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Review

Recent Advances in Bio-management of Plant Diseases

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Abstract
Constantly increasing global human populations has put agricultural sector under astounding pressure to fulfil food demands growing worldwide. In order to optimize crop production, usage of agrochemicals in intensive agronomic practices have increased alarmingly. The negative impact of excessive application of agrichemicals on food production, human health and environment raises concerns about its long-term field application. Exploration of alternative means of crop protection and optimization, therefore, warrants inexpensive and environmentally friendly strategy. Use of microbes or microbes-based products among many options is one such important strategy that provides solution to the problems. In this regard, many biocontrol measures have been practiced over time, and some of them have shown exceptional potential and success. Realizing the importance of soil microbiota in crop optimization while reducing the chemical inputs, significance of plant beneficial bacteria in the amelioration of biotic stresses especially the phytopathogens employing microbiome management, microbial volatilomes, and nano-bioformulations is discussed. The relationship between the agriculturally useful soil microbiomes and food crops enables the development of microbes-based antagonist strategies for low-cost production of food crops in worrying open field environment.

Keywords: biotic stress, micro-biocontrol agents, nematophagous microbiome, nano-bioformulations, microbial volatilomes, hydrolytic enzymes

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1 INTRODUCTION

The relationship between human populations and crop production has been very old but complex as well. World population is growing exponentially and therefore, food insecurity is increasing at greater pace worldwide[1]. Global human populations are likely to reach approximately eight billion in 2022 which will further increase gradually to 10.4 billion in 2100 (UN 2022). Due to this huge population size, there is tremendous pressure on agriculture sector to optimize crop production and to fulfil human food demands. The global food mandates that agriculture production must increase by 70% to circumvent human food hunger[2]. Despite all efforts, production of food crops faces massive challenges from biological/microbiological enemies which cause huge losses to yield and quality of eatable crops worldwide. According to some estimates, loss in crop production in India due to insect-pests and diseases is 30-35%[3]. Among phytopathogens, fungi cause 80%, viruses and phytoplasmas cause 9% and bacteria cause more than 7% yield losses[4]. Scientists are trying hard to find ways as to how to control such losses. In this regard, various methods like, use of agrichemicals, antibiotics, and host resistance[5,6] are applied to prevent the crop damage due to phytopathogens. These methods have been proved as a short-term option in disease management strategies. Moreover, the inappropriate application of agrochemicals leads to unintended toxic impacts on soil-plant environment, soil/rhizosphere microbiome[7] and human health via food chain[8]. The resilience of insect-pests or other microbial phytopathogens toward expensive toxic chemicals is yet another major concern. So, considering all factors, there is urgent need to find an eco-friendly and cost-effective long-term solution to solve the phytopathogens problem and to enhance crop production. Evidence reveals that among all applied methods, use of biological formulations to manage plant diseases, often called "biological control" has attracted greater attention as a sustainable and inexpensive disease management strategy[9].

Indeed, different kinds of biological control measures are available but among all options, application of rhizobacteria that occupy about 7-15% of rhizosphere, is most preferred and widely used method[10]. The biological control agents (BCAs) employ different mechanisms such as competition, lytic enzymes and iron chelating compounds "siderophore", antagonism and induced systemic resistance (ISR) to suppress the severity and extent of diseases[11]. Attempts have been made herein to provide a broader and comprehensive view of new and emerging biocontrol strategies that focuses explicitly on microbial volatilome, plant microbiome engineering, and bio-nano-formulations for controlling phytopathogens.

2 CURRENT GLOBAL PERSPECTIVE OF CROP DISEASES

The loss in food crops due to insect-pests is increasing globally. Each year, plant diseases severely damage the crops resulting in losses in world economy which accounts for about $220 billion while pests alone cause $70 billion monetary losses. The plant diseases therefore, contribute significantly to crop yield losses which puts additional financial pressure on the agrarian community[12]. Like other countries, Indian economy which depends heavily on agriculture sector also suffers hugely from the menace of phytopathogens[13]. Among major food crops, the production of cereals especially maize, rice, and wheat[14] has been reported to decline by 30-70% due to huge biotic stresses[15], this is indeed an alarming situation regarding world food security. Savary et al.[16] projected yield loss at a global level for wheat, rice, maize, potatoes, and soybeans at 22, 30, 23, 17 and 21%, respectively. The maximum losses in the food production could be due to food-deficit areas where the population is growing rapidly and due to the emergence or re-emergence of similar or new plant diseases in the same agro-ecological regions. Put together, there is a pressing need for increasing crop production while minimizing/reducing chemical inputs in agricultural practices. Such ameliorating techniques employed for the management of crop diseases should however, be ecologically sustainable, highly reliable, greatly profitable, socially acceptable, and biologically/agronomically/medically and environmentally safe[17].

3 BIOCONTROL: CONCEPTS AND IMPLICATIONS IN DISEASE MANAGEMENT

Plant diseases caused generally by the phytopathogens belonging to different groups such as fungi, oomycetes, bacteria, nematodes, and viruses, primarily invade the plant root systems and gradually affects the other parts of the host plants[18]. The destruction of disease-causing ability of phytopathogens at any stage of infected plants therefore, becomes imminent. This can be achieved by employing one or simultaneous options like, biological approaches, chemical measures, plant genetic strategies or soil disinfection (fumigation, soil solarization, and anaerobic soil disinfestation) strategies[19]. Of all options, use of chemicals especially pesticides have been found rapid and effective. Ironically, the application of chemicals in the management of plant diseases pollute soil through drift or runoff, leaching and food via consumption of contaminated foods causing phytotoxicity to plants and human health[20]. Agrichemicals are also exorbitantly expensive and when applied injudiciously to control plant diseases, disrupt soil fertility, and crop productivity[21,22]. Considering this, interest in biological control via microbial agents has grown as an alternative to pesticides[23]. In order to limit the usage of synthetic agents, biological control measures involving microorganisms is considered an important component of integrated management strategies[23].

The term "biological control" or "biocontrol" refers to the use of living organisms to compete for resources or space, parasitise other organisms, or fight against certain plant diseases or pests[5]. Due to differences in understanding among scientists, the term biocontrol has been defined differently. For example, the use of biological agents, such as viruses, to combat pestilential organisms, such as pathogens, pests, and weeds, for a variety of objectives to benefit humans has been defined as biocontrol by some workers[24]. The beneficial organisms that are used to cope with the diseases are termed as BCAs by others. With the molecular advancement in biological control strategies, the term has been expanded further to include specialised metabolites, which can be effective for treating diseases and are often isolated from interactions or plant extracts. They are frequently referred to as "biopesticides" or "bioprotectants" and comprise compounds having signalling, antimicrobial or attractant properties (such as pheromones)[25]. Some of the widely used BCAs belongs to genera, *Bacillus*, *Pseudomonas*, *Agrobacterium*, *Burkholderia*, *Azotobacter*, *Frankia*, *Azospirillum*, *Bradyrhizobium*, *Rhizobium*, *Serratia* and *Thiobacillus*[26]. Apart from disease suppression, they also enhance plant growth by different direct/indirect mechanisms, biological nitrogen fixation, solubilizing essential elements such as P, Zn and K, secretion of iron chelating compounds (siderophores), phytohormones excretion, production of antibiotics, volatile organic compounds (VOCs), exopolysaccharide, hydrogen cyanide (HCN) and lytic enzymes[27]. Yan et al.[28] in a recent study, isolated *Bacillus velezensis* YYC strain from tomato rhizosphere and observed enhancement in tomato growth following inoculation by suppressing *Ralstonia solanacearum* through secondary metabolites such as plantazolicin, fengycin, difficidin and bacilysin and fengycin. Among all secondary metabolites, fengycin promoted plant disease resistance and reduced the growth of *Sclerotinia sclerotiorum*. Overall, BCAs are considered important in agriculture because they are inexpensive, environment friendly, simple to convey, easy to use, long shelf life and generates no toxic residues[29]. Also, BCAs can be used along with biofertilizers without contaminating soil as well as without causing any damage to the human health[30]. Considering all, there is need to scale up the BCAs production for aggressive application in real field situations for optimizing the crop yields[31,32].

4 PLANT MICROBIOME: AN EMERGING CONCEPT OF DISEASE SUPPRESSION

Plant microbiome, also known as the phyto-microbiome, is relatively a new concept that plays significant roles in disease suppression leading to crop optimization. The term microbiome has been defined as "a characteristic microbial community occupying a reasonably well-defined habitat which has distinct physio-chemical properties". In simple terms, microbiome refers to both composition and functions of microbes thriving well in any given environment. Broadly, plant microbiome, can be divided into the rhizosphere, phyllosphere and endosphere microbiomes, all of which harbour antagonists that may inhibit various phytopathogens in a plant system[33]. Overall, the plant microbiome benefits plants through different mechanisms such as synthesis of a specialised antagonistic metabolite (rhizobitoxine) that causes resistance against severe infections, suppression of soil-borne disease, antibiosis, competition for nutrients in the rhizosphere and hormone regulation[34]. Plant microbiome is affected by many factors related to plant itself for example, genotype, species, organs and plant health and abiotic factors like, land use and climate, agriculture practices like crop rotation, fertilizers and microbial applications[35].

Rhizosphere microbiome, also considered as the "second genome of plants"[36], consists of bacteria, protozoa, fungi, archaea, oomycetes, algae, nematodes, and viruses[37,38]. Some of these microbial populations exhibit antagonistic effects, while others benefit plants by other mechanisms[39]. Like rhizosphere microbiome, phyllosphere microbiome consists of mostly non-pathogenic microbial community whose interaction with plants can be positive, negative, neutral, or commensal[40]. According to some estimates, the total aerial surface of phyllosphere is about $6.4\times10^8 km^2$ worldwide that provides a common and vital place for terrestrial microbiota including bacterial cells[41]. Phyllosphere microbiome aid plants in maintaining health by reducing the overgrowth of phytopathogens. For instance, *Brevibacillus brevis*, isolated from Chinese cabbage phyllosphere, when used as a biocontrol agent against *Botrytis cinerea* produced the antibiotics gramicidin S and another cyclic antibiotic, non-ribosomal decapeptide, and some major component of tyrothricin[42]. In addition, phyllosphere microbiome enhances plant productivity and health by influencing seed weight, apical growth, blooming, and fruit development, as well as eliminating pollutants[43]. Phyllosphere microbial populations, such as *Microbacterium*, *Stenotrophomonas*, and

Methylobacterium have been found to improve the growth and nutritional quality of edible crops by producing natural growth regulators (such as IAA) and fixing di-molecular atmospheric N[44]. The importance of plant associated microbiome in phytopathogen suppression and consequently crop optimization is discussed in the following section.

4.1 Microbial Biocontrol Agents: A Conventional Biocontrol Approach

4.1.1 Bacterial Biocontrol Agents

Soil contains a diverse group of microbial populations which may be deleterious or beneficial to the plants. Among beneficial microorganisms, plant growth-promoting rhizobacteria (PGPR) or plant beneficial bacteria (PBB), firstly described by Kloepper and co-workers were isolated from the rhizosphere which after seed inoculation, quickly colonized plant roots and enhanced crop yields[45]. Also, any soil has the capability to prevent the establishment of diseases in host plants, even in the presence of a pathogen with a substantial inoculum density[46]. However, the abundance, diversity, and composition of PGPR/PBB depends largely on plant species and soil properties[47]. Despite this, the rhizosphere is considered a hotspot for interactions between plants and soil inhabiting heterogenous microbial populations and offer several advantages to mutualistic and symbiotic microorganisms, for example, PGP bacteria, archaea, mycorrhizal fungi, endophytic fungi, and other groups of organisms[48]. The scientific evidence suggests that PBB have been/being used in agriculture as potential biocontrol agents in place of agro-chemicals[49]. Some of the notable PBB commonly applied as bacterial antagonists belongs to genera *Alcaligenes*, *Azospirillum*, *Arthrobacter*, *Acinetobacter*, *Bradyrhizobium*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Pseudomonas*, *Rhizobium*, *Frankia*, *Azoarcus*, *Exiguobacterium*, *Paenibacillus*, and *Pantoea*[26,50,51]. These bacterial BCAs mitigate the phytopathogens populations both directly and/or indirectly[52] as presented in Figure 1. In order to inhibit the phytopathogens directly, PBB synthesize secondary metabolites, organic compounds, antimicrobial compounds, toxins and various hydrolytic enzymes like beta-xylosidase, chitinase, catalase, pectin methylesterase, β-1,3-glucanase etc. (Table 1). Of these, production of enzymes is however, one of the key mechanisms evolved within microbial populations that disintegrate the glycosidic linkages of pathogen cell wall leading consequently to the death of target pathogens[5].

The antagonists also inhibit the growth of phytopathogens indirectly by other mechanisms, hyperbiotrophy, ISR and competition. They also promote the growth of plants through effector and elicitor molecules released from the BCAs without killing the targeted pathogens[60]. Effectors are substances that are secreted by or linked to an organism that change the physiology, composition, or function of another organisms. Effectors are pathogen specific compounds that can alter the function and structural constituents of host cells to facilitate infection and/or elicit immune reactions allowing access to nutrients, proliferation, and growth[61]. A very few studies however suggests that effectors/elicitors may aid in uplifting the BCAs' capacity to manage plant diseases. For example, some species of Pseudomonas synthesize and excrete different elicitors such as lipopolysaccharides, phenazines and siderophores (pyochelin and pseudobactin) that efficiently stimulates the defence responses in host plants whereas growth and ISR were induced by 2,4-diacetylphloroglucinol and phosphogluconate dehydratase. The antibiotic compounds produced by *Pseudomonas* may have superior effectiveness when they are excreted in the rhizosphere because ISR may be triggered in plants prior to pathogen attack. As a result, they protect host plants from the damaging impact of pathogens and enhances overall growth of infected plants[62].

ISR is other beneficial trait of plant associated microbiomes that are used to suppress pathogens present either in soil or aboveground. The purpose and pathways underpinning ISR triggered by different beneficial biocontrol agents such as *Bacillus* spp., and *Pseudomomas* spp. etc. in containment of plant diseases is, however, poorly researched even though they can suppress numerous crop diseases[63]. Thus, systemic acquired resistance (SAR) and ISR both cause systemic resistance in plants and offer long-lasting defence against different phytopathogens. Among phytocompounds, salicylic acid (SA) is a necessary signal molecule for SAR, whereas ethylene and jasmonic acid (JA) acts as ISR signal molecules[64]. For instance, the seed inoculation of *B. pumilus* INR7 was found effective against the bacterial spot disease of pepper caused by *Xanthomonas axonopodis pv. Vesicatoria*[65]. PBB also manage biotic stresses indirectly through competition which occur among microbes for nutrients, oxygen, and appropriate niches both at root surface and in rhizosphere regions. The root exudates or the nutritional photosynthates released from different plant genotypes attracts PBB and favours their colonisation on appropriate plant surfaces. Rhizosphere microbiome, however, have a competitive advantage over plant pathogens due to their superior nutrient absorption and metabolic capabilities[66].

4.1.2 Fungal Biocontrol Agents

Majority of plant growth-promoting fungi are considered one of the safest methods for ISR and growth promotion of crops due to their ability to activate the

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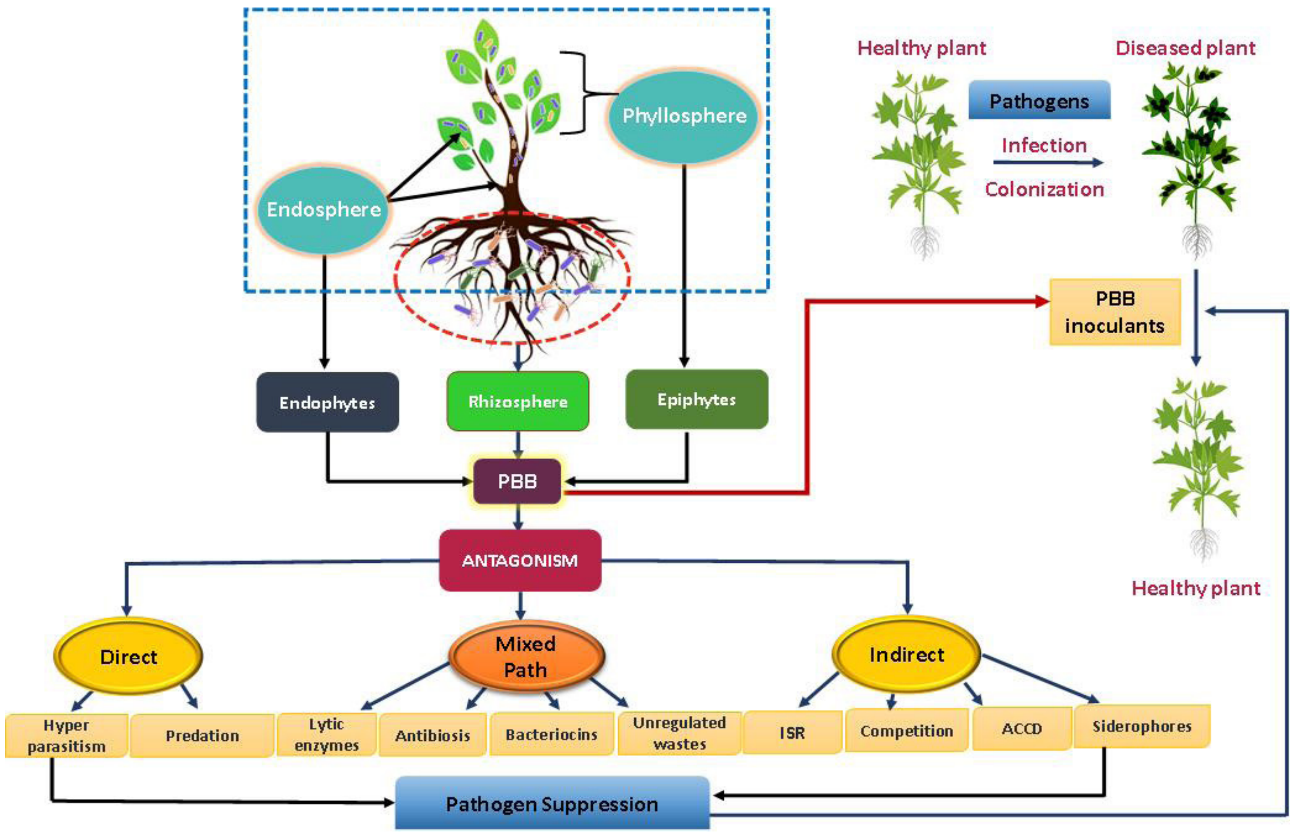

Figure 1. A mechanistic model explaining the plant disease suppression adopted by plant beneficial microbiome (Adapted from Khan et al.[53])

Table 1. Hydrolytic Enzymes Associated with Disease Suppression Produced by Bacterial Biological Control Agents

Antagonists	Biocontrol Agents	Target Phytopathogens	Disease Caused by Phytopathogens	Enzymes Involved	Mechanisms of Destruction	References
Pseudomonas spp.	Bacterial	*Ralstonia solanacearum*	Bacterial wilt of tomato	Lipase Amylase Protease	Cell wall degradation	[54]
Bacillus subtilis	Bacterial	*R. solanacearum*	Bacterial wilt of potato	Protease	Hydrolyze proteins and peptides	[55]
Pseudomonas fluorescens	Bacterial	*Fusarium oxysporum f.sp. cumini*	Cumin wilt	Chitinase, β-1, 3 Glucanase, and Protease	Inhibits mycelial growth, cell wall degradation	[56]
Bacillus velezensis	Bacterial	*Coniella vitis*	Grape white rot	Cellulase, Protease, Amylase and Lipase	Inhibits mycelial growth and spore germination	[57]
Serratia sp. *Enterobacter* sp.	Bacterial	*F. oxysporum f.sp. ciceris*	Chickpea wilt caused	Amylase, Protease, Cellulase, Chitinase	Cell wall degradation	[58]
Pseudomonas aeruginosa	Bacterial	*A. alternata*, *R. solani*, *X. euvesicatoria* *C. michiganensis subsp. michianensis, P. infestans*, *P. colocasiae*, *and B. cinerea*	Black spot of vegetables, Root rot and damping off vegetables	Proteases and Lipases	Destruct cell membrane and cell wall	[59]

plant immune system against pathogenic attack[67]. As a BCA, fungi are preferred due to - (i) a very high reproductive rate, (ii) a quick generation time, and (iii) they are target specific. Also, they can survive by switching from parasitism to saprotrophism in the absence of the host, thus preserving the sustainability of the environment[68]. Among fungi, *Trichoderma*, a genus with 25 BCAs have been used largely as a potential candidate to suppress a range of fungal phytopathogens. In addition to *Trichoderma*, other fungal genera such as *Alternaria*, *Aspergillus*, *Candida*, *Fusarium*, *Penicillium*, *Pichia*, *Pythium*, *Talaromyces*, and *Verticillium* have also been found as promising fungal biocontrol bioagents (FBCAs)[68]. The fungi adopt different mechanisms including secretion of hydrolytic enzymes (Table 2) to suppress the pathogenicity of the diseases. Furthermore, FBCAs activate host defence responses by producing pathogen-associated molecular patterns (PAMPs) or microbe-associated molecular patterns (MAMPs). These receptors can easily be sensed by the plants and in return induce PAMP/MAMP-triggered immunity to plants, antibiosis, hyperparasitism, competition and production of secondary metabolites[69]. Hyperparasitism is a fungal phenomenon exhibited by many antagonists wherein hyperparasites penetrate and kill cells of bacterial pathogens as well as the mycelium, spores, and dormant fungal pathogens[70].

Overall, the mycoparasitism includes different stages: (i) close contact with the pathogens, (ii) mutual/specific recognition and interaction between the pathogen and antagonists, (iii) secretion of lytic enzymes by the antagonists, dissolution of cell wall and penetration inside the host, and (iv) proliferation of the antagonists inside the host, and exit to the exterior environment[71]. In this context, mycoparasites such as species of *Trichoderma* have traditionally been considered as necrotrophic hyperparasite and fast colonizer of the spermosphere (seed zone) and rhizosphere (root zone). Following colonization and successful establishment, release of various hydrolytic enzymes such as chitinases, proteases, glucanases and other secondary metabolites, like, polyketides, non-ribosomal peptides, terpenoids and pyrones have been reported to suppress the fungal pathogen diseases and hence relieving plants from biotic stresses[72]. It has now become possible to enhance fungal strains and introduce fungal genes into the host plants using biotechnologies, genetic modification, and DNA recombination[68]. Employing these techniques, the gene encoding for trichodermin (tri5-trichodiene synthase) was cloned into *T. brevicompactum* Tb41tri5 which increased the production of trichodermin with greater antifungal efficacy against *Aspergillus fumigatus* and *Fusarium* spp.[73]. This and other developments in biological approaches for disease management warrants further use of genome editing technology (such as CRISPR/Cas9)[74].

4.1.3 Fungal and Bacterial BCAs Against Plant Parasitic Nematodes: An Overview

Plant-parasitic nematodes (PPNs) among soil dwelling nematodes pose a serious global challenge to food crops. The annual global economic losses due to PPNs has been reported as USD 173 billion[79]. When food crops are attacked by PPNs, no specific symptoms appear on plants and hence the damages are quite often erroneously confused with abiotic stresses. This mis concept, allows PPN to proliferate and increase in density beyond threshold limit in the field. Some of the agronomically destructive nematodes are root-knot nematodes (*Meloidogyne* spp.), cyst nematodes (*Globodera* spp. and *Heterodera* spp.), root-lesion nematodes (*Pratylenchus* spp.), the burrowing nematode (*Radopholus similis*) and the stem and bulb nematode (*Ditylenchus dipsaci*)[80,81]. So, considering the nematode threats, chemical control with synthetic nematicides has been attempted to offset PPN populations under real field conditions. The broad-spectrum activity, environmental pollution, emergence of resistance among PPNs and lack of proper regulatory and legislative guidelines regarding use of synthetic chemicals to contain and maintain PPNs within limit warrants alternatives strategies[82]. In this regard, BCAs especially nematophagous fungi (NF) and nematophagous bacteria (NB) offers a promising alternative to expensive chemical measures. In this section, the role of some fungal and bacterial BCAs in the management of PPNs are highlighted.

Plant beneficial microbiome inhabiting soil/rhizosphere or colonizing and penetrating endophytically plant surfaces (endophytes/spermophytes) also adopts different strategies to protect plants from the damaging impact of PPNs[83,84]. Generally, such nematophagous microbes (NMs) including fungal (Table 3) and bacterial BCAs (Table 4) target various life stages/processes including both motile and sedentary growth stages of PPNs and eventually kill them. Broadly, the NF controls the PPNs through bionematicides by parasitism, secretion of lytic enzymes and toxins and induce defence and resistance mechanisms in plants against PPNs[85-87]. Essentially, the NF traps (nematode-trapping fungi) and prevent PPNs from escaping through-(i) specialized structures, such as constrictor rings that capture nematodes in their mycelium (ii) three-dimensional hyphae networks and (iii) adhesive spores[88,89]. For example, the opportunistic saprotrophic fungi attack non-motile stages, like eggs, cysts, and *Meloidogyne* females[90]. On the other hand, the endoparasitic fungi do not produce specialized structures but infect PPNs by spores (conidia or zoospores). Such spores produced for example by *Harposporium* spp. are either ingested or adheres onto the cuticle of PPNs and later the whole NF content is injected into the nematode as reported in

Table 2. Some Examples of Hydrolytic Enzymes Associated with Disease Suppression Secreted by Fungal Biological Control Agents

Antagonists	Target Phytopathogens	Disease Caused by Phytopathogens	Enzymes Involved	Mechanisms of Destruction	References
Trichoderma harzianum sensu lato	*Bipolaris sorokiniana*	Wheat spot blotch	Chitinase	Decompose cell wall chitin	[75]
Trichoderma asperellum,	*F. oxysporum, F. fujikuroi, F. tricinctu, F. cantenulatum*	Fusarium wilt of banana	Chitinase and β-1,3, Glucanase	Degradation of chitin and cell wall	[76]
Cladosporium omanense	*Pythium aphanidermatum*	Cucumber and radish damping-off disease	Cellulase, β-1,3-Glucanases	Cellular leakage mycelium and inhibited oospore production.	[77]
Trichoderma species	*F. solani* and *R. solani*	Root rot of pea and bean	Chitinase, Peroxidase, and Polyphenol oxidase	Hydrolysis of cell wall	[78]

Table 3. Some Examples of Potential Fungal BCAs Against Plant-parasitic Nematodes

Antagonists	Major PPN	Nematode Species	Host Plants	Major Findings	References
Pochonia chlamydosporia	Root-knot nematodes	*Meloidogyne incognita*	Tomato and Cucumber	Reduced infection by 32-43% and female fecundity by 14.7-27.6%, induced the expression of salicylic acid (SA) pathway and upregulated jasmonate signalling pathway	[98]
Purpureocillium lilacinum			Tomato	Namaticidal effect on second stage juvenile's survival and egg hatching of nematode, reduced nematode populations, number of galls and egg masses in plant roots	[99]
Arthrobotrys oligospora (MRDS 300)			Tomato	Reduced the number of females, galls and nematodes in different developing stages	[100]
Pochonia chlamydosporia var. chlamydosporia			Pistachio	Reduced reproduction parameters; Number of galls were significantly reduced	[101]
Pochonia chlamydosporia	Cyst nematodes	*Globodera pallida*	Potato	Integrative characterization offers novel perspectives on the biology and biocontrol potential of *P. chlamydosporia*	[102]
Hirsutella minnesotensis		*Heterodera glycines*	Soybean	Microscopic examinations revealed soybean root surface colonization by H. *minnesotensis*, H. *minnesotensis* inoculation significantly improved the biomass, colonization efficiency, relationship between nematode parasitism and fungal density, and enhancement in soybean growth provide evidence that H. *minnesotensis* may be used as a potential BCA.	[103]
Arthrobotrys oligospora, Purpureocillium lilacinum and *Pochonia chlamydosporia, Glomus fasciculatum*	Root lesion nematodes	*Pratylenchus zeae*	Sugarcane	Individual or combined inoculations of BCAs increased shoot and root growth, *G. fasciculatum* with *A. oligospora* showed maximum shoot weight, *P. zeae* population reduced in all BCA inoculated plants, nematode reductions in roots varied between 50 and 77%, mycorrhizal colonization increased in combined treatments of AMF and antagonistic fungi	[104]

Fusarium oxysporum f. sp. cepae (foc)	Stem and bulb nematode	*Ditylenchu dipsaci*	Garlic	Interaction of *D. dipsaci* and Foc reduced the severity of disease in bulb and lowered the nematode populations	[105]
Fusarium inflexum, Thielavia terricola, Trichoderma brevicompactum, T. harzianum, T. longibrachiatum, Penicillium citrinum	Reniform nematode	*Rotylenchulus Reniformis*	Coriander and Cowpea	The NF fungi caused nematode mortality, allowed only 5 to 20% of the juveniles to hatch, fungal filtrates significantly reduced the number of egg masses and the reproductive factor of *R. reniformis*.	[106]
Purpureocillium lilacinum	White tip nematode	*Aphelenchoides besseyi*	Rice	Significantly reduced white tip symptoms and kernel numbers in panicles and panicle weight	[107]
Volutella citronella	Cyst nematode	*Aphelenchoides besseyi, Bursap-helenchus xylophilus,* and *Ditylenchus destructor*	Potato	The mortality rate was 100, 100, and 55.63%, respectively for each nematode	[108]
Monacrosporium thaumasium	Beer mat nematode	*Panagrellus redivivus*	*In vitro*	BCA produced chitinases of two distinct molecular weights, 27 and 30 kDa with nematocidal activity, enzymes significantly reduced number of *P. redivivus* larvae by 80%.	[109]

Table 4. Some Examples of Potential Bacterial BCAs Against Plant-parasitic Nematodes

Bacterial BCAs	Major PPN	Nematode Species	Host Plants	Major Findings	References
B. cereus, B. subtilis, B. thuringiensis, B. megaterium	Root-knot nematodes	*Meloidogyne* spp.	Soybean	The filtrate mixture of BCA caused approximately 85–90% immobility of second- stage juveniles (J2) of *nematode* after 96 h	[115]
Bacillus subtilis			Sugarcane	Effectively controlled the nematodes in all three cycles of sugarcane production	[116]
Pasteuria penetrans		*M. arenaria*	Peanut	Local change in specificity on a yearly basis, exhibited ability to infect and suppress target pest	[117]
Bacillus cereus, B. pumilus, B. subtilis, B. flexus, B. megaterium	Cyst nematodes	*Globodera rostochiensis*	Potato	BCAs were nonpathogenic and had protease and chitinase activity; could be used as potential BCA for golden cyst nematode	[118]
Ensifer fredii		*Heterodera glycines*	Soybean	The mortality of J2 treated with BCA increased with exposure time, reduced egg hatching within cysts, *H. glycines* were repelled by the BCA	[119]
Pseudomonas donghuensis, Pseudomonas sp.	Root lesion nematodes	*Pratylenchus Penetrans*	Onion	PGPR application decreased *nematode* populations on onion roots, enhanced root length and dry weight, PGPR strains showed nematicidal activity, produced chitinases and proteases, and formed biofilms	[120]
Combination of *P. fluorescens* and *Purpureocillium lilacinum*	Burrowing nematode	*Radopholus similis*	Banana	*P. fluorescens* with *P. lilacinus* effectively reduced the burrowing nematode populations in soil and roots	[121]
Bacillus sp. (CBSAL02), *Pseudomonas* sp. (CBSAL05)	Stem and bulb nematode	*Ditylenchus* spp. and *M. javanica*	Garlic	Bacterial BCAs CBSAL02 and CBSAL05 significantly reduced the hatching of *M. javanica* eggs by 74% and 54.77%, respectively and motility of *Ditylenchus* spp. by 55.19% and 53.53%, respectively	[122]

Bacillus amyloliquefaciens (FR203A), *B. megaterium* (FB133M), *B. thuringiensis* (FS213P), *B. thuringiensis* (FB833T), *B. weihenstephanensis* (FB25M), *B. frigoritolerans* (FB37BR), and *P. fluorescens* (FP805PU)	Fanleaf virus nematode	*Xiphinema index*	Grapevine	The three initial consortia showed effective control of parasite, significantly lowered the reproductive indices, damages caused by *X. index* were declined by all BCAs without any difference among BCA formulations.	[123]
Xenorhabdus bovienii	White tip nematode	*Aphelenchoides besseyi*	Rice	The *X. bovienii* suppressed the *A. beseyi* populations	[107]

Drechmeria coniospora and *Verticillium* spp.[91,92]. As an example, the *Arthrobotrys oligospora*, a nematode-trapping fungus has been found to have a significant deleterious effect on *Meloidogyne javanica* infecting tomato by forming a specialized penetration tube to pierce the nematode cuticles[93]. The killing of PPNs by NF is also done through nematicidal or nematostatic compounds released into the soil[94,95]. Among toxic metabolites, mycotoxins are commonly used by toxin-positive NF to immobilize or kill PPNs[96,97].

Bacterial mechanisms to antagonize PPNs may include the production of antibiotics, endospores, hydrolytic enzymes, VOCs, Cry proteins (pore-forming toxins) etc[110,111]. Apart from directly suppressing the PPNs, many soil microbiome including arbuscular mycorrhizal fungi (AMF), indirectly facilitate the growth and development of agriculturally important crops by inducing plant defense mechanisms against PPNs, for example, inducing signal substrate production, regulating gene expression, and enhancing protein production and maintaining plant hormone levels[112-114]. Acknowledging the importance of interaction between NMs and PPNs, the area looks interesting because nematophagous BCAs can be used to manufacture inexpensive and environmentally friendly namatocides as an alternative to synthetic chemicals used to manage PPNs. Some hydrolytic enzymes such as serine protease, chitinase and toxins released by NMs into soils can play important roles in destroying infection and thereby protecting crops from the PPNs attack.

5 MICROBIAL VOLATILOMES: A RECENT APPROACH FOR CONTROLLING PHYTOPATHOGENS

Control agents also synthesize VOCs that mitigates the crop diseases by preventing root colonization of plant pathogens. The VOCs released by microbiome, varying in chemical composition is preferred in sustainable agriculture over synthetic fungicides due to- (i) long-range of action, (ii) easy decomposition, and (iii) higher biocontrol efficiency[124,125]. Approximately 2000 bacterial VOCs are known to be secreted by almost 1000 microbial species, the predominant VOCs are alkenes, alcohols, ketones, terpenes, benzenoids, pyrazines, acids, and esters[124,126]. The fungal volatiles are dominated by alcohols, benzenoids, aldehydes, alkenes, acids, esters, and ketones[127]. Bacterial species that produce VOCs belongs to genera *Bacillus*, *Burkholderia*, *Collimonas*, *Pseudomonas*, *Serratia*, *Stenotrophomonas* and *Streptomyces* while fungi include *Aspergillus*, *Fusarium*, *Muscodor* and *Alternaria* (Table 5). The co-inoculations of *B. cereus* Rs-MS53 and *P. helmanticensis* Sc-B94 have been found to effectively suppress the pathogenic fungus *R. solani*[128]. Similarly, *R. solani*, a soil-borne pathogen, secreted a variety of VOCs that facilitated plant growth, development, altered plant emissions, and decreased insect resistance[129]. The synthesis of HCN by some *Pseudomonas* spp., such as *P. fluorescens* CHA0, is a well-known example of volatile-mediated fungal inhibition against *Thielaviospis* induced tobacco root rot[130].

6 NANO-BIOFORMULATIONS IN DISEASE MANAGEMENT

Nanotechnology, an exciting technology with broader applications in different disciplines including agriculture, biomedicine, food packaging and environment[141] has generated exceptional interests among global researchers due to their unique features[142-144] such as size (10 to 100nm), large surface area to volume ratio, high surface energy, quantum confinement and many other catalytic and magnetic activities of nanoparticles (NPs)[145,146]. The application of NPs or NPs based formulations are increasing in agriculture including plant disease management also[147,148] due to- (i) precise delivery of NPs to targeted sites (ii) capability of NPs to enhance nutrient use efficiency and (iii) its ability to reduce nutrient losses during application or leaching into water systems[149]. The NPs based formulation often called nanoformulations or nanobioformulations involves the use of biological resources such as microbes. The nanoformulations should contain all properties of NPs like shape, size, no eco-toxicity, easy transport delivery and disposal[150]. Due to these properties, nanoformulations are considered potential plant growth enhancer in crop production practices[151-153]. Realizing the phytopathogen inhibiting abilities of NPs, the nanomaterial-based formulations have been applied and found useful in up-regulating crop production by impeding the phytopathogens[154,155].

Table 5. Volatilomes Synthesized by Antagonist Microbiomes Against Phytopathogens

Antagonists	Target Organisms	Main VOCs	Effects of VOCs	References
Lysobacter	*Pythium ultimum Rhizoctonia solani, and Sclerotinia minor.*	2,5-Dimethylpyrazine, 2-ethyl-3-methoxypyrazine and 2-isopropyl-3-methoxypyrazine	Induce resistance against abiotic and biotic stresses and Inhibits spore germination and mycelial growth	[131]
Trichoderma gamsii	*Panax notoginseng*	dimethyl disulfide, dibenzofuran, methanethiol, ketones,	Controls plant pathogens, activate plant immunity, and enhance plant growth	[132]
Streptomyces sp.	*Rhizoctonia solani, Phoma medicaginis, Fusarium solani Fusarium oxysporum and Sclerotium rolfsii*	3-carene 2,5-dione, geosmin, beta-cubebene and Phenol, 2-(1,1-dimethylethyl)-6-methyl-	Alter hyphal morphology and inhibits conidial germination	[133]
Pseudomonas sp.	*Verticillium dahlia*	1-undecene, (methyldisulfanyl) methane and 1-decene, tridecane, 1-decene	Plant growth promotion and anti-fungal activity	[134]
Bacillus spp.	*Macrophomina phaseolina*	Benzene, 1, 3-diethyl- and Benzene, 1, 4-diethyl followed by naphthalene, m-ethylacetophenone and ethanone, 1-(4-ethylphenyl)	Mycelial growth inhibition, deformity of mycelium, inhibition of sclerotia germination, and ultrastructural alterations of cell organelles	[135]
Bacillus spp.	*Fusarium oxysporum f. sp. niveum*	2-heptanone, 2-ethyl-1-hexano, and 2-nonanone	Plant growth promotion and antifungal activities	[136]
Corallococcus sp.	*Fusarium oxysporum f. sp. Cucumerinum*	trans-1, 2-pentyl-1-heptene, 259 1H-cyclopenta-1,3-cyclopropa-1,2-benzene and 3-Undecanone. 2-hexyl-1-decanol and 2-octyl-1-dodecanol	Damage cell wall and cell membranes, Apoptosis, accumulation of reactive oxygen species (ROS), inhibits mycelial growth, antifungal activity	[137]
Bacillus spp.	*Fusarium kuroshium*	ketones and pyrazine compounds,	Inhibits mycelial growth, antifungal activity	[138]
Stenotrophomonas sp.	*Bacillus pumilus*	dodecane, 2,6,10-trimethyl dodecane, 2,6,11-trimethyl	Antibacterial activity, inhibits root attachment, chemotaxis and motility, damages the cells	[139]
Pseudomonas putida	*Ralstonia pseudosolanacearum*	2, 5-dimethyl pyrazine; 2-methyl pyrazine; dimethyl trisulphide; 2-ethyl 5-methyl pyrazine; and 2-ethyl 3, 6-dimethyl pyrazine	Antibacterial, antifungal, completely inhibits oomycetes	[140]

Due to many problems linked with the application of synthetic pesticides in disease management, metal oxide NPs (MONPs) have received greater attention as nanoformulations in plant disease management because they are- (i) much smaller than bulk molecule, (ii) required in small quantities, (iii) inexpensive relative to expensive conventional agrichemicals, and (iv) benign[156-158].

Nowadays, *Bacillus* based nanoformulations are preferred against phytopathogens since *Bacillus* spp. secretes a variety non-ribosomically antagonist substance, including iron chelating compounds, lipopeptides, antimicrobial peptides, and polyketide compounds[159]. The *Bacillus* species such as *B. stearothermophilus*, *B. laterosporus*, *B. circulans*, *B. licheniformis*, *B. amyloliquefaciens*, *B. pabuli*, *B. magaterium*, *B. thuringiensis* and *B. subtilis* produce chitinase which can break the cell wall chitin of the conidia, hyphae, sclerotia as well as chlamydospores and have shown antifungal activity against *Aspergillus favus, A. niger* and *Penicillium chrysogenum*[151]. Nanoformulations are also used as carrier materials for the controlled release of BCAs due to slow delivery of the active ingredient and improved solubility to have maximum inhibitory effect against phytopathogens[160]. Recently, bacterial based nanobioformulations prepared using carbon nanotubes and silicon oxide NPs was found effective against *Phytophthora drechsleri*, capable of causing pistachio gummosis, and increased the growth

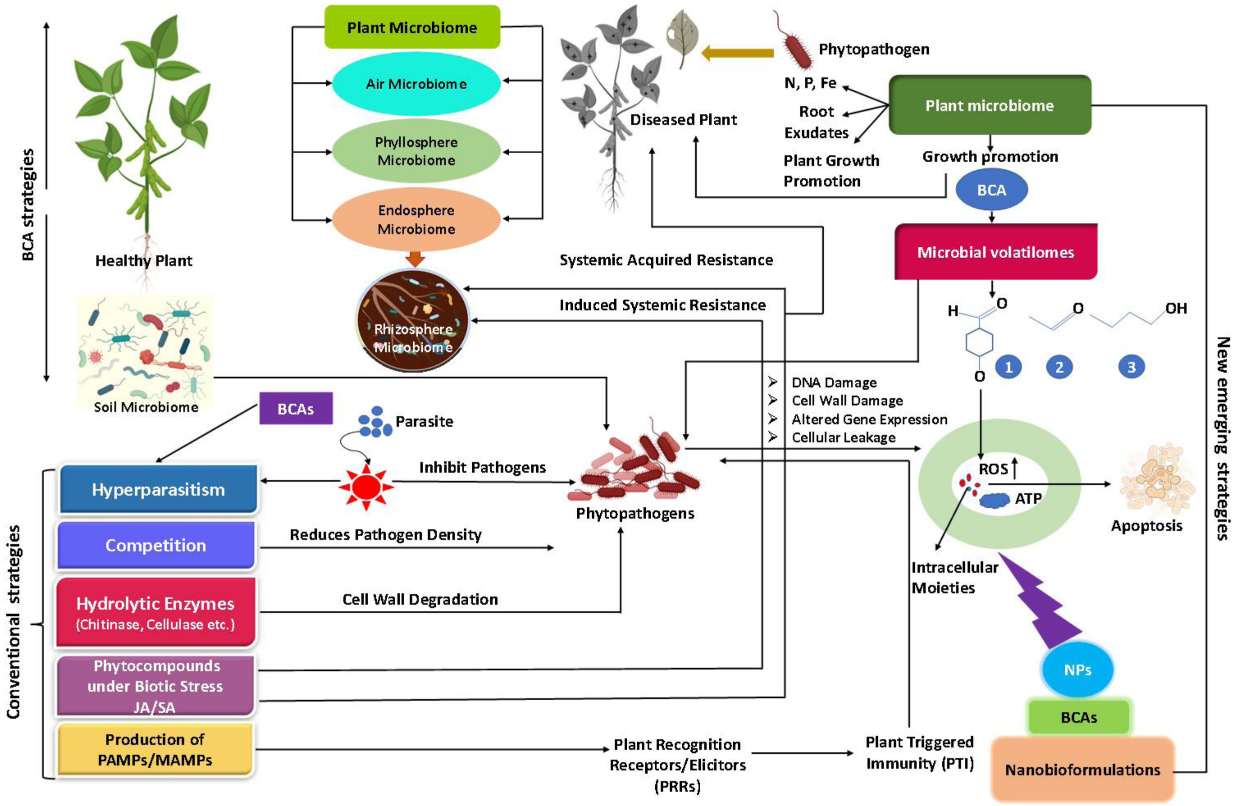

Figure 2. Schematic overview of recent approaches involving plant microbiome, microbial volatilomes and nanobioformulations strategies that can be adopted and integrated to generate a more holistic picture of microbiome consortia and mechanisms involved in phytopathogen suppression leading to crop optimization. BCA, Biocontrol agents; JA, Jasmonic acid; SA, Salicylic acid; ROS, Reactive oxygen species; N, P and Fe indicates nitrogen, phosphorus and iron respectively; NPs, Nanoparticles.

and crop yields[161]. Besides bacteria-based formulations, fungus-based formulations are also used against the phytopathogens. In a study, two types of nano-capsules, nanoemulsion, and powdered nanoformulations were prepared using fungus *Talaromyces flavus* and tested against the pathogenic fungus *F. oxysporum* f. sp. *cucumerinum*. The nanopowder was found as the most potent nanoformulation that maximally inhibited the pathogen compared to nanoemulsion based nanofungal formulations[162]. Similarly, the biocontrol capability of *Serratia marcescens* SU05's bovine serum albumin (BSA) NPs loaded with extra cellular chitinase had inhibitory effect against phytopathogenic fungus *Alternaria alternata*. Nano-enzyme conjugate at all concentrations significantly reduced the fungal biomass, with maximum damage to fungal hyphae fragments. It was suggested that the nanoformulations could be developed and applied in field environments for efficient control of phytopathogenic fungi[163]. The conventional and new emerging trends highlighting the importance of microbiomes in disease suppression are summarized in Figure 2.

Besides controlling the phytopathogens, NPs also play significant roles in plant growth and development beginning from seed germination to optimization of crop yields[164]. In a study, selenium NPs were found to exhibit positive effects on the length of shoots, roots, and the germination percentage of *Hordeum vulgare*[165]. Similarly, the silver and titanium oxide NPs revealed positive impacts on seed germination, seedling growth, chlorophyll content, antioxidant activity and carotenoid content of tomato plant[166]. In yet other reports, Zinc oxide nanoparticles, prepared from foliage of *Coriandrum sativum*, when used as nanofertilizer had stimulatory effects on growth of various pulses, such as Bengalgram, Turkishgram, and greengram. The effects were obvious on seed germination, chlorophyll, and protein content leading to overall improvement in plant performance[167].

7 CONCLUSION

Crops in general are susceptible to many biotic stresses including soil borne bacterial and fungal pathogens that distinctly diminish the food quality and crop yields. The reduction in production can be managed by adopting both traditional and advance approaches. The unreasonable cost, development of resistant pathogens and environmental hazards resulting from pesticidal applications are serious concerns. The intervention of microbial formulations and nanobioformulations in intensive crop production practices provide a safe and an effective solution to the problems of biotic stresses. They can also act as growth enhancer by supplying nutrition to plants and consequently enhances crop yields under stressed open field conditions. The microbiome endowed with many disease suppressing abilities could be developed and commercialized for upregulating the food production under real field conditions. The genetic manipulation of microbial antagonists especially genes associated with disease suppression/growth promotion into bacterial/fungal microbiome lacking such activity are needed.

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Conflicts of Interest
The authors declared no conflict of interest.

Author Contribution
Rizvi A and Nigar D contributed to the literature search strategy, manuscript screening, data compilation and validation. Khan MS and Rizvi A contributed to original draft preparation. Ahmed B, Ahmed E and Rizvi A contributed to graphics design and reviewed the manuscript. Khan MS conceptualized, supervised, and edited the whole manuscript. The manuscript was read and approved by all the authors for publication.

Abbreviation List
AMF, Arbuscular mycorrhizal fungi
BCAs, Biological control agents
BSA, Bovine serum albumin
FBCAs, Fungal biocontrol bioagents
HCN, Hydrogen cyanide
ISR, Induced systemic resistance
JA, Jasmonic acid
MAMPs, Microbe-associated molecular patterns
MONPs, Metal oxide NPs
NB, Nematophagous bacteria
NF, Nematophagous fungi
NMs, Nematophagous microbes
NPs, Nanoparticles
PAMPs, Pathogen-associated molecular patterns
PBB, Plant beneficial bacteria
PGPR, Plant growth-promoting rhizobacteria
PPNs, Plant-parasitic nematodes
ROS, Reactive oxygen species
SA, Salicylic acid
SAR, Systemic acquired resistance
VOCs, Volatile organic compounds

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