organic amendments such as compost teas or liquid swine manure, while others attempt to treat the soil by withdrawing oxygen (anerobic soil disinfestation) or injecting hot steam to kill microbes [23,24]. More effective at killing soil microbes is the use of agrochemicals for disease control in crop fields [25,26]. These toxic chemicals are used to fumigate the soil before planting to reduce the inoculum of all bacteria, fungi and/or nematodes, and at the same time they can increase plant yields by improving traits such as root density and productivity [27]. Examples of these pesticides include pentachloronitrobenzene (PCNB), metalaxyl, triadimefon, etazol, propamocarb, furalaxyl, myclobutanil, nabam, chloropicrin and methyl bromide [6].

However effective at killing that these fumigants may be, excessive use of pesticides leads to problems such as economic waste, low nutrient use efficiency, reduction of soil quality (i.e. killing beneficial microbes, loss of organic matter), and environmental pollution [28–30]. It has been estimated that in some cases only 0.1% of the applied pesticide reaches the target pest, while the rest drifts into the surrounding environment where it can be incorporated into nutrient and biological cycles, thus persisting for long periods of time, and contaminating soil, water, and air where it continues to poison or affect non-target lifeforms [31–33]. Metalaxyl, triadimefon and chloropicrin have been observed to modify soil bacterial populations and fertility, reducing the function of biogeochemical cycles that are mediated by soil microorganisms [34–38]. Because methyl bromide has strongly negative effects on the ozone layer, its use has been banned in many countries in a campaign supported by the United Nations [39]. Chemicals like cypermethrin, chlorpyrifos, endosulfan, glyphosate, and 2,4-Dichlorophenoxyacetic acid, have been found to interfere with amphibian reproduction and survival [40]; flupyradifurone and neonicotinoids are pesticides that can also kill honey bees which are critical to the production of fruit crops [41–43]; pesticides like deltamethrin, hexachlorobenzene accumulate in animal tissues, leading to biomagnification throughout the food chain and early death in apex predators [44,45]. Chemical fumigants have also been reported to directly harm humans; according to the World Health Organization, more than 25 million farmers are poisoned each year by the use of agricultural pesticides [46]. Pentachloronitrobenzene (PCNB) is one example, considered by the EPA as a potential carcinogen [47], and propamocarb is another, which changes the intestinal microbiota and metabolism of mammals altering it normal function [48]. Toxic soil fumigants have many unintended negative effects, making it clearly necessary to look for alternatives that are more precise/targeted while retaining the efficiency at controlling soil pathogens.

A promising alternative to toxic fumigants is biological control, where plants are protected against root pathogens through soil application of antagonistic microorganisms, either fungal or bacterial, that kill or otherwise inhibit growth and activity of the infectious agent. Biocontrol of root pathogens may involve mechanisms such as the production of antibiotics, predation, parasitization, competitive exclusion of space or nutrients, production of enzymes that affect cellular components of the pathogen, or by the induction of defensive responses in the plant [49–51]. Many of the microorganisms that can be used for biological control in the soil are found in plant rhizospheres; a niche that is considered one of the most diverse ecosystems on Earth [52]. Many of these bacteria belong to genera such as *Pseudomonas*, *Bacillus*, *Enterobacter*, *Klebsiella*, *Serratia*, *Azospirillum*, *Chrysobacterium*, and *Burkholderia*, colonizing roots and stimulating plant growth through nitrogen fixation, phosphate solubilization, and production of growth-promoting hormones [53–57]. These microorganisms are known as plant growth-promoting rhizobacteria (PGPR), and within this group there are also some with biocontrol potential, as they can secrete siderophores, they can produce antimicrobial compounds and enzymes, or they can induce intrinsic plant defense responses such as systemic acquired resistance (SAR) [58–60]. Curiously, some antimicrobial compounds involved in pathogen biocontrol can also directly stimulate plant growth, thereby increasing plant productivity while aiding in plant defense [61–63]. PGPRs that offer the dual benefit of both controlling root pathogens and of increasing plant growth are likely to be ideal candidates for production of commercial inoculants, as big, healthy plants growing without pathogen pressure have higher yields than smaller plants under attack by soil pathogens [64,65]. The purpose of this review is to review the literature showing examples of PGPRs controlling root pathogens (especially soil-borne pathogens), while simultaneously stimulating plant growth.

2. Siderophore production

Iron is an essential mineral for the development of virtually all living organisms, acting as a cofactor approximately 140 different enzymes that catalyze biochemical reactions in primary metabolism, such as the reduction of ribonucleotides, the activation and decomposition of peroxides, and the transport of electrons through a variety of carriers [66,67]. In plants, iron is involved in the synthesis of chlorophyll, thylakoids, and chloroplasts [68] and is thus a critical mineral for growth. Under normal, aerobic conditions, soil iron is mostly present in an insoluble form (Fe3+) and is therefore not readily available for uptake by either roots or soil microbes [69,70]. To aid in uptake of soil iron, both microorganisms and plants secrete low molecular weight compounds called siderophores, which have a high affinity for this element and are easier to take up than the pure mineral [71]. One of the most common siderophores is pioverdine, a greenish-yellow, fluorescent pigment produced by bacteria of the genus *Pseudomonas*; cosmopolitan microorganisms that are frequently found in plant roots as growth promoters [72]. A *Pseudomonas* that has locked up a significant amount of soil iron using its pioverdine has increased the amount of iron available to itself, while blocking its access to other microbes which lack mechanisms to take up pioverdine. Next to *Pseudomonas*, *Bacillus* is the genus with the most examples of siderophore producing PGPR, where they secrete molecules like bacillibactin, hydroxamate, pyoverdine, pyochelin, 2,3- dihydroxybenzoic acid (DHBA), etc. to chelate soil iron [73–76]. Because of these properties, siderophores have become one of the best-known mechanisms of microbial biocontrol, depriving soil pathogens of this element, thus limiting their ability to proliferate and infect the root [77–79].

Siderophore based root pathogen biocontrol plus plant growth stimulation has been demonstrated by rhizobacteria such as *Pseudomonas aeruginosa*, *Pseudomonas putida* and *Pseudomonas alcaligenes*, which can inhibit up to 80% of wilt symptoms caused by *F. oxysporum* in tomato plants [80] or which significantly reduce nematode (*Meloidogyne javanica*) egg hatching, lentil root infection and disease gall formation when they are applied as a soil drench [81]. Bacteria of the genus *Bacillus* like *B. amyloliquefaciens* or *B. subtilis* also have the ability to produce siderophores such as bacillibactin, a molecule involved in the *in vitro* inhibition of pathogens like *Rhizoctonia solani*, *F. oxysporum* f. sp. *radicis-lycopersici* or *Pseudomonas syringae* pv. *tomato* [82]. Inoculation of siderophore producing strains of *Bacillus* onto roots infected with *Pyricularia oryzae* can reduce rice blast disease symptoms by up to 80% [83–85]; inoculation of biocontrol *Bacillus* into potato and banana roots inhibited disease caused by *F. oxysporum* and *P. infestans* by up to 88% and 65% respectively [86,87]. In addition to *Pseudomonas* and *Bacillus*, siderophores have also been documented in bacteria of the genera *Serratia*, *Azospirillum*, *Enterobacter, Burkholderia* and *Klebsiella*, where they have been implicated in the control of a wide range of plant pathogens such as *Colletotrichum acutatum*, *F. oxysporum* f. sp. *radicis lycopersici* (FORL), *Botrytis cinerea, Cryphonectria parasitica, Rhizoctonia cerealis, Valsa sordida* and *R. solani*, reducing plant disease symptoms by up to 48% in crops including rice, sunflower, strawberry and tomato [88–99]. Experiments with cell free, siderophore rich supernatants have various times been shown to have strong antimicrobial properties even compared with chemical fungicides like carbendazim [100,101] and have even found use as agricultural products in of themselves [72,102,103]. The use of siderophore producing strains of PGPR for biocontrol of root diseases have been reviewed especially for the application of *Pseudomonas* and *Bacillus* for controlling root pathogens [104–106] such as *Cephalosporium maydis*, *R. solani* and *Colletotrichum gloeosporioides* in maize and chilli [107,108]

Besides controlling disease, PGPR produced siderophores can also stimulate plant growth, most likely by alleviating disease pressure, reducing abiotic stress, improving plant mineral nutrition, and by influencing levels of phytohormones present in the rhizosphere. It has been shown experimentally that *Streptomyces*-derived, cell-free liquid supernatant containing siderophores and auxins, when added to heavy metal contaminated soil can increase the amount of iron absorbed by cowpeas, increase chlorophyll content, and reduce both lipid peroxidation and free radical formation, which in turn protected microbial auxins from degradation, allowing them to accumulate and enhance plant growth [109]. Inoculation of mung beans in both gnotobiotic and soil-based growth assays showed that the siderophore 17X overproducing mutant *Pseudomonas fluorescens* ATCC 13525 stimulated significantly more plant growth than inoculation with the wildtype strain did 61. Another study of a strongly wheat growth promoting and *Pythium* inhibiting strain of *Pseudomonas* showed that when siderophore production was eliminated by mutation, both biocontrol and plant growth promotion were also eliminated [110]. In several trials where *Vigna radiata* plants were inoculated with different strains of siderophore producing *Pseudomonas*, root and shoot growth stimulation correlated with an increase in chlorophyll synthesis and the iron available to the plant [61,111]. Inoculation of chickpea plants with *P. fluorescens* resulted in increases of dry root biomass of up to 70% [112]. Roots of potato plants colonized by strains of siderophore-producing *P. fluorescens*, enjoyed an enhanced tuber yield of up to 144% although the exact mechanism involved was unknown [113]. An endophytic, siderophore producing *Streptomyces* isolated from the roots of rice was able to significantly increase the length and biomass of pot grown rice and mungbean plants, in contrast to untreated controls and siderophore-deficient mutant treatments which didn't – the authors speculate that this growth promotion was due to improved plant mineral nutrition [114]. Several reports of siderophore producing and plant growth promoting bacilli exist: a strain of *B. subtilis* in pepper plants where it enhanced plant development, resulting in an increase of up to 50% and 37% in size and fruit weight respectively [115]; *Bacillus shackletonii* in pot grown soybeans had up to 20% increases in germination rate, 20% increases in root length and 230% increases in shoot length [116]; bacillibactin-producing *B. subtilis* improved the growth of *Sesamum indicum* maintained in pots by up to 32% in leaf length, 39% in shoot length, 43% in root length and 27% in fresh weight [73]. The contribution of *Bacillus* to crop biocontrol and growth promotion has recently been reviewed [117]. Meta-analysis of over 300 publications on siderophore-producing bacteria found that they also consistently stimulate plant growth, particularly in the plant families Musaceae, Solanaceae, Cucurbitaceae, Cruciferae, and Poaceae, with an average observed increase of up to 30% in plant weight, height, and germination rate [118]. Another interesting review contrasts the biocontrol and plant growth potential of the two most important siderophore producing plant growth promoting rhizobacteria (PGPR); *Pseudomonas* and *Bacillus* [119].

3. Production of antimicrobial compounds

Many growth-promoting bacteria are known to also produce antimicrobial compounds [120]. The main way that rhizobacterial biocontrol could improve plant growth is the same way that soil fumigation with toxic compounds can benefit agricultural production: killing root pathogens liberates plants from wasting resources fighting disease, allowing root systems to function at 100% capacity, delivering the maximal amount of nutrients and water to the shoot [21,121]. The genus *Pseudomonas* has been most extensively found to display these two traits [122,123], promoting plant growth while also producing antimicrobial compounds such as hydrogen cyanide (HCN) [124,125], 2,4-diacetylphloroglucinol (DAPG) [126], phenazines [127,128], cyclic lipopeptides [129,130], pyrrolnitrin [131], and pyoluteorin [132]. There are also reports of *Pseudomonas* producing volatile organic compounds (VOCs) such as 2-nonanone, acetic acids, 2-undecanone, m-cymene, dl-limonene, dimethyl disulfide and dimethyl trisulfide, which inhibit plant pathogens such as *Sclerotinia sclerotiorum* [133]. Application of antimicrobial producing *Pseudomonas* to crop plants has increased the growth rate up to 33% for bean [134]. Several recent reviews also cover the application of antimicrobial producing pseudomonads to improve crop yields [135–137]

Besides *Pseudomonas*, there are also other genera of rhizobacteria producing antibiotics that control root pathogens. Biocontrol strains from the genus *Bacillus* possess genes encoding antimicrobial compounds such as surfactins, phengicins, kurstakins, bacilicin, bacillomycins or microcin that can limit the growth of plant pathogens such as *R. solani*, *Fusarium solani, Schizophyllum commune, Macrophomina phaseolina* and *Fusarium graminearum* [138–141]. Other substances that are toxic to the plant pathogenic nematode *Meloidogyne incognita*, have also been identified in *Bacillus megaterium* and *Bacillus thuringiensis*, including benzene acetaldehyde, 2-nonanone, decanal, 2-

undecanone, dimethyl disulfide [142,143]. Other genera of PGPR such as *Enterobacter, Chryseobacterium, Burkholderia*, and *Klebsiella* contain strains having the ability to synthesize surfactins, kurstakins, phengicins, and bacillomycins, which have been shown to successfully inhibit pathogens such as *Phytophthora capsici*, *R. solani*, and others [144–147]. There are many good recent reviews about biocontrol courtesy of antibiotic producing PGPRs [104], [148–150].

Amongst the antimicrobial compounds mentioned above, DAPG is of special interest as it has a dual effect on plant phenotype as shown in Figure 1. DAPG is thought to derive its antimicrobial properties by degrading barrier structures and permeabilizing membranes/walls [151,152]. This antibiotic is produced by many growth promoting pseudomonads such as *P. protegens*, *P. chlororaphis* and *P. brassicacearum*, which have strong inhibitory effects on root pathogens such as *R. solani* [123,153]. While serving to inhibit microbial growth, DAPG can also be perceived by the plant as a growth promoting hormone and can increase carbon availability in the rhizosphere by stimulating root exudation [154]. This compound has been shown to modify *Arabidopsis thaliana* and maize root architecture [155]. In tomato and pea plants, DAPG produced by *P. fluorescens* increased the biomass of plant roots by increasing their length and weight, and also stimulated lateral root development [62,156]. Similarly, in maize plants, this compound improved plant vigor while enhancing phosphorus and magnesium uptake [157].

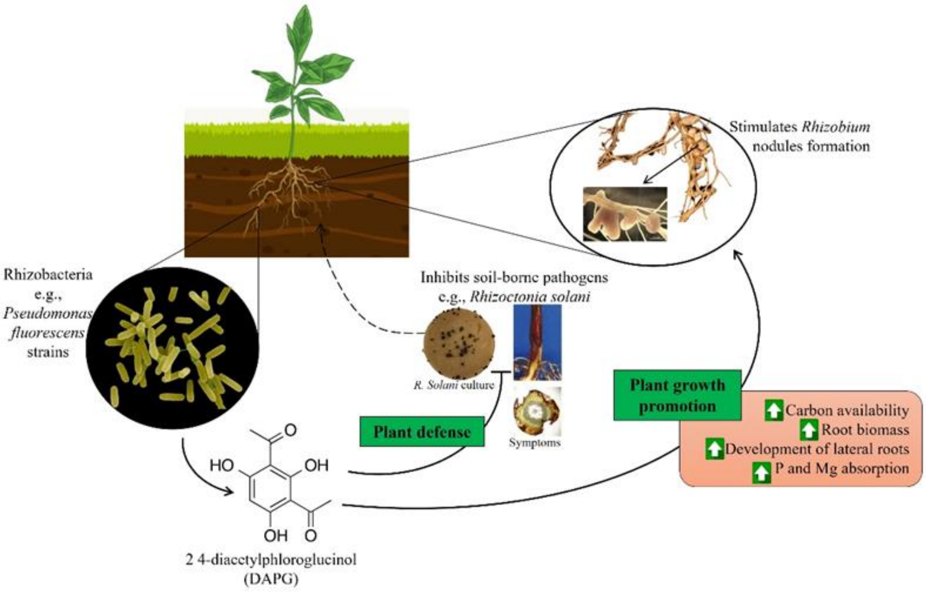

Figure 1. Mechanisms of plant growth promotion and pathogen biocontrol mediated by DAPG produced by growth-promoting pseudomonads. DAPG can directly inhibit the growth of soilborne pathogens such as *R. solani*. At the same time, DAPG may also be directly associated with the enhancement of plant traits such as root biomass and lateral root development and may also contribute to nutrient availability. This compound is also beneficial in the recruitment of Rhizobium, which promotes the formation of root nodules and nitrogen fixation.

There are reports that the use of DAPG-producing bacteria enhanced the formation of pea root nodules by *Rhizobium leguminosarum*; this plant phenotype which was lost when inoculating with mutant bacteria lacking DAPG production [158]. It was theorized by the authors that this effect occurred because DAPG increases the concentration of organic acids in the rhizosphere, providing chemotaxtic cues to help *Rhizobium* discover and migrate to the roots [159]. Yet another beneficial effect of DAPG is its ability to stimulate the growth and activity of other beneficial rhizobacteria. When DAPG producing *Pseudomonas* were co-inoculated with plant growth promoting *Azospirillum* into wheat rhizospheres, plants showed an increase in root growth relative to plants inoculated with any single strain or the DAPG- mutant *Pseudomonas* [160]. The authors observed that DAPG was stimulating *Azospirillum brasilense* Sp245-Rif by increasing its expression of phytostimulatory genes

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such as ppdC, flgE and nirK, improving the rhizobacteria's establishment and colonization of the roots and the rhizoplane.

Like DAPG, HCN can have a dual effect on plants. This compound can be produced by bacteria of the genera *Chryseobacterium* and *Pseudomonas*, controlling tomato root infections (reducing symptoms up to 80%) caused by soilborne pathogens such as *F. oxysporum* [80,161,162]. As an antimicrobial, HCN is a strong inhibitor of metalloenzymes including cytochrome c oxidase and is therefore toxic for all forms of aerobic life [163]. In plants that have evolved mechanisms to avoid cyanide intoxication, HCN can also act as a plant growth promoter, as was found in tobacco plants where HCN produced by *P. fluorescens* stimulated lateral root growth [164]. Specifically, HCN can enhance rhizosphere microbiome production of indole acetic acid, antibiotics, fluorescent insecticidal toxins, and 1-aminocyclopropane-1-carboxylate deaminase, all of which can result in plant growth promotion [165]. HCN also appears to be able to increase the bioavailability of important plant nutrients, for example by forming complexes with soil phosphorus and increasing its solubility but the exact mechanism is unknown [166].

PGPR production of the antimicrobial VOCs undecanone and heptanol also has the dual effect of fungal biocontrol and plant growth promotion. *B. subtilis* GB03 and *B. amyloliquefaciens* producing 2-heptanol and 2-undecanone, promote the growth of *Arabidopsis thaliana* [167,168] and watermelon [169] while also being the biocontrol agents in Kodiak Flowable Fungicide and Kodiak Concentrate Fungicide, suppressing root diseases caused by *Fusarium* spp. and *R. solani* on canola, mustard, rapeseed, and soybeans [170] or reducing fusarium wilt symptoms in watermelon [169].

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

PGPR can participate in the activation of intrinsic plant defense responses by releasing elicitor molecules (elicitins) or producing microbe-associated molecular patterns (MAMPs) [171,172] that modulate the plant's physiology, triggering increased resistance to pathogen invasion; these phenomena are known as induced systemic resistance (ISR) or systemic acquired resistance (SAR). Once MAMPs and elicitins are perceived by the plant, ISR or SAR involves long (or short)-distance signaling within the plant which means it can manifest systematically throughout the plant [150,173]. Plant signaling cascades involve compounds including jasmonic acid (JA), ethylene (ET) for ISR, and for SAR the most common is salicylic acid (SA) [174,175]. Plants that have undergone ISR and/or SAR are primed to respond quickly and more vigorously to pathogen invasion, having accumulated large quantities of transcription factors and signaling molecules [176,177]. ISR primed plants are also better able to resist abiotic stress, which could explain how they could show growth promotion even without pathogen pressure [178]. It has been observed that the production of compounds such as reactive oxygen species (ROS) in response to ISR or SAR plays a pivotal role in enhancing the stress tolerance of plants. This phenomenon aids in bolstering their resistance to factors like heat or elevated salt concentrations [179]. This effect was notably evident in rice plants inoculated with the *Pseudomonas* strain BaC1-38. This particular strain demonstrated the ability to activate pathogenesis-related proteins (PRs) alongside ROS. This study revealed that, besides inhibiting the pathogenic bacteria *Xanthomonas campestris*, it also conferred increased tolerance to salt concentration in the plants [180]. Furthermore, experiments with mutant plants exhibiting alterations in ROS regulation showed heightened sensitivity to a diverse range of abiotic stresses [181].

Crop plants induced to exhibit Induced Systemic Resistance through inoculation with Plant Growth-Promoting Rhizobacteria like *Serratia marcescens, Bacillus pumilus, Bacillus velezensis* or *Pseudomonas azotoformans* can demonstrate reductions of up to 50% of disease symptoms caused by pathogens like *P. capsici, F. oxysporum* in tomato [182], *Xanthomonas axonopodis* pv. *vesicatoria* in sweet pepper [183] or *F. graminearum* and *F. moniliforme* in wheat [184]. In another example, the commercial strain *B. subtilis* MBI600 inoculated onto tomato plants triggered SAR and greatly enhancing resistance to the pathogens *R. solani*, *Pythium ultimum* and *F. oxysporum* f.sp. *radicis-lycopersici*-Forl; reducing tomato disease symptoms from 38 to 47% [185,186]. The strain *B. amyloliquefaciens* SQR9 inhibits *B. cinerea* on *A. thaliana* roots by activating signaling cascades related to the salicylic acid which is typical in SAR [187].

Many of the plant signaling compounds involved in ISR and SAR signaling can also stimulate plant growth. These molecules include salicylic acid which is an important intermediary in systemic acquired resistance which has been shown to improve vegetative growth, physiological\biochemical characteristics, and to increase the number of flowers, fruits, and seeds in plants such as *Sinningia speciosa, Foeniculum vulgare* and *Artemisia annua* [188–190]. Like salicylic acid, there is some evidence that jasmonic acid (important in activating induced systemic resistance) can also act as a growth regulator, stimulating the development of buds and adventitious roots in potato cuttings, while in *in vitro* cultures of garlic, jasmonic acid significantly enhances the development of shoots and bulbs [191–193].

Microbial induction of ISR has been reported for many groups of bacteria, although one of the first was *P. fluorescens*, which had the ability to induce defense responses in carnation (*Dianthus caryophyllus*), making them more resistant to wilting caused by *Fusarium* sp. [194]. Another strain of this genus, called EA105, triggered ISR to *Magnaporthe oryzae* involving a jasmonate- and ethylene-dependent pathway – resistant plants reduced the pathogen's formation of appressoria [195]. Inoculation of rice with two different strains of *P. fluorescens* led to induction of systemic resistance against sheath blight fungus *R. solani*, increased the seedling vigor, promoted plant growth, and increased yields under both glasshouse and field conditions [196]. Similarly, application of either *P. putida* or *P. aeruginosa* (isolated from roots of healthy tomatoes in Pakistan) to tomatoes triggering ISR, significantly reducing fusarium wilt (reducing symptoms by >60%) while significantly increasing vegetative biomass and fruit yield [197].

Bacillus also has the ability to induce such responses through jasmonate- and ethylene-dependent pathways that control pathogens such as *Phytophthora infestans*, fungi, and nematodes [198,199]. In sugarcane plants, *Bacillus* strains have been reported to increase the levels of ISR-related metabolites, particularly phenylalanine ammonia lyase (PAL), polyphenol oxidase (PPO), and peroxidase (PO), which could stimulate the synthesis of phytoalexins and thus control pathogens such as *Colletotrichum falcatum* [200]. Examples of a species of *Bacillus* both triggering ISR and promoting plant growth or yield includes a *B. pumilus* strain in pepper plants that stimulates induction of plant defense against *Xanthomonas axonopodis* pv. *vesicatoria* and at the same time the plants had a higher weight and chlorophyll content [183]. Similarly, soil application of the commercial strain *B. subtilis* MBI600 to tomatoes increased shoot and root lengths (perhaps by secreting auxin) while inhibiting the soilborne pathogens *R. solani*, *P. ultimum*, and *F. oxysporum* f.sp. *radicis-lycopersici*-Forl; mechanisms involved were ISR triggered by signaling cascades depending on jasmonic acid and ethylene [186].

There are some examples of other genera of bacteria besides *Pseudomonas* and *Bacillus* that have the ability to induce ISR in plants. These include *Serratia, Azospirillum* and *Enterobacter*, which can activate plant genes related to plant defense response (i.e. PR1a, PR1b, PR2, PR5, and PDF1. 2) which can result in the increased production of reactive oxygen species [201–203] and the successful inhibition of pathogens such as *Heterodera glycines, F. oxysporum* or *R. solani* [203–205]. *Serratia marcescens* 90-166 for example can both trigger ISR and increase *A. thaliana* growth and seed yield – these responses involved jasmonate and salicylic acid-dependent signaling [63,206].

5. Quorum Sensing System (QS)

A plant's defensive responses can be triggered by the detection of molecules being released by nearby microbes. Many of these MAMPs are associated with microbial virulence, such as flagellin or the signals bacteria use to coordinate their invasion once enough cells are available; the so called "quorum sensing" (QS). QS or autoinduction, is a cellular communication mechanism mediated by the release of quorum sensing molecules, which in gram-negative bacteria are often N-acyl homoserine lactones (AHL) and in gram positive bacteria are often small peptides [207]. These systems have been reported in a wide variety of bacteria associated with plants, where they may participate in symbiotic or pathogenic relationships between microorganisms and their hosts [208,209]. Some PGPRs are known to depend on AHL for QS and to coordinate activities beneficial for plant growth. In one example, a QS- mutant *Serratia* stopped producing nucleases, lipases,

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chitinases, proteases, prodigiosin and beta-lactam antibiotics that are involved in their biocontrol activity [210]. Strains of endophytic *Pseudomonas* isolated from *Salicornia europaea* possess QS dependent bacterial phytopathogen biocontrol capacity when inoculated into tomato plants [211]. Similarly, when QS was compromised in mutant *P. chlororaphis*, its ability to control the pathogen *S. sclerotiorum* in canola was also diminished [212]. Many other reports exist of QS negative mutants such as *P. putida*, *Serratia liquefaciens* and *Serratia plymuthica* losing their capacity to produce antibiotics and inhibit pathogens such as *Pythium aphanidermatum*, *Alternaria alternata* and *Verticillium* sp. [213–215].

As many pathogens also employ QS to coordinate infections, it should come as no surprise that plants have evolved a sensitivity to the molecules involved. QS molecules such as AHLs can trigger ISR resulting in upregulation of PR1 and chitinases [203,213]. These molecules can induce plant membrane hyperpolarization, facilitating the entry of ions such as K+ into the root [216]. Additionally, QS molecules have been shown to influence the nitrogen cycle, enhance root development, and influence its architecture [207,217].

Plants so primed by exposure to QS molecules can much better survive biotic and abiotic stress [218,219]. In one example AHL-producing *Burkholderia graminis* can increase tomato salt stress tolerance [220]. The same phenomenon has been observed in wheat and *A. thaliana*, where the presence of AHL enhanced salt stress tolerance involving ABA-dependent and independent signaling pathways [221]. In another report, wheat plants inoculated with acyl homoserine lactone (AHL)-producing *Aeromonas* strains, enjoyed improved salt tolerance, and significant improvement in root growth [222].There are also examples where AHLs such as N-hexanoyl-L-homoserine lactone (C6-HL) or N-3-oxo-hexanoyl homoserine lactone (3-oxo-C6- HL) can promote root elongation by increasing expression of plant growth and auxin/cytokinin signaling genes [223–226]. Tomato and *A. thaliana* plants inoculated with *Pseudomonas* and *Serratia* strains that produce AHLs, experienced enhanced seedling vigor and also displayed modifications in their root architecture, stimulating the development of lateral roots [227,228]. In a notable study, seed application of C6-HSL (a specific type of AHL) to two Ukrainian wheat varieties followed by field growth over two years, significantly increased vegetative biomass, increased grain yield by up to 50% and improved grain quality by up to 30% [207].

6. Antibiotic enzyme Production

A mechanism employed by some growth-promoting bacteria to antagonize competing microbes is the secretion of antibiotic enzymes. This trait has been documented in a wide variety of bacterial groups such as *Bacillus, Pseudomonas, Serratia, Burkholderia, Azospirillum* and *Enterobacter*. Enzymes such as β-1,3-glucanases, proteases, chitinases, and cellulases can inactivate pathogens by degrading their structural components (i.e. cell wall) [229]. Extracellular enzymes might also interfere with pathogen quorum sensing [230] or with pathogen camouflage and chemotaxis [231]. Reports of rhizobacterially produced enzymes controlling phytopathogens include *F. oxysporum, Pyricularia oryzae, R. solani, Aspergillus niger, F. solani, Schizophyllum commune, Macrophomina phaseolina* and *F. graminearum* [80,83,99,141,201,232]. Several recent reviews also cover this subject well [233–235].

Glucanases are one powerful tool that biocontrol strains might use to control pathogens, since 1,3-glucan (commonly called laminarin) is a critical structural component of all fungal cell walls [236]. Fungi exposed to substantial quantities of microbe-derived glucanase undergo growth inhibition, as their cell walls weaken due to the degradation of polymers. This degradation ultimately results in cellular death, brought about by the loss of cellular integrity [237,238]. Examples where PGPR control fungal pathogens by secretion of glucanases include *R. solani* [239] and *S. sclerotiorum* [239–241]. There are also examples of sugarcane derived PGPR *Bacillus* secreting glucanases into the rhizosphere to control *R. solani, F. oxysporum* and *Fusarium moniliforme* [242,243]. The involvement of microbe derived hydrolytic enzymes in plant pathogen control has been reviewed recently [229]. Although there is not much published on the capacity of microbial glucanases to directly influence plant growth, there is emerging evidence that these enzymes are involved in plant-microbe interactions [244].

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Chitinases are another set of enzymes that are widely reported to be produced by PGPR; among them strains of *Klebsiella, Serratia*, and *Enterobacter* [245,246]. Chitinases are especially able to antagonize fungi whose cell walls contain chitin, which is essential for structural stability providing anchor points for other components at the cell surface. Bacteria secreting chitinases have been shown control fungal pathogens including *Botrytis cinerea* and *R. solani*, reducing the incidence of these related crop diseases in field trials by 76% and 84% respectively [88,247]. In addition to their antagonistic activity, growth-promoting bacteria with chitinolytic activity have also been associated with plant growth; for example, bacteria of the genera *Pseudomonas* and *Bacillus* with high chitinolytic activity increased germination in pigeon pea (*Cajanus cajan*) and in another example, a root inoculation with a chitinolytic strain of *Streptomyces* was associated with increased biomass in chickpea [245,248]. Cell free extracts of *Chromobacterium* sp. C61 contain both extracellular chitinase and a cyclic lipopeptide which contribute to its biocontrol activity against a number of root pathogens (e.g. *R. solani, F. oxysporum* and *Colletotrichum gloeosporioides*) in tomato plants – chitinase negative mutants had significantly lower biocontrol activity [249]. Transgenic expression in tomato plants of the endochitinase and chitobiosidase genes from *Streptomyces albidoflavus* significantly increased flowers and fruit yield [250]. The mode of plant growth promotion employed by PGPR secreted chitinases likely involves the creation of elicitins like chitosan from the breakdown of fungal cell walls, which are in turn perceived by the plant, triggering ISR [251]. In an example of this principal, externally applied chitooligosaccharides enhance the growth of *Brassica rapa* by up to 27% under greenhouse conditions [252]. The influence of microbial chitinases on plant growth has recently been reviewed [253,254].

Many pathogens coordinate their attacks by molecular communication termed quorum sensing – bacteria that secrete enzymes to degrade these molecules can thus serve as biocontrol agents. The best-known molecule involved in quorum sensing is called N-acyl homoserine lactone (AHL) – it is used by bacterial phytopathogens such as *Pectobacterium carotovorum*. Enzymes involved in degradation of AHL (also known as quorum-quenching enzymes) include lactonases and acylases [255] and there are reports of bacteria with these enzymes both controlling phytopathogens and increasing crop yields or plant growth [256,257]. Interestingly, one study describes that inoculation of chickpea with growth promoting *Bacillus* triggered the plant to increase its own production of quorum quenching enzymes, although some of these may have been bacterially produced enzymes as well [258]. While the mechanism of biocontrol is quite strait forward (disrupting pathogen communication and coordination) it is harder to imagine how these enzymes could influence plant growth. One possibility implies that since the quorum quenching system may also be related to the communication among growth-promoting bacteria, it is possible that it could influence the formation and balance of these communities, thus impacting the growth and yield of plants [259–261].

The study of fungal quorum sensing is relatively new, but it has been shown to involve pheromones, lipids, lactones, volatile organic compounds, tyrosol and farnesol [262]. To our knowledge, no studies have yet been done on PGPR enzymes interfering with fungal quorum signaling.

7. Conclusions

Rhizosphere microbiology has for many years attracted much scientific and agronomic attention, promising to help protect roots from disease while stimulating plants to grow bigger and healthier, resulting in higher yields [56,263]. Bacteria in a plant's rhizosphere that can both protect the roots against disease while stimulating plant growth and increasing yield, could be the "superheroes" that every farmer hopes will dominate in their soils. The mechanisms used by such PGPRs to both control pathogens and stimulate plant growth include production of siderophores, antipathogen enzymes, antimicrobial compounds, quorum sensing molecules (especially N-acyl homoserine lactones), and various elicitins, MAMPs and priming agents. The most common examples of these dual wielding microbes hail from the genera *Pseudomonas* and *Bacillus*, however there are some other examples including *Serratia*, *Azospirillum* and *Enterobacter*. Commercial products exist for some of these dual action PGPR, such as *Bacillus strains* MBI600 or GB03 in the products Integral® and Kodiak®

respectively [264,265] and *Pseudomonas* strain MA342 in the product Cedomon® [266]. It is easy to understand that effective biocontrol can aid the plant by reducing pathogen pressure, but how these mechanisms of biocontrol are also able to stimulate plant growth is still an area of research that needs to be developed.

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