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Journal of

Modern Agriculture and Biotechnology

ISSN 2788-810X

Open Access

Review

Amelioration of Pathogen Induced Biotic Stress to Vegetable Crops by Plant Beneficial Bacteria: A Review

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Received: September 16, 2021 Accepted: October 16, 2021 Published: January 20, 2022

Abstract

Among various crop damaging factors, biotic stresses primarily contribute to the limitation of the growth and development of plants, which leads to huge yield losses. Globally, about 25% crop yield is lost due to diseases and insect infestation. The production and consumption of vegetables is growing worldwide due to its nutritional value in human dietary systems. The vegetables are attacked by different soil borne pathogens which compromise yield and quality. To prevent such devastating effects, pesticides are applied in high throughput vegetable cultivation practices. However, the excessive and imprudent application of pesticides negatively affects the microbial diversity and soil biological activity. This in turn, detrimentally affects the yield and quality of vegetables. Eco-friendly sustainable agricultural practices that employ low cost microbial formulations can play pivotal roles in the management of biotic stresses. The use of plant beneficial bacteria to increase vegetable production may restrict pesticides application and also prevent the emergence of resistance of pathogens against toxic chemicals. Considering these, an attempt is made herein to highlight the impact of biotic stresses especially bacterial and fungal pathogens on some of the popularly grown vegetables. This review provides information about the active biomolecules associated with disease suppression and significance of plant beneficial bacteria in the amelioration of lethal vegetable diseases. The interplay between the soil beneficial microbes and vegetables will facilitate the development of bacteria-based antagonist strategies for inexpensive production of vegetables in stressful open field conditions.

Keywords: biotic stress, phytopathogens, vegetables, biocontrol, plant beneficial bacteria

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Citation: Khan MS, Rizvi A, Ahmed B, Umar S. Amelioration of Pathogen Induced Biotic Stress to Vegetable Crops by Plant Beneficial Bacteria: A Review. *J Mod Agric Biotechnol* 2022; 1(1):1. DOI: 53964/jmab.2022001.

1 INTRODUCTION

Vegetables among many food crops are one of the most important constituents of the global dietary systems owing to their role in human health. So, the demand for nutritive vegetables with high quality is growing worldwide. The vegetable crops are extremely susceptible to biotic stresses such as insect-pests^[1,2], bacterial^[3,4] and fungal^[5] phytopathogens and weeds^[6], which have caused substantive yield losses in many countries. For example, a significant loss of 40% in potato due to pathogens is reported^[7,8]. To safeguard the yield and quality of widely consumed vegetables such as tomato, potato, cabbage, ladyfinger etc. from biotic stresses, crop rotation^[9,10], usage of disease resistant varieties^[11] and other disease control measures are adopted. Moreover, various agrochemicals especially fungicides and insecticides^[12] are applied in soil-vegetable systems to offset the negative impacts of biotic stresses. Sadly, many of these management strategies failed to harvest satisfactory results. Use of agrochemicals in vegetable production has been found destructive to nutrient composition and yield of vegetables, environment and via food chain, the human health. Due to this, agrochemicals application is considered unsuitable in vegetable production^[13,14]. Considering all the harmful impact of pesticides, growers are advised to restrict the usage of agrochemicals for the maintenance of the yield and quality of vegetables. The question is how to make it feasible. Solutions, specifically the microbial formulation strategies, have been provided to the growers for the pesticide problems in vegetable production. In this regard, the use of plant beneficial bacteria (PBB): low-cost and environmentally sustainable options are advocated for enhancing vegetables quality and yield optimization^[15,16]. Unfortunately, the scientific information on the amelioration of vegetable disease employing PBB in soilplant systems are inadequate^[17,18]. However, few pieces of literature on how PBB could be useful in circumventing the biotic stresses while concurrently amplifying the yield of vegetable crops are reported^[19,20]. This review attempts to gather published information on the biotic stresses with a particular focus on the impact of phytopathogens on some widely cultivated vegetables. In addition, this review outlines the potential role of PBB in the management of diseases and their prospects in sustainable production of vegetables in different agrosystems. This review will therefore, be useful for growers to design and practice microbes-based strategies for inexpensive production of vegetables in different environmental conditions. Furthermore, the information given here will be helpful for researchers working in the area of PBB-vegetable interactions.

2 BIOTIC STRESS TO VEGETABLES AND HOW VEGETABLES RESPOND TO STRESS: AN OVE-RVIEW

Biotic stress in plants generally refers to the stresses

caused by the living organisms, specifically, pathogens, insect pests, viruses and viroids, weeds, or intra/inter specific competition for limited available resources. The biotic stresses in general, are the major constraints of vegetable production worldwide (Table 1). Physiologically, the biotic stress agents limit the uptake of nutrients which negatively affects plant vigor and in extreme cases, the death of the host plants. However, the extent and severity of biotic stress differs with the weather conditions, soil-plant systems, cropping pattern, climatic seasons, cultivation practices, vegetable genotypes, and agroecological regions^[29,30]. In general, hot and humid weather environment, nutrient-rich agrosystems and contemptible crop-management practices further predispose the vegetables to such biotic stresses.

Plants, however, have evolved defense systems (innate and systemic response) to combat different types of biotic stresses^[31,32]. Chief among them is the evolution/ identification of highly sophisticated crosstalk between different plant hormones, for instance, ethylene (ET), jasmonic acid (JA), auxin (IAA), abscisic acid (ABA), ethylene (ET), and salicylic acid (SA). These hormones are secreted in response to specific stimuli and enhance plants' endurance under stressed conditions^[33,34]. Recent findings suggest that the protection against biotic stresses occur at critical stages of plants such as morphological, structural and physiological levels^[35]. Evidence suggests that the interaction between pathogens and different plant signalling pathways determines the level of tolerance among infected plants^[36]. All these, either alone or in synergism provides tolerance or resistance against biotic stresses and give plants the strength and rigidity^[32,37]. For example, when plant is infected by any pathogen, the injured plants secrete reactive oxygen species (ROS) around the infection site called "oxidative bursts". This is considered as the primary disease resistant response against infections^[38]. Besides ROS, in response to pathogen attack, plants increase cell lignifications which blocks the invasion of pathogens and thus reduces the host susceptibility^[39]. Some of the other notable plant-based compounds secreted in response to infections and that provide protection against biotic stresses include β -aminobutyric acid (BABA)^[40,41] or benzothiadiazole $(BTH)^{[42]}$, $SA^{[43,44]}$, $JA^{[15, 45]}$ and $ABA^{[46]}$. As an example, the relationship between the endogenously secreted SA and the resistance exhibited against biotrophic and hemibiotrophic pathogens in plants have been positively correlated. The exogenous SA application induced the local and systemic acquired resistance in tomato against *F. oxysporum*^[47].

3 HOW IS BIOTIC STRESS MEASURED?

Soil borne plant pathogens among biotic stresses account for huge economic, quality, and yield losses to vegetable crops worldwide^[48], which necessitates timely detection and evaluation of the damage caused by such soil borne pathogens. The biotic-induced stresses, therefore, are monitored right from the early growth stage

Biotic Stress	Host Plant	Diseases	Causal Organism	Crop Response	Ref
Bacteria	Tomato	Bacterial canker	Clavibacter michiganensis	Systemically colonizes tomato xylem leading to unilateral leaflet wilt, marginal leaf necrosis, stem and petiole cankers, and plant death.	[21]
Viruses		Tomato root rot, Tomato yellow leaf curl virus (TYLCV)	Pythium aphanidermatum Begomovirus	Death of plants, Yield losses	[22,23]
Fungi		Early blight	Alternaria solani	Early blight can affect almost all parts of the tomato plants, including the leaves, stems, and fruits. The plants may not die, but they will be weakened and will set fewer tomatoes than normal.	[24]
Nematodes		Root-knot nematode disease	Meloidogyne incognita	Loss of fruit yield	[25]
Weeds	Okra	-	Cynodon dactylon, Eleusine indica, <i>Amaranthus</i> <i>spinosus</i> and Commelina benghalensis	Yield loss	[6]
Insect-Pests	Eggplants	-	Shoot and fruit borer	Damages foliage, flower buds and fruits	[26]
		-	Jassids	Affect leaves and fruit yields	[27]
		-	Leaf eating beetles	Feed on leaves and seriously damage plants	[28]

Table 1. Examples of Some Biotic Stresses Adversely Affecting the Vegetable Production

until harvest to identify and properly diagnose diseases on time. This will help to find a suitable management strategy to limit the damage caused by the pathogens. In this regard, researchers focus onto assess- (i) the effects of pathogens on plants (ii) pathogen growth during interactions and (iii) how plants own active biomolecules following infection overcome the biotic stresses (self-defence). Conventionally, the disease assessment of crop plants is conducted by monitoring symptoms through human naked eyes and brain to measure their incidence. Also, the detection or pathogen identification methods depend on isolation, microscopic examination and growth of recovered pathogens^[49]. The traditional approaches are, however, destructive, manual expertise demanding, labour intensive, and time consuming. Therefore, researchers apply physiologicalbased markers approach to find a better vegetable disease detection method^[50]. Some of the most commonly applied methods include (i) Diaminobenzidine (DAB) staining and luminol-based assays and nitroblue tetrazolium (NBT) staining methods: detecting reactive oxygen species (ROS) for example, hydrogen peroxide (H_2O_2) and superoxide (O_2)), respectively, (ii) Aniline blue staining method: measuring callose deposition, (iii) Membrane damage: detecting electrolyte leakage, and (iv) Trypan blue staining method: evaluating cell death. Of these, the DAB, an organic compound, when reacts with H₂O₂ and peroxidase is oxidized to an insoluble brown alcohol precipitate whereas luminol is oxidized by Horseradish Peroxidase (HRPO) in the presence of H_2O_2 and releases chemiluminescence^[51,52]. The chemiluminescence is measured by luminometer or is photographed (imaged) employing a photon detecting imaging system. The NBT reacts with O2⁻ and forms an insoluble formazan (dark blue deposit) that can be visualized. The DAB or NBT staining product is, however, proportional to the amount of H_2O_2/O_2^- in the tissue. Callose, a polysaccharide, generated in response to wounding and pathogen elicitors is deposited at the interface between the plasma membrane and plant cell wall^[53, 54]. Callose formation can be detected and quantified by staining with aniline blue. Mechanistically, the callose reacts with aniline blue and fluoresces under UV light. The death of plants after infection is attributed to the hypersensitive response^[55,56] or the collapse of the plant immune system. Trypan blue staining is the classical technique that can detect and quantify infection-induced cell death^[57,58]. Healthy plant cells with unbroken membranes preserve electrolytes within the cell boundaries. But the stability and integrity of the membrane are disrupted under the attack from infectious organisms, which, therefore, results in electrolyte leakage^[59,60]. The evaluation of electrolyte leakage from leaf discs that floats on water determines the severity of cell membrane instability and damage.

The biotic stress can also be detected by expression analyses of defense-marker genes by qRT-PCR, RNA sequencing, proteomics and microarrays. These techniques provide information about metabolic alteration caused by pathogens^[61-63]. In addition, the synthesis and accumulation of stressed-induced biomolecules such as SA^[64], JA^[65], ABA^[66] or ET^[67] have been measured in infected plants^[68-70]. Recently, chlorophyll fluorescence imaging (Chl-FI), a very pertinent and a highly delicate technique, has been used for the detection of plant stress and monitoring crop performance^[71]. The Chl-FI, a diagnostic tool, is used to determine the photosynthesis

activity at different stages of plant growth (cellular, foliage, and whole-plant) that allow researchers to perform phenotyping of plants^[72]. The Chl-FI gives knowledge about the timing and position of the pathogen development and contributes immensely to understanding the regulation of photosynthesis from foliage to crop scale. Among the extensively researched diseases detected by Chl-FI, the disease caused by fungi and oomycetes have been reported. As an example, reduction in chlorophyll content of cucumber leaves infected with viral (Cucumber mosaic virus and Cucumber green mottle mosaic virus) and powdery mildew (Sphaerotheca fuliginea) fungal pathogen has been detected^[73]. These techniques in general, provide sufficient evidence to explain variations in plant transcriptional and physiological responses due to infection caused by the soil borne pathogens. Lately, several automatic and semi-automatic techniques such as Back-Propagation Neural Network (BPNN), Support Vector Machine (SVM), K-Nearest Neighbors (KNN), Radial Basis Function Neural Network (RBFNN), Color Co-occurrence Method (CCM) and Spatial Gray-Level Dependence Matrices (SGDM) have been developed for the detection of plant pathogens^[74,75]. These techniques help to identify pathogens in healthy or diseased leaves. However, various challenges accompany these techniques during processing. For example, the automation of the detection system during complex imaging outside under intense lightning and environmental conditions is difficult.

4 WHY ARE PLANT BENEFICIAL BACTERIA PREFERRED FOR VEGETABLE DISEASES MA-NAGEMENT?

Indeed, bacterial and fungal phytopathogens among biotic stresses are the most deadly menace to the nutritional value, biomass, and yield of vegetable crops worldwide^[76]. So, it is imperative to realize the threat and devise protection strategies to maintain both the yield and quality of vegetables, for which the vegetable growers espouse different methods to suppress the disease causing bioagents. Such methods include field sanitization, use of disease resistant cultivars, crop rotation, and pesticides application^[17,77]. Agrochemicals, especially the use of pesticides among many diseases management options in general, are effective in reducing the crop damage in different agrosystems^[78,79]. The emergence of resistance among pathogens toward pesticides, the residual toxicity to neighbouring non-target organisms and environmental pollution are, however, the biggest global challenges. To date, there have been no available environmentally sustainable solutions to prevent biotic stresses. Therefore, the scientists in recent times have directed their efforts onto discover inexpensive, eco-friendly, and viable alternative that can be effective in the suppression of vegetable diseases. Such microbial formulations may achieve to optimize the production of safe and good quality vegetables under open field conditions^[80,81]. The plant beneficial bacteria endowed, especially with the disease eradication ability, often termed "microbiological control agents or "microbial antagonists", inhibit soil borne phytopathogens by secreting various antimicrobial metabolites. Additionally, they promote the growth and development of vegetables by supplying essential plant nutrients and phytohormones (Table 2). Essentially, the antimicrobial metabolites of microbial or any biological origin, are easily biodegradable compared to the frequently used agrochemicals^[100]. Considering all, an attempt is made herein to explore the role of microbial formulations in disease suppression vis-a-vis growth and yield optimization of some of the most popularly cultivated and widely consumed vegetables.

5 DISEASE MANAGEMENT BY PLANT BENEFI-CIAL BACTERIA: A GENERAL PERSPECTIVE

Plant beneficial bacteria are bacteria that infect, colonize surfaces and augment the overall development of plants by one or simultaneous growth modulating mechanisms^[101,102]. Management of biotic stresses including those of plant pathogens using PBB has indeed been one of the greatest interests to researchers^[103,104]. The PBB containing disease suppression abilities include bacteria belonging to different functional groups such as N2 fixers^[105], P-solubilizers^[106], K^[107], and Zn-solubilizers^[108,109] etc. The wide-ranging soil borne PBB protects the vegetables from pathogen attack directly by secreting pathogen-antagonizing substances^[110]. The antimicrobial metabolites include the broad-spectrum antibiotics^[111-113], cell wall degrading enzymes^[114], iron-chelating compound, siderophores^[115,116], cyanogenic compounds, HCN^[117,118] or bacteriocins^[119,120] and ACC deaminase^[121]. They also limit the pathogen populations through competition for space and nutrients or indirectly by inducing the resistance mechanisms^[122,123], all of which contribute to enhancing the yield and quality of vegetables. Of these, siderophores, lytic enzymes, antibiotics and bacteriocins that disintegrate cellular architecture and ACC deaminase that lowers the stress hormone, ethylene, have been widely studied mechanisms of antagonistic PBB. The PBB have shown effective antagonism in treating different pathogens including bacteria^[124], fungi^[125] and viral diseases^[126]. In PBB, few bacteria secrete antibiotics, pyrrolnitrin, pyoluteorin, 2, 4-DAPG, etc. to inhibit the growth of phytopathogens^[127]. The stimulation of induced systemic resistance (ISR) is yet another significant disease suppressive mechanism adopted by PBB. However, the PBB may employ simultaneous mechanisms of antagonism to provide better results (Figure 1). As an example, P. fluorescens CHA0 synthesized two antifungal compounds such as 2,4-diacetylphloroglucinol (DAPG)^[128,129] and pyoluteorin (PLT)^[130] which together suppressed various soil borne plant diseases^[131]. Below are some of the important compounds released by PBB to inhibit the pathogens and help promote growth and yield of vegetables.

Disease	Infected Plants	Bioagents	Microbial Antagonists	Inhibitory Biomolecules	Ref
Fusarium wilt	Tomato	F. oxysporum f sp. lycopersici	Bacillus aryabhattai strain SRB02	Phytohormones: Salicylic acid and amino acids	[15]
Fusarium wilt	Tomato	F. oxysporum f sp. lycopersici	Streptomyces griseus	Glucanase, chitinase, peroxidase	[82]
Bacterial wilt	Tomato	R. solanacearum	Bacillus, Brevibacillus Pseudomonas, Trichoderma	Peroxidase, phenylalanine ammonia lyase, polyphenol oxidase	[83]
Bacterial wilt	Eggplant	R. solanacearum	P. polymyxa	Lipopeptides	[84,85]
Bacterial wilt	Eggplant	R. solanacearum	P. fluorescens	Rhizosphere colonization	
Powdery mildew	Cucumber	Podosphaera xanthii (Castagne)	<i>T. harzianum, T. viride,</i> B. subtilis, P. polymyxa, S. marcescens	Peroxidase, polyphenol oxidase, phenols content (TPC)	[86]
Damping-off	Cucumber and Tomato	Pythium aphanidermatum	Talaromyces variabilis	Glucanase, cellulase and siderophores	[87]
Phytophthora crown rot	Cucumber	Phytophthora capsica	P. stutzeri, B. subtilis, B. amyloliquifaciens, S. maltophilia	Competitive root tip colonization	[88]
Phytophthora crown rot	Cucumber	P. capsica	P. stutzeri, B. subtilis, Stenotrophomonas maltophilia, B. amyloliquefaciens	Catalase	[88]
Damping off	Cucumber	Pythium ultimum	P. fluorescens, Pseudomonas sp., B. subtilis	Antibiotics and metabolites	[89]
Downy mildew	Cucumber	Pseudoperenospora cubensis	Consortium of Achromobacter sp., Streptomyces sp., B. licheniformis	Induced systemic resistance	[90]
Root and collar rot	Okra	Macrophomina phaseolina	T. viride	ND	[91]
Root rot	Okra	R. solani	P. fluorescens	Siderophores, HCN, IAA	[92]
Chilli Fruit Rot	Chilli	P. capsici	T. asperellum, T. harzianum, B. subtilis	Volatiles and non- volatile metabolites	[93]
Bacterial spot	Pepper	Xanthomonas campestris pv. Vesicatoria	Lactic acid bacteria	Siderophores	[94]
Early blight	Potato	A. solani and A. Grandis	Mycoparasitic fungus Clonostachys: C. chloroleuca, C. pseudochroleuca, C. rhizophaga	Bioactive substances and cell wall- degrading enzymes	[95]
Late blight	Potato	P. infestans	Streptomyces	Amylases, cellulases	[96]
Early blight	Potato	Alternaria solani	T. harzianum with P. fluorescens	ND	[97]
Late blight	Potato, Pepper	P. infestans; P. capsica	Chaetomium globosum; Burkholderia cepacian	Endo and exoglucanases; antimicrobials	[98,99]

Table 2. Diseases of Some Common Vegetables and Their Management by Plant Beneficial Bacteria

ND=Not Detected

5.1 Defence Molecules Produced by Plant Beneficial Bacteria

5.1.1 Iron Chelating Compounds

Siderophores are low molecular weight (≈ 2.0 KDa) iron chelating peptide molecules which are secreted under low-iron limited conditions by rhizosphere PBB ^[132,133]. Plant beneficial bacteria including N₂ fixers, for example, rhizobia and *Azotobacter*^[134], P-solubilizers^[116], K and Zn solubilizers^[92] excrete functionally different types of siderophores (hydroxamates, catecholates, phenolates, and carboxylates). The released siderophores form a complex with soil iron and limit its availability to phytopathogens^[135]. Moreover, the siderophore regulates the population size by restricting the Fe supply to phytopathogens and therefore, protect plants from further infection^[136,137]. As an example, the siderophores positive PBB, *P. aeruginosa* (strain FB2) and *B. subtilis* (strain RMB5) demonstrate significant antagonistic activity against different fungal plant pathogens, *F. oxysporum*, *F. moniliforme*, *R. solani*, *Colletotrichum gloeosporioides*, *C. falcatum*, *A. niger*, and *A. flavus*^[115]. Pyoverdines produced mainly by pseudomonads such as P. protegens, P. aeruginosa and P. fluorescens have shown adequate antagonistic activity against many pathogenic bacteria and fungi such as Pythium and Fusarium species. The tomato plants were then protected from pathogen-based damage and achieved healthy growth^[138]. Similarly, the siderophore pseudobactin secreted by P. putida suppresses the growth and infection of F. oxysporum and R. solani by reducing the Fe availability^[127]. Species of Azotobacter also secretes different types of siderophores, azotochelin, protochelin, aminochelin, and azotobactin that shield the food crops from phytopathogens such as Alternaria, Fusariun and Aspergillus. Given the direct impact on disease progression, the siderophores-mediated suppression of soil borne pathogen provides a promising avenue for PBB engineering and pathogen control.

5.1.2 Pathogen Modulating Enzyme

Plant beneficial bacteria also produce the growth modulating enzyme, 1-aminocyclopropane-1-carboxylate (ACC) deaminase that induces tolerance against biotic stresses^[139,140]. The ACC deaminase lowers the concentration of ethylene (ET) produced under severe biotic stresses^[141]. Ethylene (C_2H_4 or $H_2C=CH_2$), a stress phytohormone, induce chlorosis, senescence, and abscission in plants which aggravates the fatal impact of different pathogens^[142,143]. When produced by PBB, the ACC deaminase splits the ACC (a precursor of ethylene) into α -ketobutyrate and ammonia that reduces the precursor levels by inducing the ACC oxidase activity and ACC synthase in stressed conditions^[144, 145]. Accordingly, the ET concentration declines in the surrounding environment and thus plants are relieved from ET pressure. Plants therefore exhibit better growth and yields^[146,147]. The ACC deaminase produced by PBB Paenibacillus lentimorbus have induced tolerance in tomato against Scelerotium rolfsii, a causal organism of southern blight disease. The bacterized tomato plants displayed modulated ET pathway and antioxidants activities. The systemic tolerance was substantiated by pathogen related gene expression analysis^[148].

5.1.3 Unregulated Waste Products: Cyanogenic Compounds

Plant beneficial bacteria, in particular, fluorescent pseudomonads, studied extensively owing to their abilities to produce toxic antimicrobial metabolites including cyanogenic compounds are implicated in plant disease management^[149,150]. Many authors have reported HCN (a volatile poisonous secondary metabolite) producing PBB and their use as the antagonist in disease suppression and growth and yield enhancement of vegetables^[151]. Mechanistically, HCN cracks and distorts the fungal hyphae leading to alteration in cellular structure and function due to vacuolation and protoplast leakage^[152]. Cyanide, a toxic substance, acts by forming stable complexes with some of the essential elements such as Cu²⁺, Fe²⁺, and

 Mn^{2+} which consequently disrupts the functional aspect of protein. HCN effectively blocks the transport of electron and interrupts the supply of energy to the cell, and the death of biotic forms including pathogenic microbes occur under HCN positive environment. In a greenhouse study, Hyder and co-workers^[153] observed that the HCN positive P. putida, P. libanensis, P. aeruginosa, B. subtilis, B. megaterium and B. cereus significantly suppressed the infections caused by a notorious fungus Phytophthora capsici by 52.3-63% and concurrently enhanced the growth characters of chilli pepper. In addition, the HCN positive P. japonica (strain NBRC 103040), B. megaterium (strain CtST3.5), Pseudomonas sp. (strain Gamma-81), P. tolaasii (strain ATCC 33618), P. chlororaphis (strain Lzh-T5) and P. mosselii (strain CV25) inhibited the growth of pathogenic A. tumefaciens and affected the survivability of Meloidogyne incognita juveniles^[154]. Additionally, the gall formation on tomato plants by A. tumefaciens was prevented by P. japonica and Pseudomonas sp. Other PBB such as B. megaterium, P. chlororaphis, P. tolaasii, and P. mosselii, however, decline the number and biomass of galls produced on A. tumefaciens inoculated tomato plants grown either in the presence or absence of *M. incognita*. In general, all HCN producer PBB declined the M. incognita population and nematode gall numbers when used against M. incognita. Conclusively, the HCN-positive PBB caused a significant increase in overall performance of tomato plants colonized by A. tumefaciens and/or M. incognita.

5.1.4 Antibiosis and Antimicrobial Peptides

Production of antimicrobials such as lipopeptides, polyketides, and antifungal metabolites with broadspectrum action is yet another vital defense strategy adopted by PBB to control the attack by phytopathogens^[25] ^{155,156]}. 2,4-diacetylphloroglucinol (DAPG), phenazine-1carboxylic acid, oomycin, zwittermycin A, pyrrolnitrin, fengycin, iturin, phycocyanin and kanosamine^[154,157, 158] etc. are some of the common antibiotics that inhibit the growth and infective ability of phytopathogens. The notable PBB being capable of producing such antimicrobials are B. subtilis, B. amyloliquefaciens, B. velezensi, P. putida, P. fuorescens, P. brassicacearum, and P. polymyxa^{[103,} ^{159]}. Functionally, the antimicrobials adversely affect the cell wall^[160], damage the membrane integrity, and destruct protein synthesis by blocking the formation of initiation complexes on the small subunit of the microbial ribosomes^[161], which inhibits the growth and development of phytopathogens. DAPG, a polyketide antimicrobial compound released by pseudomonads is used to control many soil-borne plant pathogens^[162,163]. The DAPG produced by cell free culture filtrates of P. fluorescens (VSMKU3054) expressively prevents the in vitro growth of R. solanacearum, a causative agent of bacterial wilt disease of tomato, and other fungal pathogens, R. solani, S. rolfsii, M. phaseolina and F. oxysporum. Following inoculation, DAPG positive P. fluorescens (VSMKU3054) significantly

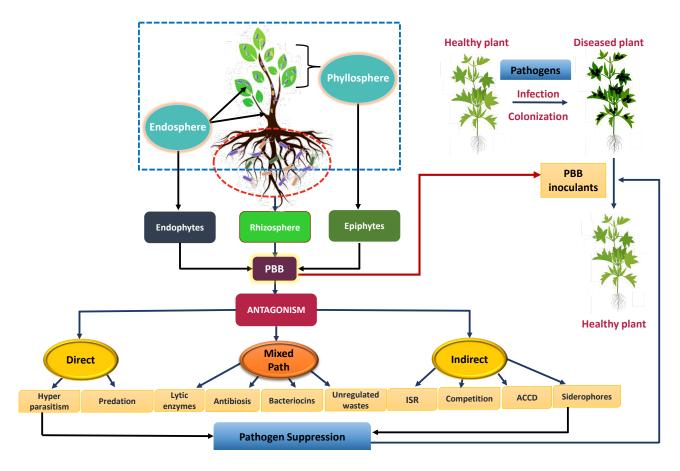


Figure 1. A mechanistic model explaining the bio-management of phytopathogens adopted by plant beneficial bacteria.

control the wilt disease of tomato^[164]. Other PBB, like, *Burkholderia* sp. HQB-1 produces phenazine that possesses redox activity and has been reported to suppress wilt causing F. oxysporum^[165]. In addition to *Pseudomonas sp.*, several Gram negative and Gram positive PBB strains are also known to produce antibiotics, polymyxin, circulin and colistin, that can limit the growth of many bacterial and fungal plant pathogens^[161,166].

Antibacterial peptides synthesized ribosomally by PBB termed "bacteriocins" are proteins with an antimicrobial activity that are used by producing strains to reduce competition from related bacterial strains^[120]. Once excreted into the environment, the bacteriocins destruct the bacterial cells which are closely related to the producer strains^[167,168]. In crop production systems, the bacteriocins have been found effective in suppressing the growth of phytopathogens^[127]. However, unlike conventional antibiotics, bacteriocins are narrow-spectrum proteinaceous toxins that can be bacteriostatic or bactericidal even for the synthesizing bacteria. Megacins, marcescins, cloacins and pyocins are some of the notable bacteriocins excreted by B. megaterium, S. marcescens, E. cloacae and P. pyogenes, respectively^[169]. Bacteriocins produced by species of Bacillus have received great attention due to their wide spectrum activity against multiple pathogens^[170]. As an example, the bacteriocins including known compounds such as fengycin, surfactin, bacillibactin, subtilin, etc. produced by Bacillus strains show inhibitory activity against bacterial and fungal phytopathogens, *E. carotovora*, *P. syringae*, *R. solani*, *B. cinerea*, *V. dahlia* and *P. infestans*^[119].

5.1.5 Cell Wall Degrading Enzymes

Several lytic enzymes are released by PBB that hydrolyse fungal/bacterial polymeric compounds, cellulose, hemicellulose, chitin, and proteins^[171]. The hydrolytic enzymes, for instance, chitinase^[172], glucanase^[173], β -1, 3-glucanase^[174], cellulases^[175], proteases^[176], phenylalanine ammonia lyase, peroxidase, polyphenol oxidase, catalase^[177], lipases^[178] etc. secreted by PBB degrade the cell wall of pathogens and ultimately cause their death. Since the fungal cell walls are mainly composed of chitin and beta-glucans, the PBB through lytic enzymes inhibit the growth of pathogenic fungi. Symbiotic N₂ fixing (SNF) rhizobium, S. fredii and free-living P. fluorescens produces chitinase and beta-glucanases, which have been reportedto inhibit the growth of F. udum. Accordingly, the PBB could manage the fusarium wilt disease caused by the fungus^[179]. Antagonistic bacteria S. marcescens hamper the mycelial growth of S. rolfsii through chitinase^[180] while Lysobacter enzymogenes suppress the growth of Bipolaris and Pythium *sp.* by glucanase^[181]. The secretion of defense enzymes such as SOD, guaiacol peroxidise, catalase and ascorbate peroxidase by Paenibacillus lentimorbus in wake of inoculation ameliorate the biotic stress caused by S. rolfsii in tomato plants^[148]. Also, E. asburiae BQ9 exhibits resistance

against tomato yellow leaf curl virus. The expression of defense-related genes and antioxidant enzymes, including phenylalanine ammonia lyase, peroxidase, catalase, and superoxide dismutase contributes to the disease resistance^[126].

5.1.6 Induced Systemic Resistance (ISR) and Competition

Apart from directly inactivating the phytopathogens, the PBB may also activate plant defence systems and induce resistance against different pathogens. The signalling cascade and wide-spread mechanism called "induced systemic resistance (ISR)"[182] evolved within plants are induced by different biotic agents including rhizobacteria^[183]. When a powerful pathogen attacks the host plant, the ISR is activated^[123,184] (Table 3). Notable PBB that induce ISR in potato, tomato, and Chinese cabbage against potential pathogens such as Bemisia tabaci, Fusarium, M. phaseolina, R. solani, R. solanacearum, Colletotrichum orbiculare, B. cinerea, and Pectobacterium carotovorum belongs to Pseudomonas, Alcaligenes, Paenibacillus, and Chryseobacterium^[196,182]. The PBB such as *B. amyloliquefaciens*, *Lactobacillus* paracasei, P. fuorescens, and P. putida have been found to protect plants including tomato by inducing ISR against phytopathogens^[197,198]. The ISR is though, not specific against any individual pathogen, plays a critical role in the management of plant diseases. The ISR is developed by PBB colonization of plant roots and is mediated by plant hormones for instance, JA, ET or phenolic compounds etc.^[199,200] produced by infected plants.

Competition for space and nutrients between PBB and pathogens is considered an important strategy in plant protection^[67,201]. The PBB usually compete with the pathogens both for physical space and growth supporting nutrients with limited amounts, both of which can alter the growth and infection ability of the pathogens^[202,203]. Among PBB, pseudomonads in general are the better colonizers^[204] of the plant root surface and through this ability can restrict the spread and growth of pathogens. Furthermore, in colonizing and aggregating onto seeds or soils, PBB strive for the limited available nutrients. Through active nutrient uptake mechanisms, PBB deter the growth of pathogenic fungi and bacteria by preventing the accessibility of nutrients to competing pathogens. For example, the soil suppressiveness to Fusarium wilt of tomato is attributed to competition for carbon and iron between the rhizospheres pathogenic F. oxysporum and F047 of F. oxysporum, a non-pathogenic endophytic strain and the wild population of fluorescent pseudomonads, respectively^[205,206]. Conclusively, the PBB consisting of biocontrol potentials serve as an inexpensive and environmentally friendly approach for maintaining the yield and quality of vegetables while eliminating/reducing the use of agrochemicals in vegetable cultivation practices.

6 MANAGEMENT OF VEGETABLE PATHOG-ENS BY PLANT BENEFICIAL BACTERIA: FEW EXAMPLES

Microbes-based strategies broadly known as "Microbial control" is receiving increasing attention as an environmentally comprehensive substitute to pesticides in vegetable production practices worldwide. The role of PBB in the management of phytopathogens causing severe losses to some of the most common vegetables are described.

6.1 Bacterial and Fungal Wilt of Tomato and Brinjal 6.1.1 Bacterial Wilt of Tomato

Tomato (Solanum lycopersicum L.), commercially the second most important edible vegetable crop after potato, owing to its high nutritive value (a rich source of vitamin A and C) is cultivated and consumed worldwide^[207]. The yield and quality of tomato, however, suffers heavily from attack by nearly 200 species of plant pathogens including bacteria, fungi such as Fusarium, Pythium, Rhizoctonia, and Verticillium and viruses etc.^[208,209] Wilt, among vegetal diseases, is the most common and devastating one against tomato caused by the microbial pathogens^[210] in the tropical and subtropical areas of the world^[211]. Among bacterial pathogens, R. solanacearum is the second most damaging bacterial pathogen that causes vascular wilt in tomato plants with swift and lethal wilting symptoms^[212,213]. The yield loss of tomato due to this pathogen varies between 2 to 90% in different cultivation areas^[214,215]. Different strategies such as, agrochemicals, antimicrobial plant extracts, soil disinfection, antibiotics, crop rotation and resistant cultivars etc. are adopted to reduce the losses caused to tomato by bacterial pathogens^[216,217]. Notwithstanding the effectiveness of in restricting the growth, development and infection potential of phytopathogens, their harmful effects on microbial diversity, soil biological activity^[218,219] and tomato yields^[220] raise global concerns. In order to prevent the lethal effect of chemicals, biological control measures in the management of bacterial wilt disease are desirable^[221]. Several antagonistic PBB for example, P. fluorescens, P. putida, Bacillus sp. etc. applied in soilplant systems suppress the tomato wilt disease^[83,222,223]. The tomato plants inoculated with B. velezensis (B63) and P. fluorescens (P142) significantly reduce the population densities of R. solanacearum (B3B) and hence, the wilt systems. Analysis by Confocal Laser Scanning Microscopy (CLSM) revealed an aggressive colonization of bacterial antagonists in roots, root hairs, epidermal cells and within xylem vessels that primed the plant defence against fungal pathogens. Similarly, the disease intensity was minimum (17.95%) while the biocontrol efficacy was maximum (68.19%) when tomato plants were bio-primed with B. amyloliquefaciens DSBA-11. The B. amyloliquefaciens strain DSBA-12 and B. subtilis strain DTBS-5 on the other hand had poor biocontrol ability which resulted in slightly higher disease intensity due to R. solanacearum infection.

Vegetables	Elicitor PBR	PBR Strains	Resistant Against Pathogens	Ref
Tomato	B. cereus	EPL1.1.3	Ralstonia syzigiisub	[185]
	P. fluorescens	PF15	Fusarium wilt	[186]
	E. asburiae	BQ9	Yellow leaf curl virus	[126]
	P. putida	BTP1	B. cinerea	[187]
	P. putida	WCS 358	Broad spectrum	[188]
Chilli	Bacillus sp.	BSp.3/aM	Colletotrichum capsica	[189]
	B. vallismortis	EXTN-1	Phytophthora capsica	[190]
Black pepper	P. fluorescens	Pf1	P. capsica	[191]
Cucumber	B. megaterium	L8	Pythium aphanidermatum	[192]
Potato	B. vallismortis	EXTN-1	Potato Virus Y and X	[193]
	P. fluorescens	89B61	P. infestans	[194]
French bean	P. putida	WCS 358	Broad spectrum	[188]
Radish	P. fluorescens	WCS-374	F. oxysporum f. sp. raphanin	[195]

Table 3. Examples of induced systemic resistance against diseases in vegetable crops

Bacillus strains in general, declined the *R. solanacearum* populations in infected plants and consequently optimized the vegetative growth, yields and quality of tomato^[223]. The innate immunity triggered by environmentally friendly PBB to plants was owing to the secretion of peroxidase, phenylalanine ammonia lyase and polypehenol oxidase^[83].

6.1.2 Fusarium Wilt of Tomato

Vascular wilt caused by the soilborne fungus F. oxysporum f. sp. lycopersici (FOL) is one of the most destructive fungal diseases of tomato in many vegetable growing countries. As a soil inhabitant, the fungus spreads to different agronomic areas through infested soil transport, good quality water (irrigation water), infected plants and seeds^[224]. The pathogenic fungus enters through the root via wounds or natural openings. After massive aggregation, they cause stern vascular damage by disrupting water transport leading to wilting and subsequently plant death^[225]. More than 80% of crop loss that has been reported is attributed to infections^[226]. Traditionally, growers apply fungicides to control this disease but the emergence of resistance among pathogens against chemicals becomes a major concern worldwide^[227]. Considering this, the use of many PBB such as species of Pseudomonas and Bacillus entailing antifungal activity have been recommended for examining the spread of fungal wilt disease^[228,229]. Inoculation of B. aryabhattai SRB02 for example significantly improves the growth while tumbling the disease in both tolerant and susceptible tomato cultivars^[15]. The susceptible and tolerant tomato cultivars bacterized with B. aryabhattai (strain SRB02) have significantly higher amounts of amino acids following infection by F. oxysporum. The plant defence hormone analysis revealed maximum concentration of SA with gradual reduction in JA in diseased plants. These observations fairly proved the antagonistic potentials of strain SRB02 which triggered the release of endogenous phytohormones and amino $acid^{[15,230]}$. Several other researchers have also concluded that the antibiotics for instance zwittermicin, bacillomycin, fengycin, bacilysin and difficidin produced by *B. amyloliquefaciens* strains can be useful in the management of fusarium wilt that consequently could improve the growth and yield of tomato^[231,232].

6.1.3 Bacterial Wilt of Eggplant

Bacterial wilt of eggplant (Solanum melongena) is one of the most destructive diseases of brinjal caused by R. solanacearum. This disease has threatened brinjal production throughout the temperate and tropical regions of the world^[233,234]. Owing to the long survivability and variable forms of the pathogen in soil and the ability to reinfect the healthy plants, chemical means failed to manage this pathogen^[235]. In greenhouse experiment, the application of P. polymyxa (IMA5) markedly optimized the growth, above/underground seedling/root length and biomass of R. solanacearum infected eggplants while exhibiting greatest biocontrol efficiency. The MALDI-TOF MS analysis revealed the production of antimicrobial lipopeptide by bacterial antagonist and therefore, the antagonistic activity was ascribed to the production of polymyxin and tridecaptin^[84]. Also, the *P. fluorescens*, a widely studied antagonist when applied as bacterial formulations enhanced the growth and yield features such as leaf area, number and biomass of fruits, height and yield of R. solanacearum infested brinjal plants^[85]. The bacterial formulations applied to seed, root and soil further reduce the occurrence and sternness of the bacterial wilt disease. The substantial

aggregation and colonization of the antagonist onto the seed surface from where it moves to the expanded roots is considered the best place for microbial colonization^[236]. This PBB strategy for disease suppression is considered promising in brinjal cultivation practices for reasons explained earlier.

6.1.4 Fusarium Wilt of Eggplant

Fusarium wilt of eggplant caused by F. oxysporum f. sp. melongenae is a serious vegetable disease. The pathogenic fungus invades the vascular bundles, blocks the xylem tissues, and disrupts the water transport, leading to severe wilting and consequently the death of the plants^[237]. Sadly, the Fusarium spores resist abiotic stresses and persist in the soil indefinitely. The control of this fungal pathogen and the deadly disease secondary to its impact is, therefore, utterly challenging. The use of PBB has, however, given some ray of hope as an alternative strategy to other modes of wilt management. Recently, two Gram positive PBB, B. amyloliquefaciens (KY568716) and B. velezensis (KY568715) showing broad-spectrum antifungal activity against F. oxysporum, A. alternata, C. capsici, M. phaseolina, S. hydrophilum, R. solani and P. digitatum, when applied on diseased eggplants, effectively reduced the lethal Fusarium wilt disease owing to lytic enzymes. Accordingly, the antagonists significantly promoted the biological features such as length, biomass and chlorophyll content of eggplants after stress was ameliorated^[238]. In other investigation, P. aeruginosa (P07-1), P. putida (P11-4), P. aeruginosa (85A-2), B. amyloliquefaciens (76A-1) and B. cereus (B10a) substantially inhibited the mycelial growth leading eventually to a massive reduction (85%) in the incidence of the disease. The P. aeruginosa (P07-1) and P. putida (P11-4) among all bacterial antagonists, colonize aggressively within eggplants, prevent the entry of the fungal mycelium inside the host tissues, and consequently alleviate the disease effect. The reduction in brinjal wilt disease is attributed to the ISR and secretion of several enzymes, peroxidase, polyphenol oxidase, catalase and cell wall degrading enzymes^[239].

6.2 Root Rot Disease of Okra

Okra (*Abelmoschus esculentus* L. Moench) is regarded as an integral component of balanced food systems owing to its amino-acid composition which is rich in lysine and tryptophan, dietary fibers, and other essential nutrients^[240,241]. Like other edible vegetables, cultivated okra is susceptible to many pathogens including fungi of genera *Rhizoctonia* (root rot), *Fursarium* (wilt), *Pythium, Phytophthora, Macrophomina* (damping off), *Colletotrichum* (anthracnose), *Cercospora* (leaf spot), *Erysiphe* (powdery mildew) and *Botrytis* (pod rot), bacteria such as *Xanthomonas esculenti* (leaf spot) and viruses (yellow vein mosaic) and different insect pests^[242-244]. Root rot of okra among many *R. solani* driven diseases is one of the most distressing diseases which has endangered the cultivation of okra worldwide. The application of PBB either alone or in combination with other bioagents have, however, been found successful in mitigating the destructive impact of root rotting fungi. Furthermore, the PBB application stimulates the synthesis of polyphenols and improve the antioxidant levels in okra plants^[245]. Pseudomonas (P. flourescens PF-7 and PF-8) as an antagonist suppressed the R. solani growth significantly leading to a considerable increase in the vigour index of okra plants^[92]. The excretion of secondary metabolites including pigments, siderophores, and cyanogen, etc. in addition to the release of IAA, SA and P solubilization by P. fluorescens causes an overall improvement in the yield and quality of okra. The biocontrol potentials and ability to secrete different growth modifying substances makes P. fluorescens a most ideal microbiological agent for upgrading the production of okra in different agrosystems.

6.3 Early and Late Blight of Potato

Potato (Solanum tuberosum L.) is the most important edible food crop which is cultivated widely in the temperate, sub-tropical, and tropical regions. Early blight caused by A. solani is one of the most common foliar diseases of potato around the world and causes yield losses of up to 80%^[246]. After infection, the disease symptoms appear first onto the lower senescing leaves that subsequently turn chlorotic and abscise prematurely. Eventually, the brown spot enlarges gradually and leads to complete destruction of plant foliage. Also, the stem canker or collar rot, sunken spots, lesions on upper stems and petioles or dark leathery fruit spots, etc. are other visible symptoms that appear in wake of infection^[247]. Moreover, the early blight may also cause dry rotting of tubers which spoils the yield and quality of tubers. However, the incidence and severity of disease depends on different factors such as cropping season, cultivation regions, cultivar genotypes and the health and stage of potato plants. Though, chemical fungicides are generally used to control potato early blight, the residual toxicity to non-target organisms and environmental hazards can be not underestimated. Therefore, the bacterial antagonists have been attempted to optimize the yield and quality of potato^[248]. For instance, a formulation consisting of P. fluorescens and T. harzianum, when applied in combination with the fungicide mancozeb, inhibited the growth of A. solani and greatly reduced the severity and incidence of the disease. The reduction in disease then produces a substantial improvement in the growth and yield of potato^[97].

Late blight is another most devastating disease of potato and is the re-emerging problem worldwide. The yield losses due to this deadly disease caused by the oomycete *Phytophthora infestans*^[249] varies from countries to countries depending upon the adopted plant protection measures and growing cultivars^[250,251]. For example, the yield loss in potato due to late blight has been reported as 100% under epidemic condition in Pakistan while in India the reduction in potato production due to this

disease averages 15% across the country^[252]. On the other hand, the total cost of late blight in Europe arising out of yield loss and the cost associated with its control has been estimated over one billion euros per year^[253]. In traditional cultivation practices, potato growers adopt different management strategies for late blight disease. They use chemicals, host resistant cultivars, biological control measures and cultural control methods^[254], among which the bio-based measures involving the use of bacterial antagonists especially the genera Pseudomonas and Bacillus for potato late blight have been proved effective and economical^[255,256]. In a greenhouse experiment, P.</sup> chlororaphis (strain R47) efficiently reduced the incidence of P. infestans, and demonstrated the highest level of P. infestans inhibition which was followed by P. fluorescens (R76) and P. marginalis (S35). The inhibitory action of Pseudomonas strains was mediated through the antifungal compounds^[257,258]. As a result, the growth of *P. infestans* were suppressed significantly that leads to a significant enhancement in potato production^[259]. The application of single bacterial antagonist against P. infestans sometimes, however, is counterproductive because the pathogen can attack its host by multiple routes. To be specific, this pathogen can enter through direct sporangia germination or via the release of motile zoospores; both situations involve host cell penetration and mycelial development^[249]. Therefore, the approaches based on multiple rather than single antagonist strain each targeting different route of infection are desirable. This strategy shows great potential to further improve the amelioration efficiency of cocultures. To date, very few studies have been conducted to address this issue and test the effect of composite PBB antagonists for potato diseases control. De Vrieze and coworkers achieved significantly improved protection of potato against P. infestans-induced blight disease when using combination of five Pseudomonas strains than when applying each *Pseudomonas* strain separately^[260]. This finding indeed paves the way for better understanding of antagonists' microbiome management that subsequently could be integrated into global potato production strategies.

6.4 Bacterial Soft Rot of Cabbage

Cabbage (*Brassica oleracea* L.), one of the most widely cultivated crucifers worldwide suffers heavily from bacterial soft rot disease^[261]. The disease caused by *Pectobacterium carotovorum* subsp. *carotovorum* (Pcc)^[262,263] is a major constraint in Chinese cabbage production^[264,265]. Chemical methods though generally effective are considered unsuitable due to environmental pollution and the emergence of resistance among target pathogens^[266]. Bacterial antagonists is one of the most effective and economical microbiological approaches for soft rot disease^[264]. Among bacterial agents, *Bacillus, Pseudomonas, Lactobacillus, Lactococcus*, and *Paenibacillus* have been used for soft rot management^[267,268]. Studies by Cui and co-

workers revealed that the extent of soft rot in Chinese cabbage and transmission of *P. carotovorum* to the stem progeny in greenhouse conditions and its persistence in the rhizosphere was significantly declined due to the antibacterial activities of *B. amyloliquefaciens* KC-1^[269].

6.5 Damping-off and Root Rot of Cucumber

Long English cucumber (Cucumis sativus L.; Cucurbitaceae) is grown as a vegetable crop in greenhouses in many regions of the world. Damping-off and root rot caused by soil borne fungal pathogen Pythium sp. is a serious and widespread disease^[270,271]. Generally, the intensity of damping-off and root rot pathogens are maximum during the cool and wet environment. Pathogenically, this fungus affects almost all growth stages and organs (e.g., radicle, hypocotyl, cotyledons, seed coat, endosperm, and embryo) of plants^[272,273]. The infectious magnitude of dampingoff and root rot pathogens can be suppressed by certain fungicides, such as captan, thiram, iprodione, fenaminosulf, fosetyl-Al, and metalaxyl^[274,275]. The microbiological control measures are, however, desired to clean up the damping-off and root rot diseases due to least/no hazards to the environment^[87,276]. A few species of PBB especially the genera, Pseudomonas and Bacillus, have been found useful in alleviating the effect of damping-off and root rot pathogen P. ultimum^[277,278]. In a study, Khabbaz and Abbasi reported that the three antagonistic PBB, P. fluorescens (9A-14), Pseudomonas sp. (8D-45) and B. subtilis (8B-1) when used alone or in combination enhanced the overall growth of cucumber by suppressing the unpleasant impact of *P. ultimum-induced* damping-off and root rot diseases^[89]. The pre- and post-planting application of PBB caused a substantial reduction in the intensity of the cucumber diseases by 27%-50% leading thereby to a considerable increase in plant growth. The enhancement in cucumber yield and quality was attributed to the production of antibiotics and other anti-fungal metabolites by PBB^[86, 102]. In conclusion, the sole or composite formulations of PBB could be developed as a safe and inexpensive biofungicides on commercial scale to optimize cucumber production globally under real field conditions. This will substantially reduce the dependence on fungicides being applied in traditional production systems to offset the damping-off and root rot disease in cucumber.

7 CONCLUSIONS AND FUTURE PROSPECTS

Vegetables are one of the most important constituents of human food systems. Most of the vegetable crops are susceptible to many biotic stresses, among which soil borne bacterial and fungal pathogens markedly reduce the yield and quality of widely grown and pleasantly consumed vegetables. The loss in vegetable production can be reduced by employing conventional approaches such as the use of resistant cultivars, crop rotation, field sanitization, and biocides. The exorbitant cost, the emergence of resistance among pathogens, and environmental pollution caused

by pesticide applications, however, remain major global issues to be addressed. The success that has been achieved so far at the bench scale clearly suggests that the microbial formulations could safely and inexpensively be exploited as an antagonist to alleviate the biotic stresses. Furthermore, they can act as biological enhancers for the nutrition and yield optimization of vegetables under stressed open field conditions. Despite the incredible developments made in this area to date, scientists/researchers need to identify the soil microbiota with profound disease suppression abilities from the unexplored soil ecosystems. Such PBB with multiple plant growth-enhancing traits demonstrate great potential in enhancing vegetable production under biotic stressed open field conditions. The molecular engineering of antagonists and transferring the desired genes coding for disease suppression/growth promotion into PBB deficient in such features are desirable. The use of advanced microscopic and some molecular techniques like cryo-SEM and HR-TEM, RFLP analysis, FISH, automated DNA sequencing methods, etc. may be valuable in deciphering the physiological details of PBB and devising the strategies for uplifting vegetable production in open field conditions.

Acknowledgements

Dr. Rizvi thanks DST-SERB for National Post-Doctoral Fellowship (PDF/2020/000127).

Conflicts of Interest

The authors declare that there is no conflict of interests.

Author Contribution

Khan MS conceptualized, designed and edited this manuscript; Rizvi A surveyed, collected and organized the latest scientific information and edited the original draft; Ahmed B revised the scientific literatures for important intellectual content; Umar S critically revised and proofread the manuscript; all authors approved the final version.

Abbreviation List

ABA, Abscisic acid ACC deaminase, 1-Aminocyclopropane-1-carboxylate deaminase BABA, β -aminobutyric acid BPNN, Back-propagation neural network BTH, Benzothiadiazole CCM, Color co-occurrence method Chl-FI, Chlorophyll fluorescence imaging DAB, Diaminobenzidine DAPG, 2,4-Diacetylphloroglucinol ET, Ethylene FISH, Fluorescence in situ hybridization H₂O₂, Hydrogen peroxide HCN, Hydrogen cyanide HRPO, Horseradish peroxidase HR-TEM, High-resolution transmission electron microscopy

IAA, Indole acetic acid ISR, Induced systemic resistance JA, Jasmonic acid KNN, K-Nearest neighbours NBT, Nitroblue tetrazolium $O2^{-}$, Superoxide PBB, Plant beneficial bacteria PLT, Pyoluteorin RBFNN, Radial basis function neural network RFLP, Restriction fragment length polymorphism ROS, Reactive oxygen species SA, Salicylic acid SEM, Scanning electron microscopy SGDM, Spatial gray-level dependence matrices SNF, Symbiotic nitrogen fixation SVM, Support vector machine TYLCV, Tomato yellow leaf curl virus

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