Review

Bacterial Bioprotectants: Biocontrol Traits and Induced Resistance to Phytopathogens

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Abstract: Plant growth and nutrition are adversely affected by various factors such as water stress, high temperature, and plant pathogens. Plant-associated microbes play a vital role in the growth and development of their hosts under biotic and abiotic stresses. The use of a rhizosphere microbiome for plant growth stimulation and the biological control of fungal disease can lead to improved crop productivity. Mechanisms used by plant-growth-promoting rhizobacteria (PGPR) to protect plants from soilborne pathogens include antibiosis, the production of lytic enzymes, indole-3 acetic acid production, decreasing ethylene levels by secreting 1-aminocyclopropane-1-carboxylate deaminase, competition for nutrients and niches, parasitism and induced systemic resistance. In this review, we emphasize the biological control of plant pathogens by root-associated microbes and discuss traits involved in pathogen reduction. Future research should focus on the effect of root exudation on plant–pathogen interactions under various abiotic factors. Moreover, the development of microbial fungicides with longer shelf lives will help farmers to opt for organic agriculture, reducing the use of chemical fertilizers. This trend is expected to drive the adoption of biological control methods in agriculture. The future prospects for the biological control of plant diseases are bright and are expected to play an increasingly important role in sustainable agriculture.

Keywords: root-associated microbes; biological control; plant-beneficial traits; pathogens

1. Introduction

Crop production is essential for feeding the world's growing population, which may reach 9.8 billion by 2050 [1]. Sustainable crop production is necessary to ensure that everyone has access to a sufficient and nutritious diet. Moreover, proper crop production ensures income for farmers, creates jobs in the agricultural sector, and contributes to overall economic growth.

There are several reasons why crop production is reducing in many countries. Climate change can have a significant impact on crop production, as extreme weather events, drought, floods, and changes in temperature and rainfall patterns can negatively affect crop yields and quality. Pests and diseases can cause significant damage to crops, leading to reduced yields and lower-quality produce. Moreover, soil degradation and water scarcity can limit crop production. Overall, these factors, either alone or in combination, can lead to

reduced crop production and threaten food security for communities and regions around the world. It is therefore important to address these challenges and develop sustainable agricultural practices to ensure food security and environmental sustainability for current and future generations [2,3].

Plant pathogens and pests cause economic losses with decreasing global annual agricultural production [4]. Plant pathogens are spreading due to abiotic factors such as drought, salinity, temperature, the overuse of agrochemicals, and the development of pathogens resistant to pesticides. Approximately 20–40% of these losses occur due to pathogenic infections caused by bacteria, viruses, and fungi, and the estimated economic losses due to this equal USD 40 billion annually [5]. Plant susceptibility is a vital factor in disease development and host–pathogen interactions, which are affected by abiotic stresses such as drought, salt stress, temperature and humidity [6]. While chemical-based fungicides have played a significant role in securing crop production, their indiscriminate use has led to the development of resistance in plant pathogens and potential risks to human health and the environment. The search for new bioactive natural products, particularly from endophytic fungi, is crucial in the development of sustainable and environmentally friendly methods for controlling plant diseases [7,8].

The plant rhizosphere is a very complex system that includes various microbes such as bacteria and fungi that compete for the nutrients and niches [9,10]. Bacteria that reside in the rhizosphere region and have a symbiotic relationship with the plant are known as plant-growth-promoting rhizobacteria (PGPR) [11–14]. Soil microbial activity plays important roles in nutrient cycling, also regulating the dynamics of organic matter decomposition. This process ensures nutrient availability for plant growth and physiological processes [15]. It is well-known that plants are associated with beneficial microbes, which play a key role in plant health and fitness [16–18]. Microbe–plant signaling is an important process in the selection of bacteria by the host plant, which is crucial for the colonization of plant tissues [19,20]. Among these microorganisms, endophytes are quite effective against plant phytopathogens. Endophytic bacteria colonize the internal tissues of the root, the root cortex, phloem, and xylem and form biofilms [21–23]. Plant-beneficial microorganisms belong to several genera and are able to modulate plant physiological process, helping them to survive in their environment [24,25]. Many of these species show an antagonistic effect against a wide range of plant pathogenic fungi such as *Fusarium*, *Phizoctonia*, *Aspergillus*, *Cylindrocarpon*, *Phytophthora*, *Pythium*, etc., and are considered as biological control agents (BCAs) [26,27]. BCAs are potential alternatives for agrochemicals used in horticulture, vegetables and crops [28]. For example, the *Pseudomonas* spp. strain with biological control traits was able to inhibit *Verticillium* wilt of cotton in the field [29]. It is known that *Pseudomonas* actively colonize the rhizosphere and effectively reduce the incidence of root disease in many plants [30]. *Bacillus* species are also known as potential biocontrol agents against plant fungal pathogens. Khan et al. [31] observed the strong antagonistic activity of *Bacillus subtilis* 30VD-1 against *Fusarium* spp. under in vitro conditions. The inoculation of pea seeds with *B. subtilis* 30VD-1 reduced wilt severity in plants and improved plant growth and development compared to uninoculated plants growing in *Fusarium*-infested soil. The authors also studied the mechanisms of action in pathogen suppression and plant growth by bacterial inoculants and found that *B. subtilis* synthesized chitinase, volatiles, and other antifungal compounds. Similar results were observed for cucurbis, where *B. subtilis* reduced powdery mildew caused by *Podosphaera fusca* [32] and tomato root rot caused by *Fusarium oxysporum* f. *spradicis-lycopersici* [33].

The traits involved in plant growth stimulation and tolerance to abiotic stresses by endophytic bacteria have been commonly reported and reviewed in previous studies [34,35]. PGPR act as biotic elicitors that carry out the synthesis of secondary metabolites in plants [36]. When plants are damaged by pathogens such as fungi, bacteria and pests, various defense mechanisms are initiated. A plant cell, attacked by pathogens and pests, is self-destructive (hypersensitive) and produces antimicrobial secondary metabolites (phytoalexins) and proteins with antimicrobial properties. Many scientific reports have described and tried to

understand the ability of endophytes to protect the host from pathogens. Some examples of direct and indirect mechanisms exploited by endophytes are summarized and discussed in this review. The possible mechanisms of the biocontrol of plant pathogens by beneficial microbes are (i) indole-acetic acid (IAA), gibberellin and cytokinin production, [37,38], and the synthesis of ACC deaminase, cellulase, chitinase, proteinase, and glucanase enzymes; (ii) the production of antifungal and antibacterial compounds [39]; (iii) the induction of systemic resistance (ISR) [34]; and (iv) competition for nutrients and niches in the rhizosphere [40]. Some examples of microorganisms with biological activity against plant disease are given in Table 1.

Table 1. Biological control of plant pathogen by plant-beneficial bacteria.

Plant Beneficil Bacteria	Host Plant	Pathogen(s)	Reference
Microbispora sp. *Streptomyces* sp.	Field mustard *(Brassica rapa)*	*Plasmodiophora brassicae*	Lee et al. [41]
Streptomyces sp.	Tomato *(Solanum lycopersicum)*	*Fusarium proliferatum*	Passari et al. [42]
Streptomyces sp.	Black kennedia, *(Kennedia nigriscans)*	*Pythium ultimum, Rhizoctonia solani, Phytophthora cinnamomi*	Catillo et al. [43]
Streptomyces ochraceiscleroticus Leifsonia xyli, Microbacterium sp.	Red sage *(Salvia militiorrhiza),* Tumeric *(Curcuma longa)*	*Fusarium oxysporum, Curvularia lunata, Botrytis cinerea*	Zhao et al. [44]
Brevibacterium sp.	*Ferula sinkiangensis*	*Alternaria alternate, Verticillium dahlia*	Liu et al. [16]
Bacillus sp.	Sugar beet *(Beta vulgaris L.)*	*S. rolfsii*	Farhaoui et al. [45]
Bacillus licheniformis	Banana *(Musa sp.)*	*Fusarium oxysporum f.sp. cubense*	Yadav et al. [46]
Lysinibacillus sp., *Pseudomonas fluorescens*	Potato *(Solanum tuberosum)*	*Ralstonia solanacearum that*	Dijaya et al. [47]
Bacillus velezensis a	Rice *(Oryza sativa)*	*Burkholderia glumae*	Perea-Molina et al. [48]
Pseudomonas aeruginosa Bacillus subtilis	Turmeric *(Curcuma longa)*	*Rhizoctonia solani Fusarium solani*	Chenniappan et al. [49]

Moreover, plant-beneficial bacteria are capable of solubilizing insoluble forms of phosphorus (P) in soil, making it available for plant uptake. These bacteria play an important role in the biogeochemical cycle of P, which is a vital nutrient for plant growth [50]. They can solubilize the insoluble form of phosphorus by secreting organic acids, phosphatases, and other enzymes that break down the complex phosphorus compounds into simpler forms, such as soluble orthophosphate, which plants can readily absorb. These mechanisms can work alone or in combination to suppress plant pathogens and protect crops from disease.

2. Mechanisms of Action of Microbial Biocontrol Agents

2.1. Production of Phytohormone

Rhizosphere bacteria have the ability to produce the phytohormones that play important roles in processes such as cell division in symbiotic as well as non-symbiotic plant

roots [51]. Phytohormones are mainly classified as gibberellins, cytokinins, ethylene and auxins that affect plant–microbe associations [52,53]. They can enter plants through different mechanisms. One is through direct contact with the plant roots, whereas microbial hormones diffuse into the root cells and are transported throughout the plant [54]. Additionally, some microbes can produce hormones that are released into the soil, where they can be taken up by the roots of nearby plants. This is known as allelopathy, where one plant produces chemicals that affect the growth of other plants [55]. The microbial phytohormones stimulate plant development and enhance plant tolerance to abiotic and biotic stresses [35,56]. Moreover, previous studies have reported that phytohormones stimulate the innate immunity of plants against pathogens such as bacteria and fungi [18,51,57]. Kapoor et al. [58] reported the inhibition of *Verticillium dahliae* and *Fusarium oxysporum* growth and development by up to 70% by an IAA-producing endophytic fungi. In another study, *Bacillus amyloliquefaciens* induced disease tolerance against the pathogen *Rhizoctonia solani* through the modulation of phytohormone signaling [59]. A similar observation was reported by Zebelo et al. [60], where the inoculation of cotton with *Bacillus* sp. increased jasmonic acid synthesis and suppressed the beet armyworm *Spodoptera exigua.* Zhao et al. [61] observed the biological control ability of IAA-producing bacteria against *Phytophthora sojae*, which indicates that the use of phytohormones could be one of the mechanisms to increase plant immunity against pathogens. Bacterial cytokinins are also known to induce plant immunity against pathogen infections [62]. Karimi et al. [63] reported increased plant growth and the biological control of *F. oxysporum* f. sp *ciceris* in chickpea by *B. subtilis*, which produce IAA.

The ethylene phytohormone acts as a signaling molecule in defense against pathogens and signals systemic resistance caused by rhizobacteria [64]. For example, Dixit et al. [65] observed an amendment of ethylene levels in inoculated plants with ACC deaminase-producing *Paenibacillus lentimorbus*, which are infected by *S. rolfsii*. The plant-beneficial bacteria were able to control southern blight disease through the modulation of the ethylene pathway and antioxidant enzyme activities (Figure 1).
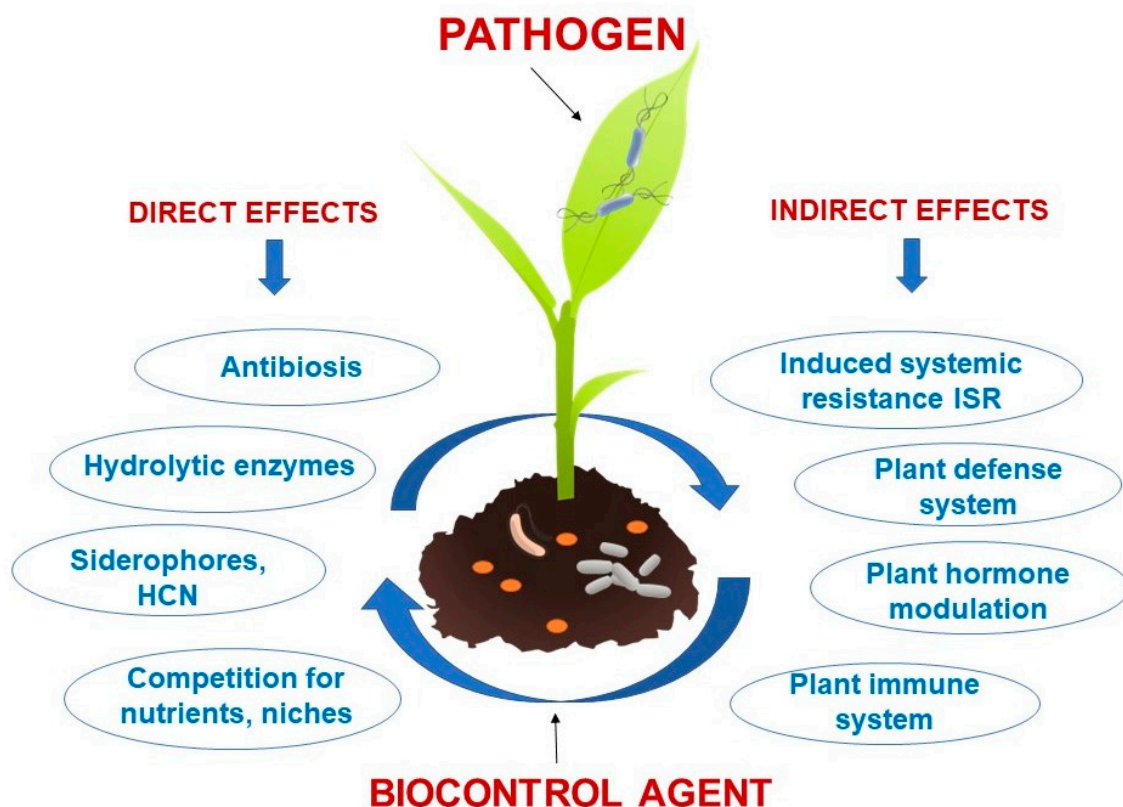

Figure 1. Mechanisms of action of microbial biocontrol agents against plant pathogens.

The production of these phytohormones by microbes can have beneficial effects on plant growth, development, and stress responses. Overall, phytohormones are important signaling molecules that can activate various defense mechanisms in plants against biotic stress. The modulation of phytohormone signaling pathways could be a promising strategy for developing new plant protection methods against pathogens. It is important to note that the effects of microbe-produced phytohormones on plants can depend on various factors, such as the type of hormone, the type of microbe, and the environmental conditions.

2.2. Lytic Enzymes

Microbial enzymes, also called cell-wall-degrading enzymes, such as cellulases, chitinases, glucanases, lipases, pectinases, and proteases, have drawn attention for their inhibition of phytopathogens [66,67]. They also play an important role in nutrient cycling in the ecosystem, through decomposing organic matter. These enzymes degrade the structural component of the fungi cell wall and thus inhibit spore germination and germ-tube elongation [68]. Egamberdieva et al. [69] isolated bacterial endophytes from horseradish, Armoracia rusticana, and they displayed some o lytic enzyme activities, such as lipase, protease, chitinase, and glucanase. Most of the bacterial strains have been shown to suppress plant pathogens such as *Fusarium culmorum*, *F.solani*, and *Rhizoctonia solani.* In another study, Muniroh et al. [70] observed a reduced basal stem rot of oil palm caused by *G. boninense* by plant-beneficial bacteria *Pseudomonas aeruginosa.* The strain produced hydrolytic enzymes such as chitinase, cellulase and 1, 3, β-glucanase. Similar results, reported by Woo et al. [71], highlight the degradation of cell wall of fungal pathogen by biocontrol *Trichoderma* spp. through the production of β-1,3-glucanases, chitinase, cellulose, and proteases. Overall, lytic enzymes produced by microbes can degrade the cell walls of plant pathogens and prevent their growth and spread. This can help to protect plants from various diseases and promote their overall health and growth.

2.3. Antifungal Compounds

Endophytes with biocontrol abilities produce secondary metabolites, such as antibacterial and antifungal compounds, which assist in the inhibition of phytopathogens [66]. There are many reports on the antifungal production abilities of endophytic fungi and bacteria, which can be related to the induction of systemic resistance in plants [67,72]. Microbial antifungal compounds play a critical role in plant defense systems and the biological control of emerging plant pathogens [17,73,74]. According to previous reports, the most well-known antibiotic-producing endophytes are *Bacillus*, *Aspergillus*, *Penicillium*, *Trichoderma* and *Streptomyces* species [17,75]. *Streptomyces* sp. was reported to produce dimethyl sulfide and trimethyl sulfide, which play an important role in reducing tomato bacterial wilt caused by *Ralstonia solanacearum* and red pepper leaf spot caused by *Xanthomonas euvesicatoria* [76]. The *Bacillus* sp. that showed biocontrol ability against *Phytophthora sojae* and isolated from soybean produced two types of antifungal compounds [61]. In another study, iturin A synthesized by *Bacillus* sp. CY22 was responsible for the inhibition of *Rhizoctonia solani*, the causal agent of root rot of balloon flower [77].

Endophytic fungi have yielded numerous antifungal natural compounds with potential use in the development of biopesticides [78]. These compounds have been found to exhibit a range of bioactivities, including antifungal activity against various plant pathogenic fungi [79,80]. For example, a new natural sesquiterpene compound with antifungal activity has been isolated from *Lophodermium sp.*, an endophytic fungus derived from *Pinus strobus*. The compound, 5-(hydroxymethyl)-2-(20,60,60-trimethyltetrahydro-2H-pyran2-yl)phenol, exhibited antifungal activity against the phytopathogen *Microbotryum violaceum,* with a minimum inhibitory concentration (MIC) of 2 μM [81]. Two new halogenated cyclopentenones, bicolorins B and D, were isolated from the endophytic fungus *Saccharicola bicolor* obtained from *Bergenia purpurascens.* Bicolorins B and D showed strong antifungal activities against *P. dissimile* with MIC values of 6.2 and 8.5 μg/mL, respectively, compared with the positive control cycloheximide (MIC of 8.6 μg/mL). Moreover, bicolorin D has been

found to exhibit potent antifungal activity against the plant pathogenic fungus *Sclerotinia sclerotiorum*, both in vitro and in vivo [82]. In another study conducted by Chen et al., [83], two tetranorlabdane diterpenoids, 13,14,15,16-tetranorlabd-7-en19,6β:12,17-diolide and botryosphaerin H, were isolated from the endophytic fungus *Botryosphaeria* sp. P483 was obtained from *Huperzia serrata*. These compounds showed strong antifungal activity against several plant pathogenic fungi, including *F. solani*, *F. oxysporum*, *G. graminis*, *F. moniliforme*, and *Pyricularia oryzae* at a concentration of 100 μg/disk. According to Talontsi et al. [84], three polyketides, epicolactone and epicoccolides A and B, were isolated from an endophytic fungus, *Epicoccum* sp. CAFTBO, derived from *Theobroma cacao*. These compounds showed significant inhibitory effects on the mycelial growth of two peronosporomycete phytopathogens, *Pythium ultimum* and *Aphanomyces cochlioides*, and the basidiomycetous fungus *Rhizoctonia solani*.

Microbial antifungal compounds can be used as potential alternatives to chemical fungicides in agriculture, which can have negative impacts on the environment and human health. They can inhibit the growth and spread of fungal pathogens, helping to protect plants from various diseases.

2.4. Siderophore Production

Endophytes produce volatile compounds that can directly inhibit pathogen development [85]. Siderophores are low-molecular-weight compounds produced by some beneficial microbes that play an important role in plant protection by enhancing iron uptake and inhibiting the growth of some plant pathogens. Iron is an essential nutrient for plant growth and development, but it is often limited in soil. Siderophores can enhance iron uptake in plants by chelating ferric ions and making them more available for plant absorption. [86]. Siderophore secretion by endophytes enhances plant growth making plant pathogens compete with iron and protecting the host plant [87]. Moreover, some pathogenic microbes, such as fungi and bacteria, require iron for their growth and survival. Siderophores produced by beneficial microbes can compete with these pathogens for iron, limiting their growth and survival. This can help to protect plants from various diseases caused by iron-dependent pathogens.

The usage of siderophore-producing endophytes as biocontrol agents is considered as a promising solution to overcome plant diseases. For instance, in a study by Yu et al. [88], the siderophore-producing *Bacillus subtilis* CAS15, with ability to control Fusarium wilt and improved the growth of pepper, was reported. In another study, *Pseudomonas* species showed the ability to produce siderophores to control *F. oxysporum* f. sp. *dianthi* by improving competition for nutrients and niches [27]. Chowdappa et al. [89] reported that the endophytic fungi *Penicillium chrysogenum*, *Aspergillus terreus* and *Aspergillus sydowii* from *Cymbidium aloifolium* had siderophore-producing ability. The isolates were able to control plant pathogens such as *Ralstonia solanacearum* and *Xanthomonas oryzae* pv. *oryzae*. In summary, siderophores produced by beneficial microbes can enhance iron uptake in plants, compete with iron-dependent pathogens, and even have direct antibiotic activity against plant pathogens.

2.5. Induction Systemic Resistance (ISR)

Induced resistance has been identified as a promising tool to overcome plant diseases in sustainable agriculture applications [66,90]. Most of the endophytic microorganisms have the ability to protect their host plants against pathogens via two common mechanisms: induced systemic resistance (ISR) and systemic acquired resistance (SAR) [91–93]. ISR improves pathogen resistance in host plants through the activation of pathogen-related proteins, polyphenols, and phytoalexins or the induction of signal transduction pathways triggered by jasmonate (JA)/salicylic acid (SA) or ethylene (ET) [94,95]. The PR proteins decrease plant pathogen effects and simplify the protection against the plant pathogens to stimulate biotic stressors. The PR proteins include enzymes such as chitinases and 1, 3-glucanases. These enzymes have a critical role in the lysing of invading fungal cells

and recruitment of cell wall lines to resist infection and cell death [96]. For example, *P. polymyxa* elicited ISR in pepper, which protects plants against the bacterial spot pathogen *Xanthomonas axonopodis* pv. *vesicatoria* and reduces disease severity [97]. In another study, *Penicillium citrinum* enhanced the resistance of *Helianthus annuus* L. to stem rot caused by *Sclerotium rolfsii* through the SA and JA signaling networks [98]. Kavroulakis et al. [99] reported an increased ISR in tomato against the pathogen *Septorialyco persici* by activating the PR7 and PR5 genes. The inoculation of *Aradiopsis* with *Bacillus velezensis* reduced the reproduction of green peach aphid *Myzus persicae* by expressing senescence-promoting gene phytoalexin deficient4 (PAD4) [100]. Peng et al. [101] observed induced reactive oxygen species accumulation and the activation of the SA signaling pathway in tobacco by *Paecilomyces variotii*, which enhanced resistance to Potato X viruses. According to Ahmad et al. [102], the *Burkholderia gladioli* strain E39CS3 strongly inhibited the corm-rot pathogen *F. oxysporum* by chitinases and β-1,3-glucanase production, antibiosis, enhanced the endogenous JA levels and expression of JA-regulated plant defense genes (Table 2). Similar results were observed for paddy plants inoculated with *P. pseudoalcaligenes*, which showed the induction of PR proteins such as enzymes β-1,3-glucanase and catalase in plants infected with *Pyricularia grisea* [103].

In an earlier study, Schuhegger et al. [104] found that the plant-beneficial bacteria *Serratia liquefaciens* and *P. putida* produce Acyl-homoserine lactones (AHL) and induce systemic resistance in tomato against *Alternaria alternate*. In another study, *Bacillus* sp. upregulated the expression of the genes PR1a, PR2a, and PR3, which are responsible for the production of glucanases and chitinases and inhibit the growth and development of *S. rolfsii* [105]. *Pseudomonas aeruginosa* showed biocontrol ability in pea against *Fusarium oxysporum* f.sp. *pisi* through the induction of ISR in infected plants and by enhancing antioxidant enzymes such as peroxidase, polyphenol oxidase, ascorbate oxidase, catalase and total phenolic content [106]. Examples of ISR against plant pathogens due to beneficial microbes are given in Table 2. ISR is involved in plant protection by priming the plant for defense, inducing systemic signaling, activating defense genes, and crosstalking with other defense pathways. This phenomenon can enhance the plant's ability to defend against pathogens and improve its overall health and growth.

Table 2. Bacteria-induced systemic resistance (ISR) in plant.

Endophytes	Properties/Mechanisms	Refernce
Paecilomyces Variotii SJ1	Reactive oxygen species accumulation, increased SA and activated SA signaling pathway	Peng et al. [101]
Penicillium citrinum LWL4 and *Aspergillus terreus* LWL5	Production of SA and JA	Waqas et al. [98]
Fusarium Fo47	Production of SA, JA, and ET	Constantin et al. [107]
Burkholderia gladioli	Production of chitinases and β-1,3-glucanase; enhanced endogenous JA levels; overexpression of JA-regulated and other plant defence genes	Ahmad et al. [102]
Enterobacter asburiae	Expression of defense-related genes and antioxidant enzymes	Jayaraj et al. [108]
Serratia liquefaciens and *P. putida*	Acyl-homoserine lactones	Schuhegger et al. [104]
Azospirillum sp. B510	The induction of signal transduction pathways triggered by ET	Kusajima et al. [109]
P. aeruginosa and *P. pseudoalcaligenes*	Production of phenolics and flavonoids; induction of PR proteins such as enzymes β-1,3-glucanase and catalase	Jha [103]
Bacillus sp. 2P2	Higher activity of phenylalanine ammonia lyase, peroxidase, polyphenol oxidase, an ascorbate oxidase; upregulated the expression of three pathogenesis-related genes, PR1a, PR2a, and PR3	Sahu et al. [105]
Bacillus velezensis YC7010	Higher expression of PAD4 with suppression of BIK1	Rashid et al. [100]

2.6. Antioxidant Enzymes

It is known that abiotic stresses can increase reactive oxygen species (ROS) in plant cells and oxidative damage occurs in plant tissues [110]. The proteins and DNA may get damaged, whereas OH·- produce lipid peroxides, which may modify protein configuration and cause loss of biological function [111]. Antioxidant enzymes play an important role in plant protection by scavenging harmful reactive oxygen species (ROS) that are produced during various stress conditions, including pathogen attack [112]. Plants synthesize enzymatic and non-enzymatic antioxidants to reduce ROS damage. Among them, superoxide dismutase (SOD), peroxidase (POD), and ascorbate peroxidase (APX) can help to maintain the dynamic balance of reactive oxygen species. Microbes associated with plants may also help stimulate the antioxidative system in the host plants [113]. For example, *Bacillus* sp. induced ISR and strengthened the cell wall through lipid peroxidation and the synthesis of peroxidase, ascorbate oxidase and polyphenol oxidase [105].

Pathogens can induce the production of ROS in plants as part of their attack strategy. Antioxidant enzymes can help to counteract this by scavenging the ROS produced by the pathogen and limiting their damaging effects on the plant [114]. Peroxidases (POD) play a vital role in plant disease resistance [115], whereas superoxide dismutase (SOD) is involved in the plant defense against ROS [116]. ROS can also act as signaling molecules in plants, activating defense responses against pathogens. Antioxidant enzymes can regulate the level of ROS in the plant and help to fine-tune these signaling pathways. Yan et al. [117] found that yeast with antifungal activity induced resistance to pathogens in plants by increasing plant defense enzyme activity, catalyzing phenol oxidation to quinones and causing an inhibition of pathogen growth [118]. Sebestyen et al. [119] found that *Bacillus subtilis* and *Hypocrea atroviride* inhibited the growth of fungal pathogen *Eutypa lata*, which causes grapevine trunk diseases through the synthesis of iron-binding metabolites and antioxidants. Antioxidant enzymes play a critical role in plant protection by scavenging ROS, defending against pathogen attack, regulating signaling pathways, and cross-talking with other defense pathways. These mechanisms can help to protect plants from various diseases and improve their overall health and growth.

2.7. Competition for Nutrient and Niches

Soil and rhizospheres are complex environments with high carbon concentrations, oxygen, nutrients, and microorganisms. Rhizosphere-inhabiting microbes such as beneficial bacteria and pathogenic fungi compete for nutrients and niches [120,121]. In biocontrol, competition for nutrients and niches can be an important factor in determining the success or failure of a biological control agent. Nutrients are essential for the growth and reproduction of all organisms, and competition for these resources can be intense in natural ecosystems. [122].

When introducing a biocontrol agent, it is important to consider the existing microbial community in the target environment. The biocontrol agent must compete with other microorganisms for nutrients and space [123]. If the biocontrol agent is not able to compete effectively, it may not be able to establish itself in the environment or may not be able to maintain its population at a level sufficient for effective pest control. It is found that limiting nutrients such as carbon, iron, mineral elements and space will cause the inhibition of the spore germination of fungal pathogens and formation of infection on host tissue [124]. The biocontrol bacteria should actively colonize the root system and occupy niches to consume nutrient sources from root exudates and compete for the resources that the pathogen also uses for its proliferation [125,126].

Therefore, efficient root colonization by bacteria is the delivery system for biological active metabolites, including antifungal compounds, cell-wall-degrading enzymes and HCN, which negatively affect the physiology of fungal pathogens [127]. Kamilova et al. [40] reported on the biological control strain *P. fluorescens* strain PCL1751, which effectively colonized the rhizosphere and reduced tomato foot and root rot caused by *F. oxysporum f. sp. radicis-lycopersici*. The *P. extremorientalis* strain TSAU20 was reported as an enhanced

root colonizer and reduced cucumber root rot caused by *F. solani* by 10%. The strain was not able to produce antifungal compounds against *Fusarium*, was negative for the HCN, cellulase, lipase, and glucanase production, and it seems its major mechanism of biocontrol is competition for nutrients and niches [30]. It has been indicated that motility, chemotaxis toward root exudates, induces the colonization of *Pseudomonas* in the rhizosphere and their interaction with plant [128]. Another report observed a suppression of disease symptoms in *A. thaliana* caused by *P. syringae* for *Sphingomonas* strains. The authors indicated that competition for a carbon source among bacteria plays an essential role in inhibiting pathogen development [129]. Colonization and biofilm formation are considered as essential traits for the biocontrol bacteria. Ji and Wilson [130] found that *P. fluorescens* and *Stenotrophomonas maltophilia* have overlapping niches with the pathogen *P. syringae* on the phyllosphere of beans. They are able to suppress disease caused by plant pathogens.

Understanding the niche requirements of both the BCA and the target pest is therefore essential for successful biocontrol [131]. Competition for nutrients and niches can be an important factor in determining the success of a BCA. It is important to carefully consider the existing microbial community and the niche requirements of both the BCA and the target pest when designing a biocontrol strategy or product.

3. Conclusions and Future Perspectives

The published research findings show evidence that plant-associated microbes may protect plants from various soilborne pathogens. Thus, they are considered as BCAs and used widely in crop protection. The traits of plant growth stimulation and development, as well as reduced pathogen infection, include: the production of antimicrobial compounds, siderophores, the secretion of plant growth regulators, which improve plant immunity, ISR against various pathogens, competition for nutrients and niches among microbes, including pathogens, and the modulation of antioxidant enzymes, which enhance the plant defense system. The use of secondary metabolites produced by endophytic microorganisms for biological control and induced resistance to plant pathogens shows great promise for sustainable agriculture, as it offers an environmentally friendly alternative to synthetic fungicides. However, the performance of biocontrol microbes depends on their environment and interactions among plants and pathogens as well. Thus, the physiological properties of biological control microbes, their interactions with other microorganisms, including pathogens, and the mechanisms involved in the plant-beneficial effect under hostile climatic conditions still need to be researched. Moreover, the root exudates have a potential effect on bacterial colonization and proliferation in the rhizosphere, and thus the survival of biocontrol agents in the root system and shelf remains a significant challenge. The future prospects of the biological control of plant disease are promising. New methods such as genomics, transcriptomics, and proteomics are being used to identify and characterize new beneficial microorganisms that can control plant pathogens. In addition, advances in nanotechnology and formulation technology are improving the delivery and efficacy of biological control agents.

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