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Abstract	grown vegetals variety of phy The major fun oxysporum f. Sclerotium rolletc. Even thou combat fungal leave negative.	chum lycopersicum L. (tomatoes) is the second most widely ble. This crop is sensitive to over 200 diseases caused by a topathogenic microorganisms, specifically, soil-borne fungi. Ingal pathogen causing diseases in tomatoes are Fusarium sp. lycopersici, Botrytis cinerea, Verticillium dahliae, lysii, Colletotrichum sp., Alternaria sp. Rhizoctonia solani, tegh a wide range of chemical fungicides is now available to diseases, the overuse of these chemicals has been shown to dadverse influences on the texture, yield and nutritive value of its regard, to manage the fungus-induced tomato diseases, plant

growth-promoting (PGP) bacteria are one of the most environmentally friendly, effective, safe and economically sound solutions. A variety of beneficial soil microorganisms (BSMs) are currently being employed as soil or plant inoculants in several crop plants, including tomatoes, as biocontrol agents (BCAs). These BCAs also work as growth regulators, in addition to preventing fungal diseases. The current chapter discusses the application of beneficial and antagonistic BCAs, their effectiveness as well as bacterial-mediated mechanisms involved in the management of diseases in tomatoes. The specific mechanisms are antibiosis, competition, production of cellulolytic enzymes, cyanogenic compounds (HCN) and siderophore and induced systemic resistance (ISR). The ability of PGP rhizobacteria to antagonize a pathogen and suppress the disease through multiple pathways has been intensively studied to use them as effective BCAs. As a result, this chapter highlights a full explanation of various bacterial-mediated biocontrol mechanisms used by BCA. As environmental and health issues highlight the need to transition to a more sustainable agriculture system, the use of indigenous PGP rhizobacteria in plant disease prevention is gaining attraction. It's also recommended that using a bacterial consortium guarantees that BCA performs consistently in field settings.

Keywords (separated by '-')

Solanum lycopersicum - Tomatoes - Fungal diseases - Biocontrol agents (BCAs) - Antifungal metabolites

Chapter 15 1 **Bacterial Inoculants for Control of Fungal** 2 Diseases in Solanum lycopersicum 3 L. (Tomatoes): A Comprehensive Overview 4

Mohammad Shahid, Udai B. Singh, Talat Ilyas, Deepti Malviya, Shailesh K. Vishwakarma, Zaryab Shafi, Babita Yadav, and Harsh V. Singh

Abstract Globally, *Solanum lycopersicum* L. (tomatoes) is the second most widely 8 grown vegetable. This crop is sensitive to over 200 diseases caused by a variety of 9 phytopathogenic microorganisms, specifically, soil-borne fungi. The major fungal 10 pathogen causing diseases in tomatoes are Fusarium oxysporum f. sp. lycopersici, 11 Botrytis cinerea, Verticillium dahliae, Sclerotium rolfsii, Colletotrichum sp., 12 Alternaria sp. Rhizoctonia solani, etc. Even though a wide range of chemical 13 fungicides is now available to combat fungal diseases, the overuse of these 14 chemicals has been shown to leave negative/adverse influences on the texture, 15 yield and nutritive value of the fruits. In this regard, to manage the fungus-induced 16 tomato diseases, plant growth-promoting (PGP) bacteria are one of the most environmentally friendly, effective, safe and economically sound solutions. A variety of 18 beneficial soil microorganisms (BSMs) are currently being employed as soil or plant 19 inoculants in several crop plants, including tomatoes, as biocontrol agents (BCAs). 20 These BCAs also work as growth regulators, in addition to preventing fungal 21 diseases. The current chapter discusses the application of beneficial and antagonistic 22 BCAs, their effectiveness as well as bacterial-mediated mechanisms involved in the 23 management of diseases in tomatoes. The specific mechanisms are antibiosis, 24 competition, production of cellulolytic enzymes, cyanogenic compounds (HCN) 25 and siderophore and induced systemic resistance (ISR). The ability of PGP 26 rhizobacteria to antagonize a pathogen and suppress the disease through multiple 27 pathways has been intensively studied to use them as effective BCAs. As a result, 28 this chapter highlights a full explanation of various bacterial-mediated biocontrol 29 mechanisms used by BCA. As environmental and health issues highlight the need to 30 transition to a more sustainable agriculture system, the use of indigenous PGP 31 rhizobacteria in plant disease prevention is gaining attraction. It's also recommended 32 that using a bacterial consortium guarantees that BCA performs consistently in field 33 settings.

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Keywords Solanum lycopersicum · Tomatoes · Fungal diseases · Biocontrol agents
 (BCAs) · Antifungal metabolites

15.1 Introduction

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Tomatoes (Lycopersicum esculentum Mill.), commonly known as 'golden apples', 38 are the world's second most widely farmed vegetable crop after potatoes, due to their 39 flavourful fruit and high nutritional content (Costa and Heuvelink 2018). Vitamin A, 40 vitamin C and β-carotene, as well as vital minerals, are abundant in tomatoes (Colak 41 et al. 2020). It is also high in phosphorus (P), potassium (K), magnesium (Mg) and 42 iron (Fe), all of which are needed to keep nerves and muscles functioning normally 43 (Ali et al. 2020). Tomatoes contain β-carotene (a precursor to vitamin A) and 44 phytosterols, making them the third-best source of vitamin C and the fourth-best 45 source of vitamin A in human diet (Poiroux-Gonord et al. 2010). A strong antiox-46 idant found in natural lycopene is a phyto-nutrient found in red, ripe and cooked 47 tomatoes that helps prevent heart-related diseases and sarcoma (Kaur and Kaur 48 49 2015). Other preventive processes, such as anti-inflammatory and antithrombotic functions, are also attributed to this fruit. The short growing season, cheap cost and 50 great economic returns have enticed growers to cultivate the crop throughout the 51 year, even in hotter climates (Villareal 2019). Because of the diverse nature of the 52 fruit, tomatoes are often considered a cash and industrial crop in several countries 53 54 like India, the USA, China, Turkey and Egypt (Costa and Heuvelink 2018). China is the world's biggest tomato producer, with yearly production of approximately 55 34 million tonnes, according to international statistics (Nicola et al. 2009). Tomato 56 output in the world is expected to be 145 million tonnes per year, covering 4.36 57 million ha (Chohan et al. 2017). 58

Tomatoes are grown all over the world due to their resilience to a wide range of soils and climates (Morganelli 2007), but their softness makes them vulnerable to insect pests and various abiotic (pesticides, heavy metals, salinity and drought) and biotic stresses (Atkinson et al. 2011). Diseases caused by phytopathogens are the primary limiting factors in overall crop losses around the world, and they are becoming increasingly important as the global population grows. Over 200 pathogen-caused illnesses have been recorded in tomatoes around the world (Watterson 1986). Seed-borne infections, on the other hand, can quickly travel from one location to another and act as the first source of inoculum (Rennie and Cokerell 2006). Highquality seeds, therefore, play an important role in producing long-term, lucrative veggies, and tomatoes are no exception to this. Microorganisms such as fungi, bacteria, viruses and nematodes cause seed-borne illnesses. Among disease-causing parasitic microbes, fungi are the most commonly seen on seeds. As a result, infected seeds have a negative impact on seed health, limiting germination capacity, poor seedling vigour, transmitting fungus pathogen to seedlings, speeding up storage deterioration, transferring pathogens into new areas and expanding the inoculum source in the field. Fungi, a crucial category of microorganisms, are responsible for a number of seed-borne illnesses of tomato, which result in significant yield losses.

Several seed-borne fungi, such as Aspergillus flavus, Rhizopus solani, Curvularia 77 spp. and Fusarium stolonifer induce problems in tomato seeds, including wilt, 78 necrosis, rotting and toxification of seeds (Neergard 1997). Late blight, a disease 79 of tomato (caused by *Phytophthora infestans*), is one of the most destructive tomato 80 diseases, resulting in significant financial losses (Fry 2020). Sclerotinia rot (caused 81 by Sclerotinia sclerotiorum) is another major fungal infection that is threatening 82 tomato crop productivity (Jnr 2000). Several studies have been published on Fusar- 83 ium species-caused wilt, crown and root rot infections in tomatoes (Yezli et al. 84 2019). The wilt (Fusarium oxysporum f. sp. lycopersici) and early blight (Alternaria solani) diseases are regarded the most damaging fungal diseases that affect tomato 86 plants.

Since the fungal diseases are pandemic, simple cultural cleanliness is ineffective. 88 To protect the fungal diseases, chemical fungicides are often used for better yield and 89 productivity of tomatoes. Even though agrochemicals have long been employed as a 90 reliable method of harvest insurance, their increased use has resulted in several 91 undesirable consequences, including disease resistance and non-target natural 92 effects. Furthermore, the increased use of fungicides to combat tomato diseases 93 has resulted in an increase in health risks due to phytotoxic residues and environ- 94 mental consequences. As a result, it is strongly recommended that alternate disease 95 management methods be used in place of agrochemical substances.

Managing fungal diseases using biological means is seen to be a viable method 97 for reducing disease severity. In comparison to the previously mentioned use of 98 chemical fungicides, the use of soil beneficial bacteria that colonize the underlying 99 foundations of harvest plants and suppress the soil-borne illnesses is becoming an 100 elective alternative. In this regard, PGP bacteria can be used as soil inoculants to 101 reduce soil-borne illnesses, which is an organic solution. Because they have the 102 potential to colonize the rhizosphere swiftly and spread down the root from a single 103 seed treatment or soak application into the soil, PGPR with the viability of their 104 biocontrol activity typically provide long-term protection from soil-borne diseases at 105 the root surface. A huge number of PGPR have been recovered and characterized in 106 the hopes of developing them as biocontrol agents for tomato illnesses. For example, 107 Kilani-Feki et al. (2016) also employed B. subtilis strains to suppress the Botrytis 108 cinerea, the pathogen that causes tomato fruit rot. In another study, biocontrol agents 109 (BCAs) were recovered to combat the tomato wilt disease. It was observed that 110 Ochrobactrum intermedium and B. amyloliquefaciens, among strains, potentially 111 inhibited the disease incidence and increased the seedling growth and vigour indices 112 of tomatoes (Gowtham et al. 2016). Furthermore, the effectiveness of *P. fluorescens* 113 strains against a variety of fungal diseases (leaf blight, damping-off, stem canker, 114 and root rot) in tomatoes (Singh et al. 2017) has been reported. Under in vitro and 115 pothouse settings, BCAs, viz. P. aeruginosa, P. fluorescens, B. amyloliquefaciens 116 and B. subtilis were able to successfully suppress the canker and wilt disease of 117 tomato (Abo-Elyousr et al. 2019). Recently, a new technique for inducing systemic 118 resistance (ISR) in plants by employing PGPR has been investigated by Attia et al. 119 (2020). They confirmed that PGPRs were found to be effective in reducing the 120 growth of A. solani (causing early blight disease) in tomato plants. In comparison to 121

non-treated plants, they achieved an 84.3% protection rate. Effective selection, screening and safety investigation of promising PGPR strains are required for incorporating soil microbes for disease control/plant growth promotion in cropping systems and eliminating the need for chemicals. Furthermore, information on disease targeting, mass-scale production costs and procedures of registration must all be updated to improve the market standing of these BCAs. The current chapter aims to look into the potentiality of antagonistic PGP bacteria (BCAs) in managing the major fungal diseases of tomatoes. This chapter also discusses the challenges and benefits of commercializing these bacteria in the agriculture sector.

131 15.2 Prevalence of Seed-Borne Mycoflora: A Historical Perspective

133 Seed-borne fungi are microorganisms that can host the seeds both within and externally, causing diseases or contaminating the environment (Amza 2018). Phy135 topathogenic fungi may cause post-germination death, rendering them poisonous
136 and lowering their quality for human food and seed production. The conidia,
137 oospores, sclerotia, hyphae and chlamydospores are some examples of the main
138 forms in which they are present (Arora 1986). The tomato, which is employed as a
139 model crop in genetics, is susceptible to a variety of seed-borne fungal diseases.

A total of 12 phytopathogenic fungi were recovered from the fruits and seeds of 140 Solanum lycopersicum. It was found that the majority of the pathogens were 141 habitants of fruits; however, the species of Cladosporium were detected in seeds (Dhekle and Bodke 2013). In reality, a considerable number of fungal isolates belonging to genera Fusarium, Pythium, Botrytis, Alternaria and Rhizoctonia were found in tomato seeds, causing several seeds-borne diseases. Mycoflora are isolated 145 as surface contaminants, internally seed-borne flora, and are known to cause major 146 field diseases depending on the presence of fungi on the seed coat or in the seed. Various fungal phytopathogens, viz. F. oxysporum, Alternaria solani, Aspergillus flavus, A. fumigatus, etc., have been detected and identified from infected tomato plants and reported to cause serious seed damage (Fig. 15.1) as reported by several workers. The investigation of grey mould disease in tomato leaves was done using a 151 hyperspectral imaging technique based on competitive adaptive reweighted sampling (CARS) and correlation analysis (WANG et al. 2017). Similarly, tomato plants 153 were infected by fungal pathogens like F. semitectum (1-3% infection), 154 F. moniliforme (0.5% infection), and Curvularia lunata (0.5-7.5% infection) and Bipolaris spp. (1.5% infection) (Bhatti et al. 2010). The duration of storage has a 156 157 significant impact on the prevalence of various mycoflora. On a modest scale, Phytophthora infestans has caused the full destruction of tomato harvests around 158 the world (Panthee and Chen 2010). Hormonema spp., one of the most prevalent 159 genera on tomato seeds, were discovered by Nishikawa et al. (2006) while assessing 109 species of seed-borne fungi from three cultivars of tomato. The seed could be

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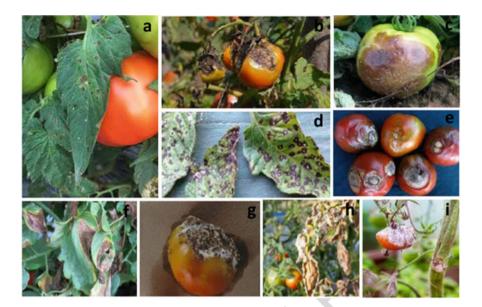


Fig. 15.1 Major tomato diseases caused by fungal pathogens. Early blight (Alternaria solani) (a), late blight (Phytophthora infestans) (b), buckeye rot (Phytophthora) (c), septoria leaf spot (Septoria lycopersici) (d), anthracnose (Colletotrichum) (e), verticillium wilt (Verticillium dahliae) (f), southern blight (Sclerotium rolfsii) (g), fusarium wilt (Fusarium oxysporum f. sp. lycopersici) (h) and grey mould (Botrytis cinerea) (i) (source: https://www.google.com/)

diseased within or be contaminated on the exterior. The fungus F. oxysporum f. sp. 162 lycopersici causes fusarium wilts, one of the most destructive diseases of tomatoes. 163 Similarly, previous researchers found a total of 17 fungal phytopathogens linked 164 with tomato var. local seeds, with Aspergillus niger, A. flavus, Fusarium moniliform, 165 Rhizopus nigricans, Curvularia lunata and Alternaria alternata being the most 166 prevalent. In the Indian state of Gujarat, 12 fungi were discovered with four tomato 167 cultivar seeds. A. alternata, A. flavus and A. niger were the most common, whereas 168 A. amstelodami and Cunninghamella echinulata were discoveries.

15.3 **Management of Fungal Diseases in Tomatoes**

In the fight against crop diseases, seed health is crucial. The rise of endemic diseases 171 as a result of changing global environment poses a difficulty in maintaining the 172 health of the plant. As a result, timely and precise diagnosis of the problem, as well 173 as pathogen surveillance, gives time for mitigation actions to be implemented. 174 Treatment of seeds to destroy pathogens carried within or on the seed has been 175 demonstrated to be effective in preventing epiphytotic plant diseases. Seed-borne 176 fungi, on the other hand, are easy to control compared to airborne or soil-borne 177

fungi. Farmers are encountering financial difficulties as a result of significant crop losses caused by seed-borne mycoflora on their crops. Controlling seed-borne infections via various approaches is a crucial element in every agricultural crop production and protection programme. To eliminate pathogens from seeds both inside and externally, as well as to protect seeds from soil-borne diseases, a variety of chemical, biological, physical, and mechanical techniques have been applied (Shahid et al. 2017).

185 15.3.1 Use of Chemical Fungicides (Chemical Method)

Mycotoxins released by seed-borne fungal pathogens cause serious issues in 186 humans. Hence, seeds should be treated with appropriate chemical before planting. Chemical fungicides are used since pre-historic times for the management of phy-188 topathogenic fungi and for obtaining a better yield of crops. Historically, treating 189 seeds with chemical fungicide using spraying, drenching of soils and dusting has been important (Copping and Duke 2007). These methods could protect the seeds 191 and seedlings from the soil-dwelling fungal pathogens causing damping-off and rot 192 diseases (Divya Rani and Sudini 2013). Amini and Sidovich (2010) conducted 193 in vitro and in vivo experiments where they used six chemical fungicides, viz. 194 fludioxonil (FLN), bromuconazole (BMZL), benomyl (BML), carbendazim (CBZM), azoxystrobin (AZBN) and prochloraz (PCZ), against the fusarium wilt 196 disease in tomato crop. When administered to seedlings at prescribed levels, PCZ 197 and BMZL were found to be the most effective against Fusarium oxysporum f. sp. 198 lycopersici. Among the fungicides tested, FLN and BMZL showed a phytotoxic 199 impact on tomato seedlings. Similarly, in another investigation, Al-Kassim and 200 Monawar (2000) treated (in vitro) five vegetable seeds including Solanum 201 lycopersicum, Solanum melongena, Abelmoschus esculentus, etc., in Gazan prov-202 ince with 0.2% of chemical fungicides like benomyl, cozib and mancozeb before incubation. The majority of the isolated fungi were inhibited by all of the tested 204 fungicides. Benomyl, on the other hand, was the most effective against all of the 205 206 fungi found on the seeds of the tomato.

Major fungal diseases of tomatoes, their symptoms and chemical control measures

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207	S. no.	Disease	Causal agent	Symptoms	Chemicals used	Effectiveness	Reference
207	S. no.	Early blight	Alternaria solani	Brown-black spots (in the form of lesion 1/ 2-inch diameter) Formation of blotches (irregular) Defoliation, browning of infected leaves Appearance of lesion	Mancozeb 80WP, Bavistin 50WP, Indofil M-45, Sulcox 50WP and Tall-25EC, chlorothalonil (0.2%), kasugamycin (0.1%), propiconazole (0.1%), pryraclostrobin	Suppressed the fungal growth Reduced the disease incidence	Reference Roy et al. (2019), Arunakumara et al. (2010)
				(dark) on stems	(0.2%), perfekt (0.2%),		
				Girdling of the stem	metalaxyl (0.2%),		
				or collar rot	mancozeb (0.25%)		

S. no.	Disease	Causal agent	Symptoms	Chemicals used	Effectiveness	Reference	20
2	Septoria leaf spot	Septoria lycopersici	Disease infection on lower leaf Symptoms also occur on stems and blossom Symptoms on fruits appear in the form of small-sized water-soaked spots Development of greyish white centres with dark edges Yellowing, withering of leaves and ultimately fall off	Fungicides pyraclostrobin (116.6 ppm), fluxapyroxad (58.5 ppm), mancozeb (4000 ppm), difenoconazole (125 ppm), chlorothalonil (1500 ppm), propineb (2100 ppm), fluazinam + thiophanatemethyl (375 + 375 ppm) and metiram + pyraclostrobin (1100 + 100 ppm)	Suppressed the fungal growth Reduced the disease incidence	Monteiro et al. (2021)	21
3	Late blight	Phytophthora infestans	Younger/older leaves infected Appearance of palegreen water-soaked spots starting at leaf tips that enlarge rapidly, forming irregular, greenish-black blotches Development of white moulds at the margins of infected areas Under the favourable condition, whole plants rapidly defoliated Infection on petioles and stems occurs as brown streaks	Fungicides oxathiapiprolin, chlorothalonil, azoxystrobin, mandipropamid and mefenoxam were effec- tive against the disease	Chemicals single or in mixture con- trolled the disease Suppressed the growth of pathogens Improved the growth and yield of tomato	Cohen et al. (2018)	21
4	Fusarium wilt	Fusarium oxysporum f. sp. lycopersici	Development of leaves Affected leaves soon wilt and dry up, but they remain attached to the plant The wilting continues successively on younger foliage and eventually results in plant death The stem remains firm and green on the outside but exhibits a narrow band of brown discolouration in the vascular tissue Brown streaking in the vascular tissue of infected plants becomes plugged during the attack by the fungus, leading to wilting and yellowing of the leaves	Chemical fungicides difenoconazole (200 mg/L), benomyl, carbendazim, prochloraz, fludioxonil, bromuconazole and azoxystrobin were effective		Amini and Sidovich (2010)	21:
5	Verticillium wilt	Verticillium dahliae	Leaf edges and areas between the veins turn yellow and then brown Infected plants often have a characteristic V-shaped lesion at the edge of the leaf	Nano-fungicide (leaf extract olive oil-loaded chitosan nanoparticles)	Diminished the disease symptoms	Mazzotta et al. (2022)	21

214	S. no.	Disease	Causal agent	Symptoms	Chemicals used	Effectiveness	Reference
				occurring in a fan pat- tern • As the disease pro- gresses, younger leaves begin to wilt and die, until only a few healthy leaves remain at the top of the plant			
214	6	Anthracnose	Colletotrichum	Symptoms appear first as small, circular, slightly sunken lesions on surface of ripening fruits Spots quickly enlarge, become bruise like depressions and develop a water-soaked appearance directly beneath the skin (epidermis) of the fruit As these spots expand, they develop dark centres or concentric rings of dark specks the rings consist of numerous small spore-producing bodies	Azoxystrobin-based fungicides Onestar 23% SC and Amistar 23% SC	Decreased the incidence of disease (69–71%)	Saxena et al. (2016)
215	7	Buckeye rot	Phytophthora	Symptoms appear as water-soaked greyish- green/brown spots Further, spot enlarges and develops into a lesion with a target-like pattern of concentric rings of narrow dark- brown and wide light- brown bands	Application of fungicides metalaxyl, cymoxanil, mancozeb and copper oxychloride	Reduced the incidence of disease	Gupta and Bharat (2008)
216	8	Southern blight	Sclerotium rolfsii	Formation of wilting on plants Development of water-soaked lesion on stems Produced sclerotia are white, later becomes dark-brown (spherically structured) White mycelium and sclerotia at stem base of infected plants are the main symptoms of disease	Fungicides pyraclostrobin, quintozene and fluxapyroxad were used	Chemicals significantly reduced the disease incidence	Keinath and DuBose (2017)
217	9	Grey mould	Botrytis cinerea	Appearance of grey- brown velvety mould covering on stems/ younger leaves Grey spores cover dying flowers and the calyx of fruit	Difen Super, 55% WP fungicide concentration of 0.08% with active ingredient, difenoconazole, and fungicide Skor, 250 g/l EC with concentration of 0.05% and 0.07%	Effective against the pathogen	Zuparov et al. (2020)

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15.3.2 Biological Management

Chemical fungicides have a significant impact on seed-borne fungal infections, but 219 they also have a negative impact on beneficial microbial diversity in soils as well as 220 crop productivity. Furthermore, irregular fungicidal usage is not only harmful to 221 animals and humans but also leads to development of resistance among the patho- 222 gens targeted. Because fungicides are harmful to non-target organisms (Marinho 223 et al. 2020), scientists are turning to more environmentally benign and cost-effective 224 means of disease management, such as acid treatments, and the use of antagonistic 225 microbes (Droby et al. 2022), and plant extracts (Shuping and Eloff 2017). These are 226 interesting and viable options for releasing plant growth regulators that influence 227 overall crop development and improve morpho-physiological features. The method 228 of biocontrol has been utilized for over 2000 years, and it has been widely used in 229 managing pests since the end of the eighteenth century. The types of biological 230 control can be classified into natural, conservation, inoculative (classical) and 231 augmentative biocontrol. Natural biocontrol has been used to reduce pests since 232 evolution, whereas conservation biocontrol comprises human measures to stimulate 233 and protect the performance of natural foes. The inoculative mode of biocontrol is 234 the most extensively used type of biocontrol, in which natural enemies are dispersed 235 into new places where the pest has been mistakenly introduced. Natural enemies are 236 mass-produced in bio-factories and sent into the market for fast pest control, making 237 augmented biocontrol more appealing. This type of plant protection is regarded to be 238 both environmentally beneficial and food-safe. Moreover, gaining a better knowl- 239 edge of biocontrol mechanisms via interactions between BCAs and phytopathogens 240 may aid in the improvement and development of biocontrol systems. 241

15.4 Plant Growth-Promoting Rhizobacteria: Tapping for BCA

Rhizobacteria are a varied collection of bacteria that colonize the rhizosphere 244 environment. In the root zone, they are strong microbial competitors. They either 245 directly or indirectly influence plant development. The direct method entails PGPR's 246 positive effects that directly boost plant growth. These systems help plants grow, but 247 the ways they do so differ from species to species and strain to strain (Noori and 248 Saud 2012). Through biogeochemical cycling, the PGPR nourishes the plant by 249 converting the nutrients into the soil. They also help plant growth by facilitating the 250 transfer of these nutrients into the plant. They promote plant growth by synthesizing 251 plant hormones such as indole acetic acid (Ahmed et al. 2021), cytokinins (Liu 252 et al. 2013), fixing nitrogen from the atmosphere (Malik et al. 1997), solubilizing 253 minerals like phosphorus (Gomez-Ramirez and Uribe-Velez 2021) and generating 254 siderophores that can solubilize and sequester iron (Sultana et al. 2021) and provide 255 nutrients to plants (Etesami and Adl 2020) in addition to combating soil-borne 256 plant diseases (Hamid et al. 2021). It plays a significant effect in repelling 257

phytopathogenic bacteria in addition to promoting plant growth (Hassan et al. 2019). 258 Bacillus subtilis has a biocontrol efficiency of more than 50% on tomato plants 259 against the plant disease caused by Ralstonia solanacearum in greenhouse condi-260 tions (Chen et al. 2013). Rhizoctonia solani, which causes damping-off in tomatoes, 261 was controlled by a strong biocontrol agent, Priestia endophytica FH5 (Zhou et al. 262 2021). The biofortified vermicompost prepared from chosen BCAs (like B. subtilis 263 and P. fluorescens) could be used to successfully manage the wilt diseases in 264 tomatoes caused by Fusarium oxysporum (Basco et al. 2017). In a similar study, 265 S. pratensis strain LMM15 (having the potential of BCA) was sprayed on tomato 266 leaves 1 day before fungal inoculation. After BCA spraying, it was observed that the 267 occurrence of grey mould disease was reduced by approximately 46%. Furthermore, 268 the applied biocontrol agent significantly increased the plant stressor metabolites 269 (proline and lipid peroxidation) as well as defence enzymes in shoot tissues (Lian 270 et al. 2017). These strains of actinomycetes drastically reduced the pathogen proliferation while also improving tomato growth characteristics (Goudjal et al. 2014).

273 **15.5** Mechanisms Involved in Disease Suppression (Indirect Mechanisms)

The PGPR's antagonistic characteristics against a variety of diseases expand their 275 potential as biocontrol agents (Fatima et al. 2022). Several genera of beneficial soil bacterial strains including Pseudomonas (Kabdwal et al. 2019), Bacillus (Ni and 277 Punja 2019), Enterobacter (Xue et al. 2009), Serratia (Youssef et al. 2016), Klebsiella (Gaur et al. 2017), Azotobacter (Alsudani 2022), etc. are familiar as biological 279 control agents (BCAs) used in reducing tomato diseases. Many reports claim that 280 281 using the PGP consortium as biological control agents has some advantages over other disease control methods, such as being an environmentally safe and non-toxic 282 283 indigenous microorganism whose application is both environmentally safe and favourable to human health. Induction of systemic resistance (ISR), antibiotic 284 production, competition, secretion of cellulolytic/hydrolytic enzyme and production 285 of HCN and siderophores are all essential mechanisms involved in BCA's antago-286 nistic effects (Narayanasamy 2013). Furthermore, they can help plants cope with 287 288 numerous stressors such as salinity, drought, hunger, heavy metal toxicity and so on, allowing them to thrive in such environments. Even though various free-living 289 PGPR are regarded as plant development beneficial microbes, not all the strains 290 within the same species have the same metabolic capacity to boost plant growth. It's 291 crucial to understand the rhizosphere microbiota's capabilities, as well as its mech-292 293 anisms of action, to ensure long-term crop production (Babalola et al. 2021). The PGPR's antagonistic characteristics against a variety of diseases expand their poten-294 tial as BCAs (Verma et al. 2019). Various genera of Bacillus including Bacillus 295 megaterium, B. subtilis and B. polymyxa, P. fluorescens and T. harzianum were 296 co-inoculated with Azospirillum sp. and Azotobacter sp. and were reported to 297 effectively control the disease caused by fungal pathogens (Saad et al. 2016).

Some biocontrol agents (BCAs) involved in the management of major fungal diseases of tomatoes

	Major fungal		Biocontrol agent	Mechanism			
S. no.	disease	Causal agent	involved	involved	Effectiveness	Reference	299
1	Fusarium wilt disease	Fusarium oxysporum f. sp. lycopersici	Bacillus sp.	Production of cell wall-degrading enzymes like β-1,3-glucanase, protease, chitinase, ammonia, siderophore, HCN production, bioactive volatile and non-volatile metabolites	• Reduced the disease severity up to 55%. Enhanced the growth and physiological traits of plants	Jangir et al. (2018)	300
2	Tomato vas- cular wilt	Fusarium oxysporum	Bacillus velezensis NKG-2	Volatile organic compounds (VOCs)	• Suppressed the disease severity • Increased the growth of plants	Myo et al. (2019)	301
3	Botrytis cinerea	Grey mould disease	Bacillus subtilis L1–21	Antifungal metabolites	Completely inhibited (100%) the fungal growth Increased the plant growth and improved the fruit quality	Bu et al. (2021)	302
4	Alternaria rot disease	Alternaria alternata	Bacillus atrophaeus	Antifungal metabolites O-anisaldehyde And lipopeptides	Reduced the germination of the spore. Decreased the disease severity of Alternaria in tomato fruit.	Chacon- Lopez et al. (2021)	303
5	Black scurf disease	Rhizoctonia solani	Bacillus subtilis Hussain T-AMU	Lipopeptide, biosurfactant	Inhibited the growth of the pathogen Inhibited the incidence and severity of disease	Hussain et al. (2021)	304
6	Alternaria leaf blight	Alternaria solani	Bacillus velezensis NKMV-3	Production of lipopeptide (antibiotic synthesis genes), iturin C, surfactin A and fengycin B and D	• Controlled the growth of the pathogen	Vignesh et al. (2022)	305
7	Fusarium wilt disease	Fusarium oxysporum sp. lycopersici	Bacillus inaquosorum KR2-7	Production of BGCs fengycin, surfactin and bacillomycin F, bacillaene, macrolactin, skf, subtilosin A, bacilysin and bacillibactin	Reduced the disease severity Increased defence-related enzyme activities	Kamali et al. (2022)	306
8	Early blight disease	Alternaria alternata	Bacillus sp.	Antibiosis, pro- duction of vola- tile organic compounds	• Decreased the disease severity	Pane and Zaccardelli (2015)	307

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308	S. no.	Major fungal disease	Causal agent	Biocontrol agent involved	Mechanism involved	Effectiveness	Reference
		Wilt disease	Verticillium dahliae	Bacillus subtilis	Various antibi- otic metabolites and VOCs	• Suppressed the fungal infection, increased tomato yield	Rahman et al. (2021)
309	9	Foliar blight disease	Botrytis cinerea	B. nakamurai, B. pseudomycoides, B. proteolyticus, B. thuringiensis, E. asburiae and E. cloacae	Antifungal VOCs such as 3-methylbutan-1- ol, sulphur- containing com- pounds, 2-heptanone and dodecanal	• Increased the growth and yield of tomato	Chaouachi et al. (2021)
310	10	Anthracnose disease	Colletotrichum capsici	Bacillus sp. strain M10	Extracellular enzyme production	• Suppressed the fungal growth	Srikhong et al. (2018)
311	11	Fusarium wilt	Fusarium oxysporum f. sp. lycopersici	Bacillus pumilus	Loss of proto- plasm in fungal cell wall	• Reduced (73%) disease incidence • Increased root (60%) and shoot (84%) of tomato	Heidarzadeh and Baghaee- Ravari (2015)
312	12	Early blight and anthrac- nose disease	Alternaria solani, Colletotrichum coccodes	Pseudomonas fluorescens A506	Antifungal anti- biotics and VOCs	Suppressed anthracnose on fruit and early blight on detached leaves, controlled the disease in tomato	Cuppels et al. (2013)
313	13	Early blight disease	Alternaria solani	Pseudomonas fluorescens	Antifungal anti- biotics and VOCs	• Inhibited (45.55%) the fungal growth	Koley et al. (2015)
314	14	Grey mould disease	Botrytis cinerea	Bacillus licheniformis	Antifungal compounds	Inhibited the fungal growth Controlled the disease incidence (90%) in tomato	Lee et al. (2006)
315	15	Foot rot disease	Fusarium oxysporum f. sp. radicis- lycopersici	Collimonas fungivorans	Antifungal compounds, cell wall-degrading enzymes	Suppressed the fungal growth	Kamilova et al. (2007)
316	16	Black scurf and wilt disease	Rhizoctonia solani, fusar- ium oxysporum	Bacillus subtilis (TD11), Bacillus cereus (TD15)	Secretion of anti- fungal metabo- lites Induced systemic resistance (ISR)	• Inhibited the growth of Rhi-zoctonia solani (40%) and Fusarium oxysporum (80%) • Controlled (50%) the disease incidence in tomato	Malik et al. (2022)
317	17	Root rot disease	Sclerotium rolfsii	Bacillus sp.	Production of hydrogen cya- nide (HCN) and extracellular enzymes	• Suppressed the fungal growth • Reduced the disease incidence	Kumar et al. (2012)

~	Major fungal		Biocontrol agent	Mechanism			
S. no.	disease	Causal agent	involved	involved	Effectiveness	Reference	3
18	Fusarium wilt disease	Fusarium oxysporum	Pseudomonas sp.	Siderophore production	• Suppressed the fungal growth Reduced the dis- ease incidence	Arya et al. (2018)	31
19	Fusarium wilt disease	Fusarium oxysporum	Streptomyces SNL2	Synthesis of phe- nolate siderophore	• Reduced the prevalence of wilt disease by 88.5%	Goudjal et al. (2016)	32
20	Early blight of tomato	Alternaria solani	Lysinibacillus fusiformis L-2, Bacillus subtilis B-1 and Achromobacter xylosoxidans A-3	Production of siderophore and other antifungal compounds	Suppressed the fungal growth Controlled the disease Improved the growth features of tomato crop	Attia et al. (2020)	32
21	Fusarium wilt disease	Fusarium oxysporum	B. pumilus	Siderophore production	• Suppressed the fungal growth. Reduced the disease incidence	Heidarzadeh and Baghaee- Ravari (2015)	32
22	Fusarium wilt	F. oxysporum f. sp. lycopersici	Burkholderia contaminans AY001	Systemic induced resistance (ISR), production of antimicrobial compounds, including di (2-ethylhexyl) phthalate and pyrrolo [1,2-a] pyrazine-1,4-dione, hexahydro-3-(phenylmethyl)	Enhanced the growth of tomato plants Increase the disease resistance Improved the yield attributes	Heo et al. (2022)	32
23	Fusarium wilt	Fusarium oxysporum	Pseudomonas aeruginosa	Production of antifungal metabolites like siderophore, HCN and ammonia	• Inhibited the fugal growth (75%) • Increased the growth parameters	Parasuraman et al. (2022)	32
24	Early blight	Alternaria solani	Pseudomonas aeruginosa	Production of antifungal metabolites like siderophore, HCN and ammonia	• Inhibited the fugal growth (75%) Increased the growth parameters	Parasuraman et al. (2022)	32
25	Early blight disease	Alternaria alternata	B. atrophaeus and Brevibacterium frigoritolerans	Induced systemic resistance (ISR) Secretion of extracellular enzymes	Suppressed the fungal growth Reduced the disease inci- dence Increased the plant growth and biomass	Chacon- Lopez et al. (2021)	32
26	Verticillium wilt disease	Verticillium dahliae	Pseudomonas stutzeri	Synthesize anti- fungal metabo- lites like HCN, siderophore and other extracellu- lar enzymes	• Enhanced the growth charac- teristics (stem length, number of leaflets, leaf area and root	Essalimi et al. (2022)	32

328	S. no.	Major fungal disease	Causal agent	Biocontrol agent involved	Mechanism involved	Effectiveness	Reference
						weight) and bio- chemical param- eters (nitrate reductase activ- ity, proline and chlorophyll con- tent) of tomato.	
328	27	Fusarium wilt disease	Fusarium oxysporum f. sp. lycopersici	Pseudomonas fluorescens Pf1	Secretion of essential plant growth- regulating sub- stances, synthe- size antifungal metabolites	Decreased the disease inci- dence Improved the germination, vigour indices, growth and bio- mass of tomato	Johnson et al. (2022)
329	28	Collar rot disease	Sclerotium rolfsii	Pseudomonas fluorescens Pf1	Synthesize anti- fungal compounds	• Suppressed the growth of pathogen • Reduced the disease incidence	Johnson et al. (2022)

330 15.5.1 Production of Antibiotics

The chemical compounds which are produced by a species of microbes and are used 331 to kill other species of microbes are known as antibiotics. To survive predation, competition and other threats, microorganisms interact with each other and produce 333 these chemical molecules (Kaya and Koppenhöfer 1996). Bacterial antagonists 334 decrease phytopathogens by secreting inhibitory compounds into the extracellular 335 environment (Freitas et al. 2022). It is a highly effective and extensively researched 336 337 aspect of biocontrol. The 2,4-diacetylphloroglucinol (DAPG), pyrrolnitrin, phenazine, tensin, pyoluteorin, tropolone, oomycin A, cyclic lipopeptides and hydrogen 338 cyanide (HCN) are some of the well-known antibiotics for biological control (Saeed 339 et al. 2021). The majority of antibiotics produced by *Bacillus* sp. are effective against plant harmful fungi Fusarium oxysporum and Alternaria solani (Zhang et al. 2020). 341 B. subtilis has been reported as a strong biocontrol agent, and it inhibited the fungal 342 growth by producing a wide range of antibiotics, including bacilysin, bacillomycin, 343 fengycin, zwittermicin and difficidin (Kim et al. 2010; Telang 2010). Bacillus strain 344 TNAM5 was discovered to be effective in suppressing FOL by producing diffusible 345 and volatile organic (VO) antifungal compounds, ammonia and HCN (Prashar et al. 346 2013; Kumari et al. 2021). Phichai (2014) discovered that B. subtilis could generate 347 antifungal metabolites (bacitracin, subtilin, bacillin and bacillomycin) that inhibited 348 Alternaria spp. However, because antibiotic resistance is a problem, having too much reliance on antibiotic-producing bacteria as a BCA could be a disadvantage.

15.5.2 Competition

Effective colonization and increased competition are important factors in biocontrol; 352 thus, the biological control agents (BCAs) should be able to tolerate and multiply in 353 a natural environment (Pal and Gardener 2006). Microorganisms must efficiently 354 compete for accessibility of nutrition and niche to establish themselves in the 355 rhizosphere (Lugtenberg 2015). Biocontrol mainly relies heavily on competition 356 between pathogenic and non-pathogenic microorganisms (Daguerre et al. 2014). 357 Plant-associated bacteria are known to provide more protection to the plant by accelerating rhizosphere penetration than pathogens. Biocontrol chemicals exhaust 359 the few available substrates, rendering them inaccessible to infections. At the same 360 time, they produce metabolic chemicals that are harmful to infections (TarigJaveed 361 et al. 2021). As a result, an effective BCA must be able to safeguard the deeper root 362 sections by colonizing well and suppressing the pathogen at the growing tips. In 363 rhizobacterial populations, species of *Pseudomonads* have been identified as very efficient competitors for root exudates (Kuiper et al. 2002). Antimicrobial chemicals 365 are found in some root exudates, providing a favourable ecological niche for PGPR, 366 which may then detoxify them (Badri and Vivanco 2009). This means that PGPR competence is heavily contingent on their capacity to exploit specific environmental conditions or adapt to changing conditions (Amaya-Gómez et al. 2020). Kuiper et al. 369 (2001) found that root colonizing *Pseudomonads*' competitive colonization ability was strongly influenced by their enhanced intake of putrescine, a tomato root 371 exudate. 372

15.5.3 Induced Systemic Resistance (ISR)

Beneficial bacteria living in the rhizosphere region interact with the host plant to help 374 it fight against different phytopathogens (Kumar and Jagadeesh 2016). The 375 enhanced physiological state of defence elicited by broad-spectrum biotic and 376 abiotic stimuli is known as induced resistance. The induction of systemic resistance 377 is characterized by (1) induced systemic resistance (ISR) and (2) systemic acquired 378 resistance (SAR). ISR occurs when plants' intrinsic defence mechanisms are trig- 379 gered in response to biotic threats (Pineda et al. 2013). Plants in SAR develop greater 380 resistance to uninfected plant sections while dealing with a wide range of diseases (Pieterse et al. 2001). ISR is primarily mediated by the jasmonate or ethylene- 382 sensitive pathway, whereas SAR is mediated by salicylic acid (SA) (Mandal and 383 Ray 2011). Rhizobacteria invading plant roots can induce resistance to a wide range of illnesses. It has been reported that some strains of Bacillus (Choudhary and Johri 385 2009), Pseudomonas (Jisha et al. 2019), Burkholderia (Ahmad et al. 2022) and 386 Serratia (Singh and Jha 2016) cause ISR in response to various infections. By evoking such induced resistance, BCAs display the inhibition of diseases caused 388 by fungal, bacterial, viral and, in some cases, insects and nematodes. The genus 389

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Bacillus is an excellent BCA and the most widely used biopesticide for controlling plant diseases (Miljaković et al. 2020). Some species of Pseudomonas also play an imperative role in ISR. For example, P. fluorescens was found to provide ISR to 392 tomato plants against the diseases causing fungal pathogens (such as P. infestans and 393 F. oxysporum) (Santoyo et al. 2012). The use of potential Pseudomonas fluorescens 394 VSMKU3054, an efficient BCA, gave clear evidence of ISR-mediated biocontrol of 395 tomato grey mould disease (Suresh et al. 2022). In a study, Chunyu et al. (2017) 396 evaluated the efficiency of PGPR strain B. amyloliquefaciens SQRT3 to prevent the 397 tomato crop against pathogens by inducing a systemic resistance mechanism. In a 398 crop-based study, it was observed that by activating the various defence enzymes 399 (PPO, POX, GLU, CHI and PAL), and induction of systemic resistance, antagonistic 400 PGPR strains S. marcescens, Streptomyces cereus and Bacillus cereus increased the 401 resistance of wilt disease in tomato (Ferraz et al. 2015). Reduction in the severity of 402 disease and enhanced upregulation of defensive enzymes triggered by the combined 403 inoculation of Bacillus atrophaeus, B. subtilis, and Burkholderia cepacia exhibited a 404 direct biocontrol and ISR mode of action for suppression of vascular disease in 405 tomato crops (Shanmugam and Kanoujia 2011). Similarly, by activating and 406 upsurging the activities of peroxidase, PPO and phenylalanine ammonia-lyase, the 407 biocontrol agent Pseudomonas putida stimulated the systemic responses in tomatoes 408 against early blight disease (Ahmed et al. 2011). In another study, antagonistic 409 bacteria B. subtilis OTPB1 suppressed the early blight of tomato (caused by 410 A. solani) due to increased systemic response. The bacterial-inoculated tomato seedlings had significantly higher levels of defence-related enzymes (peroxidase, PO; polyphenol oxidase, PPO; and superoxide dismutase, SOD) than uninoculated 413 control seedlings (Chowdappa et al. 2013). In the external environment, bacteria produced exopolysaccharides (EPS). The EPS aids in drought resistance, stress resistance and phytopathogen defence (Fig. 15.2). In various crops, the significant function of bacterial EPS as an elicitor for the generation of systemic resistance has already been established. The exopolysaccharide synthesized by *Bacillus* sp. EPS has been shown to effectively minimize the occurrence of wilt disease in tomatoes caused by F. oxysporum (Thenmozhi and Dinakar 2014).

421 15.5.4 Production of Cellulolytic/Cell Wall-Degrading 422 Enzymes

423 Cellulolytic/cell wall-degrading enzymes secreted and excreted by certain bacteria 424 can disrupt pathogen development and/or activity. The secretion of these enzymes is 425 a cost-effective way to stop pathogen proliferation through the lysis of pathogenic 426 cell walls. Several bacterial genera produce and release lytic enzymes that are 427 capable of hydrolyzing a wide range of polymeric materials (proteins chitin, cellu-428 lose, hemicellulose and DNA). This technique allows the phytopathogen to be 429 directly parasitized. The release and expression of these enzymes by various

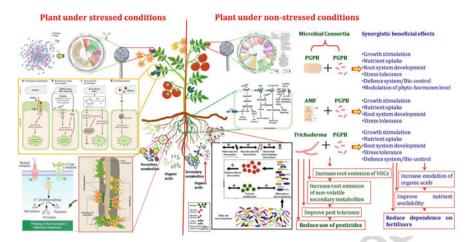


Fig. 15.2 An overview of microbe-mediated modulation of physio-biochemical and molecular mechanisms of biotic stress tolerance in plants. Photograph clearly depicts that plant secreted chemically different biochemicals/secondary metabolites which regulate recruitment of microbial strains under stressed and non-stressed conditions. These microorganisms further regulate the defence mechanisms in plants. Figure showed the multi-trophic interactions in the rhizosphere which define the active rhizosphere effects and how the microbiome served as the first line of defence and maintain defence level and plant growth under stressed conditions

microorganisms can occasionally directly decrease plant pathogen activity. Poly- 430 meric components (such as cellulose, hemicelluloses, chitin, proteins and DNA) 431 found in fungal cell walls can be digested by lytic enzymes including cellulase, 432 chitinase and protease, among others. Pseudomonas sp., among soil bacteria, has 433 gotten increased attention since it can produce a variety of cell wall disintegrating 434 enzymes, including chitinase, protease/elastase and 1,3-glucanase (Wang et al. 435 2021).

Chitinases and 1,3-glucanases are two of the most important hydrolytic enzymes 437 involved in the breakdown of fungal cell walls. Mycolytic enzymes produced by 438 rhizobia, particularly chitinases, are known to hydrolyze chitin, a significant component of fungal cell walls (Chavan and Deshpande 2013). Production of extracel- 440 lular cellulolytic enzymes (cellulase, chitinases, protease and β-1,3-glucanase) by 441 Bacillus sp. recovered from Solanum lycopersicum rhizosphere inhibited the fungal 442 pathogens and proved to be a viable bioresource for the agricultural business (Kumar 443 et al. 2012). In a study, Ramyabharathi and Raguchander (2014) found that antag- 444 onistic PGPR strain B. subtilis EPCO16 produced HCN and volatile organic com- 445 pounds (VOCs) together with proteolytic and extracellular enzymes chitinase and 446 β-1,3-glucanase. This strain retarded the growth of F. oxysporum f. sp. lycopersici 447 causing fusarium wilt disease in tomatoes and proved to be a successful biocontrol 448 agent in managing the fungal diseases. Further, strains of Pseudomonas 449 (P. fluorescences NRC1 and P. fluorescens NRC3) inhibited the phytopathogens 450

Phytophthora capsica and R. solani (the causal agents of root rot disease in tomato) by secreting different cell wall-degrading enzymes and synthesizing antifungal metabolites (Moataza 2006). Under greenhouse circumstances, the strain Bacillus 453 sp., which could synthesize different types of extracellular enzymes, reduced the 454 disease incidence of wilt disease (caused by F. oxysporum f. sp. lycopersici) by 36% in tomato plants, suggesting that it could be an effective biocontrol agent for tomato 456 wilt (Jangir et al. 2018). P. fluorescens has also been identified as a potent BCA 457 against the fungal pathogen, stimulating important enzymes such as peroxidase 458 (POX), polyphenol oxidase (PPO) and superoxide dismutase (SOD), as well as 459 1,3-glucanases (Dorjey et al. 2017). Apart from the extracellular enzymes, the 460 inhibition of phytopathogens could also be aided by other microbial by-products. 461 For instance, at picomolar concentrations, hydrogen cyanide (HCN) efficiently dis-462 ables the cytochrome oxidase pathway and is extremely hazardous to all aerobic 463 microbes. Hydrolytic enzymes produced by some identified strains of *Bacillus* have been described for the biocontrol of the phytopathogen F. oxysporum causing wilt 465 disease in tomatoes (Jadhav and Sayyed 2016). The efficiency of different 466 rhizobacterial strains is dependent on the host plant and soil factors, in addition to 467 the biocontrol methods listed above. Furthermore, their innate capacities and rhizo-468 sphere competence play a significant role in the manifestation of their biocontrol 469 features (Weert and Bloemberg 2007). In a field trial, Shanmugam and Kanoujia 470 (2011) evaluated the biocontrol potential of antagonistic PGPR strains, B. cepacia 471 and B. subtilis against Fusarium oxysporum f. sp. lycopersici causing wilt disease in tomato. They found that the bacterial strains reduced the incidence of disease by 473 secreting extracellular enzymes. Further, they claimed that leaf and root sample analyses had the highest induction of chitinase and 1,3-glucanase.

476 15.5.5 Production of Hydrogen Cyanide (HCN)

Hydrogen cyanide (HCN) is an antibacterial and antifungal molecule well known for its ability to prevent disease (Haas and Keel 2003). HCN is likely to disrupt the 479 electron transport chain (ETS) and the cell's energy source, resulting in cell death. Cytochrome oxidase is also known to be inhibited by the action of HCN (Cooper and 480 Brown 2008). This detrimental characteristic gives PGPR a competitive advantage 481 over fungal pathogens, and it can be used in plant disease biocontrol (Shaikh and 482 Sayyed 2015). Among rhizosphere microbes, *Pseudomonas* and *Bacillus* spp., for 483 484 example, produce cyanogenic compound (HCN) as a secondary metabolite (Sivasakthi et al. 2014). Bacterial cyanogenesis has also been described in the 485 species of Burkholderia (Shahid and Khan 2018), Achromobacter (Oves et al. 486 2019), Bacillus (Hassan et al. 2010), and Azotobacter (Shahid et al. 2019). However, 487 fluorescent *Pseudomonas* is the most common HCN produce (Keerthana et al. 488 2022). The majority of research suggests that HCN-producing bacteria are active

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against fungal infections and, thus, serve as a biocontrol agent (Sehrawat et al. 2022; 490 Haddoudi et al. 2021; Hernández-León et al. 2015; Pandya and Saraf 2014). In a 491 study, Kumar et al. (2012) found that HCN-synthesizing *Bacillus* sp. suppressed the 492 disease-causing pathogen Sclerotium rolfsii. Similarly, PGPR strain Beijerinckia 493 fluminensis suppressed the growth of major fungal phytopathogens while assessed 494 under in vitro conditions (Al-Shwaiman et al. 2022).

Production of Siderophore

Iron (Fe) is a necessary micronutrient for all living things and is found in the soil 497 mostly in the form of ferric ion (Fe3+), which is only sparingly soluble. As a result, 498 plants are unable to absorb it. Plants can utilize the microorganism-produced 499 siderophores to absorb iron (Radzki et al. 2013). Beneficial soil microbial diversity 500 synthesizes siderophores (low-molecular-weight Fe-chelating molecules) having 501 high affinity and selectivity for binding and forming a complex Fe complex (III) 502 (Colombo et al. 2014). It functions as a ligand, allowing iron to be sequestered and 503 transported into the cell. In recent times, this characteristic has gotten a lot of 504 attention, and the in vitro assessment of siderophore synthesized by identified 505 PGPR has been reported (Parray et al. 2016). Rather than Gram-positive PGPR 506 transport systems, siderophore-mediated iron transfer mechanisms are best 507 researched in Gram-negative PGPR transport systems. Among different varieties 508 of 500 siderophores, only 270 have been structurally studied. Siderophores have 509 been proposed as an environmentally acceptable alternative to insecticides.

Since siderophores have a higher affinity for iron than fungal pathogens, they 511 have a competitive edge when it comes to effectively reducing the proliferation of 512 phytopathogen (Govindasamy et al. 2008). When there is a lack of iron, fungal 513 pathogens become unable to reproduce and are pushed out of their biological habitat. 514 As a result, siderophore synthesis is an attractive feature of PGPR as a biocontrol 515 agent. Siderophores produced by Pseudomonas are reported to have a stronger 516 affinity than other bacterial siderophores (Patel et al. 2018). Several studies have 517 been published on the biocontrol efficacy of PGPR that produce siderophores. 518 Siderophore-producing strains of B. subtilis MF497446 and P. koreensis 519 MG209738 exhibited strong effectiveness against the fungal pathogens, reduced 520 the disease incidence and improved the crop growth (Ghazy and El-Nahrawy 2021). 521 Under field circumstances, Attia et al. (2020) found that siderophore-producing 522 PGPR strains, viz. Lysinibacillus fusiformis L-2, Bacillus subtilis B-1 and 523 Achromobacter xylosoxidans A-3 suppressed the early blight disease of tomato 524 caused by Alternaria solani. Similarly, the indigenously isolated Pseudomonas strain reduced the incidence of fusarium wilt disease in tomato crops by producing siderophore (Arya et al. 2018). In addition, siderophore-synthesizing Streptomyces 527 SNL2 reduced the prevalence of wilt disease by 88.5% (Goudjal et al. 2016).

529 15.6 Future Perspective

Managing sustainable natural reserves can help ensure food security for the world's growing population. PGPB have been shown to play an important function in 531 agricultural management in several studies. Though, there is still a knowledge 532 vacuum underpinning microbe-plant symbiosis under various stress circumstances, 533 especially pathogen stress. Understanding the rhizosphere ecology that governs 534 pathogen and antagonist dispersion could help improve biocontrol efficiency against 535 plant-based pathogens. Future studies will necessitate intense rhizosphere engineer-536 ing based on the successful discovery and separation of novel metabolites, which 537 could establish a unique environment for plant-microbe interactions. Instead, explor-538 ing and applying the combined inoculation over a single strain, on the other hand, 539 could be an efficient means for the suppression of fungal diseases. Furthermore, 540 genetic alterations to improve biocontrol values could be a new study area for 541 managing plant diseases. Transforming the strains with higher quantities of antifungal and growth-promoting essential metabolites, for example, maybe an excellent 543 option. The use of cutting-edge tools to explore microbiological, biochemical and 544 molecular interactions between plants and interacting microorganisms may provide in-depth knowledge for a better understanding of interactions between plants and 546 microbes. To summarize, the forthcoming challenge will be to improve the effec-547 tiveness and long-term resilience of biological control in the field. If this issue is handled, biocontrol efficacy could be increased by leveraging expertise to design 549 better screening processes, formulations and application procedures, as well as innovative integrated disease management strategies.

552 15.7 Conclusions

Tomato is a highly nutritious vegetable crop grown all over the world and ranks 553 second only to potatoes in terms of consumption. Tomato seed-borne infections, on the other hand, are a major source of concern in the seed industry because they have 555 a negative impact on seedling germination and vigour, resulting in a significant 556 reduction in yield and product quality. The current research shows that PGPR not 557 only have different biological promotional effects on tomato plant development 558 parameters but also operate as biocontrol agents (BCAs) to protect the plant from 559 diseases. It should become increasingly more effective and cost-effective to replace 560 fungicides with a biological pesticide. Before commercialization, molecular analysis 561 can help stabilize the effects of PGPR in biological control and determine potential 562 risks. To use PGPR effectively for disease reduction or crop protection in the future, 563 a logical selection of organisms will be required, as well as technical improvements 564 in upscaling and formulation procedures will be needed. The PGP genomic products 565 may be enhanced through the genetic engineering of PGPR. As a result, a single 566 bacterial strain or a consortium with varying features will reduce pathogen attacks

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while also promoting plant growth, which will stimulate producers. Although 568 investigations should focus on the relative contributions of each mechanism responsible for PGPR strains' significant biocontrol activity, it has become obvious that 570 they use numerous pathways to operate as an effective biocontrol agent. An in-depth 571 study of microbial interactions with plants, as well as exploitation of microbial 572 ecology in the soil and rhizosphere, will aid in revealing the many dimensions of 573 disease suppression by these biocontrol agents. Furthermore, for maximal commer- 574 cial utilization of these strains, cautiously conducted skilful field trials of tomato 575 plants inoculated with BCAs are required. Finally, the success of the microbial 576 inoculant industry, particularly those that use PGPRs, will be determined by factors 577 such as product marketing and substantial research. Furthermore, to incorporate 578 PGPR strains into the agriculture industry, they will need to be optimized for 579 improved fermentation and formulation procedures. 580

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