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Microbial antagonists: diversity, formulation and applications for management of pest–pathogens

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Abstract

Agriculture is the backbone of developing countries, which plays an essential role in primary drivers of economy. The increasing use of chemical fertilizers and toxic insecticides endangers the health of human, plant soils, and the environment. Microbial insecticides have been implemented in current scenario for crop protection. Biological agents for pest control have gained more attention in recent year as substitutes for management of pests and pathogens. It provides a sustainable approach to plant health management and assists to minimize the excessive applications of toxic substances. The antagonistic microbes belong to six different *phyla* including Bacillota, Actinomycetota, Pseudomonadota, Bacteroidota and Mucoromycota. Microbial pesticides have been developed through a number of processes, including extraction of pure culture and screening using effectiveness bioassays under controlled and natural conditions. Biological control agents (BCAs) are recognized to be the most sophisticated technology for environmentally friendly agriculture. The various beneficial BCAs have been reported for the management of plant health, but they required effective acceptance together with the standardization of bioformulation. The present review deals with the recent development of microbial control agents, mechanisms of actions, development of microbial pesticides and their potential applications for agricultural productivity.

Keywords Agricultural sustainability, Bioformulations, Microbial signaling, Pesticides, Plant microbes

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Background

The diversity of microbiome is one of the abundant sources exploited for generate a wide range of goods and process with multiple applications in the industrial, medicinal, and agricultural sectors (Yadav et al. 2017). Among all, agriculture is a crucial sector in India, and effective disease management strategies are in high demand. In the agriculture, microbiomes are mostly used as a biocontrol agent to combat pest insects. Although microbial biocontrol of pests have been documented in the middle of the 1990. These chemical pesticides obscure their effects and potential (Gurung et al. 2019). After the “silent spring” researcher erudite that chemicals intensive insect management is detrimental to environment and cannot ensure security of safe food for a growing human population (Gay 2012). Therefore, preventive pest management practices based on different economic, ecological, and human concerns have replaced therapeutic pesticidal control in modern sustainable agriculture techniques (Singh et al. 2020).

Insect pests with high population level are detrimental and destroy agricultural crops and economy as well as decrease the food security for growing human populations (Sharma et al. 2020). To achieve more sustainable agricultural practices, there is a strong push to find substitutes for chemicals in controlling diseases and pests, which have caused significant losses in food production. Now researchers are focusing on potential biological control microbiomes as viable substitutes for managing pests, due to the adverse effect of chemical fertilizers on environment and human health (Ab Rahman et al. 2018). Biotic agents such as harmful insects, pathogens, and parasitic weeds are some of the most important plant pests, which cause serious damages and losses to agricultural products. To ensure quantitative and qualitative food, feed, and fiber production, it is essential to control these plant pests (Heydari and Pessarakli 2010). Bacterial and fungal pathogens can cause plant diseases, leading to losses in agriculture productivity and poor quality of agricultural products. This can result in economic hardships for growers, reduced food supplies, and ultimately high prices (Monte 2001).

The most widely used approach for long-lasting benefits is integrated disease management, while chemicals and numerous biological methods are also employed. Microbiomes often enter plants through naturally occurring wounds, which can occur accidentally due to pests or even human intervention (Lindsey et al. 2020). Understanding the applications of microbiomes for promoting the growth and controlling diseases is crucial. Biofertilizers and biopesticides have been developed as alternative to chemical fertilizers and pesticides, but their success in the field is still inequitable (Ab Rahman et al. 2018).

Biological control is managing the plant diseases, which involves the use of beneficial microbiome, including archaea, bacteria and fungi. These microorganisms are specifically selected to attack and control plant pathogens, offering an eco-friendly approach for management of pest and pathogens. By incorporating biological control into physical and cultural controls, limiting chemical usage, it is possible to create an effective integrated pest management (IPM) system (Monte 2001). In recent times, online resources related to medicinal plants, antimicrobial peptides (AMPs), natural products (NPs), and essential oils (EOs) have significantly aided the development of cost-effective and efficient control agents for pests and pathogenic microbes (Jin et al. 2021). The various fungi, bacteria, and viruses are the primary plant pathogens, and the severity of their diseases depends on environmental factors, including temperature, humidity, altitude, and the niches of the pathogens. The present review deals the antagonistic microbes as a biocontrol agent, mechanisms of actions, diversity and their biotechnological applications for agricultural productivity.

Biodiversity of antagonistic microbes

Antagonistic microbe's importance in the sustainable management practices results in the massive amount of biodiversity study. Due to various ecological services, these microbes have been reported in diverse habitats. These microbes are found in soil, and they are also associated with diverse varieties of plants, nematodes and insects. Various microbes such as fungi and bacteria have been found as an antagonist and they are found to belong to different phylum and genera (Table 1). On a review of diverse finding, antagonistic microbes belong to six different *phyla* including Bacillota, Actinomycetota, Pseudomonadota, Bacteroidota and Mucoromycota (Fig. 1), in which Pseudomonadota was most dominant phylum followed by Bacillota, whereas Actinomycetota, Bacteroidota and Mucoromycota were least dominant. According to the report, *Trichoderma harzianum* was sorted out from rhizospheric region of sugarcane. The soil bacterium was found to inhibit the growth of *Colletotrichum falcatum* (Viswanathan et al. 2003). In a report, *Bacillus lentimorbus* associated with the weed rhizospheric region was found as an antagonist of *Fusarium oxysporum* (Kang et al. 2005). In another report, *F. oxysporum* antagonist *Pseudomonas aeruginosa* was sorted out from rhizospheric region of banana (Ayyadurai et al. 2006). The soil bacterium, *Pseudomonas putida* was found to inhibit the growth of *Alternaria alternata* (Pandey et al. 2006). In a report, *Kitasatospora* from *Fagus sylvatica* was found to inhibit the growth of *Phytophthora citricola* (Haesler et al. 2008). *Streptosporangium* sp. from *Azadirachta indica* was reported as *Phytophthora* sp. growth inhibitor

Table 1 Biodiversity of antagonistic microbes from different sources

Microbes	Source	Target pest/pathogen	References
<i>Acinetobacter rhizosphaera</i>	Wild olives	<i>Verticillium dahliae</i>	Aranda et al. (2011)
<i>Advenella incenata</i>	Tobacco	<i>Phytophthora nicotianae</i>	Jin et al. (2011)
<i>Alcaligenes faecalis</i>	Soil	<i>Fusarium oxysporum</i>	Chowhan et al. (2023)
<i>Aureobasidium pullulans</i>	Soil	<i>Rhizoctonia solani</i>	Hilber-Bodmer et al. (2017)
<i>Bacillus aerius</i>	Soil	<i>Fusarium oxysporum</i>	Chowhan et al. (2023)
<i>Bacillus amyloliquefaciens</i>	Banana	<i>Fusarium oxysporum</i>	Wang et al. (2013)
<i>Bacillus cereus</i>	<i>Arabidopsis thaliana</i>	<i>Botrytis cinerea</i>	Hong et al. (2015)
<i>Bacillus infantis</i>	Soil	<i>Fusarium oxysporum</i>	Chowhan et al. (2023)
<i>Bacillus lentimorbus</i>	Weed	<i>Fusarium oxysporum</i>	Kang et al. (2005)
<i>Bacillus licheniformis</i>	Banana	<i>Fusarium oxysporum</i>	Yadav et al. (2021)
<i>Bacillus methylotrophicus</i>	Soil	<i>Sclerotinia minor</i>	Pane et al. (2012)
<i>Bacillus paralicheniformis</i>	Rice	<i>Xanthomonas oryzae</i>	Kannan et al. (2021)
<i>Bacillus simplex</i>	Soil	<i>Phakopsora pachyrhizi</i>	Twizeyimana et al. (2023)
<i>Bacillus subtilis</i>	Ginseng	<i>Sclerotinia sclerotiorum</i>	Lee et al. (2017)
<i>Bacillus toyonensis</i>	Tomato	<i>Alternaria alternata</i>	Pane and Zaccardelli (2015)
<i>Bacillus velezensis</i>	Rice	<i>Magnaporthe grisea</i>	Jing et al. (2020)
<i>Bacillus weihenstephanensis</i>	Soil	<i>Caenorhabditis elegans</i>	Rae et al. (2010)
<i>Brevibacillus brevis</i>	Tobacco	<i>Ralstonia solanacearum</i>	Liu et al. (2013)
<i>Candida subhashii</i>	Soil	<i>Rhizoctonia solani</i>	Hilber-Bodmer et al. (2017)
<i>Cyberindnara sargentensis</i>	Soil	<i>Rhizoctonia solani</i>	Hilber-Bodmer et al. (2017)
<i>Delftia tsuruhatensis</i>	Tobacco	<i>Phytophthora nicotianae</i>	Jin et al. (2011)
<i>Enterobacter cowanii</i>	Tomato (surface)	<i>Botrytis cinerea</i>	Shi and Sun (2017)
<i>Enterobacter hormaechei</i>	Sweet pepper	<i>Ralstonia solanacearum</i>	Mamphogoro et al. (2021)
<i>Fructobacillus fructosus</i>	<i>Apis mellifera</i>	<i>Paenibacillus larvae</i>	Al-Ghamdi et al. (2020)
<i>Fusarium oxysporum</i>	Coffee	<i>Meloidogyne incognita</i>	Freire et al. (2012)
<i>Jeotgaliococcus aerolatus</i>	<i>Halodule uninervis</i>	<i>Pyricularia oryzae</i>	Bibi et al. (2018)
<i>Klebsiella oxytoca</i>	Soil	<i>Fusarium oxysporum</i>	Chowhan et al. (2023)
<i>Lysinabacillus fusiformis</i>	Nasutitermes	<i>Phytophthora capsici</i>	Fitriana et al. (2022)
<i>Moraxella osloensis</i>	<i>Halodule uninervis</i>	<i>Phytophthora capsici</i>	Bibi et al. (2018)
<i>Mortierella globalpina</i>	<i>Caenorhabditis elegans</i>	<i>Meloidogyne chitwoodi</i>	DiLegge et al. (2019)
<i>Myroides odoratimimus</i>	Tobacco	<i>Phytophthora nicotianae</i>	Jin et al. (2011)
<i>Ochrobactrum intermedium</i>	Tomato	<i>Fusarium oxysporum</i>	Gowtham et al. (2016)
<i>Paenibacillus alvei</i>	Nasutitermes	<i>Phytophthora capsici</i>	Fitriana et al. (2022)
<i>Paenibacillus jamilae</i>	Cucumber	<i>Bipolaris sorokiniana</i>	Wang et al. (2019)
<i>Paenibacillus polymyxa</i>	<i>Morinda citrifolia</i>	<i>Aspergillus aculeatus</i>	Liu et al. (2018)
<i>Penicillium oxalicum</i>	Cereal	<i>Oncopeltus fasciatus</i>	Santamarina et al. (2002)
<i>Proteus mirabilis</i>	<i>Apis mellifera</i>	<i>Paenibacillus larvae</i>	Al-Ghamdi et al. (2020)
<i>Pseudomonas aeruginosa</i>	<i>Valeriana wallichii</i>	<i>Aspergillus flavus</i>	Chandra et al. (2020)
<i>Pseudomonas brenneri</i>	Potato	<i>Alternaria solani</i>	Caulier et al. (2018)
<i>Pseudomonas fluorescens</i>	Tomato	<i>Rhizoctonia solani</i>	Solanki et al. (2022)
<i>Pseudomonas indica</i>	Cabbage	<i>Pythium aphanidermatum</i>	Al-Daghari et al. (2023)
<i>Pseudomonas protegens</i>	Potato	<i>Alternaria solani</i>	Caulier et al. (2018)
<i>Pseudomonas putida</i>	Soil	<i>Alternaria alternata</i>	Pandey et al. (2006)
<i>Pseudomonas reactans</i>	Wild olives	<i>Verticillium dahliae</i>	Aranda et al. (2011)
<i>Rahnella aquatilis</i>	Wild olives	<i>Verticillium dahliae</i>	Aranda et al. (2011)
<i>Serratia marcescens</i>	Cabbage	<i>Pythium aphanidermatum</i>	Al-Daghari et al. (2023)
<i>Staphylococcus epidermidis</i>	<i>Halodule uninervis</i>	<i>Pyricularia oryzae</i>	Bibi et al. (2018)
<i>Streptomyces rochei</i>	Tobacco	<i>Ralstonia solanacearum</i>	Liu et al. (2013)
<i>Sulftobacter dubius</i>	<i>Halodule uninervis</i>	<i>Pythium ultimum</i>	Bibi et al. (2018)

Table 1 (continued)

Microbes	Source	Target pest/pathogen	References
<i>Trichoderma asperellum</i>	Rice	<i>Xanthomonas oryzae</i>	Kannan et al. (2021)
<i>Trichoderma gamsii</i>	Lentil	<i>Pythium afertile</i>	Rinu et al. (2014)
<i>Trichoderma harzianum</i>	Sugarcane	<i>Colletotrichum falcatum</i>	Viswanathan et al. (2003)
<i>Trichoderma reesei</i>	Banana	<i>Fusarium oxysporum</i>	Damodaran et al. (2020)

(Verma et al. 2009). In another report, endophytic bacteria, i.e., *Acinetobacter rhizosphaerae*, *Pseudomonas reactans*, and *Rahnella aquatilis* in association with wild olive were reported for inhibiting the growth of *Verticillium dahlia* (Aranda et al. 2011). Similarly, in a report, *Fusarium oxysporum* from rhizosphere of coffee was found to inhibit the growth of root rot pathogen *Meloidogyne incognita* (Freire et al. 2012). Ma et al. (2013) reported *Bacillus* sp. isolated from the rhizospheric region of soil was found to inhibit the growth of *Rhizoctonia solani*.

In a report, *Brevibacillus brevis* and *Streptomyces rochei* from rhizosphere of tobacco was found as a bio-control agent against *Ralstonia solanacearum* (Liu et al. 2013). An endophytic fungus *Trichoderma gamsii* from lentil was reported for inhibiting the *Pythium afertile* growth (Rinu et al. 2014). In another report, *Trichoderma harzianum* was reported for inhibited the growth of pea pathogen, i.e., *Rhizoctonia solani* (Akhter et al. 2015). An epiphytic bacterium *Bacillus toyonensis* from tomato was found to inhibit the blight causing pathogen *Alternaria alternata* (Pane and Zaccardelli 2015). *Ochrobactrum intermedium* from tomato rhizosphere was reported as an antagonist of *Fusarium oxysporum* (Gowtham et al. 2016). In another report, various yeast, i.e., *Aureobasidium pullulans*, *Cyberlindnera sargentensis*, and *Candida subhashii* were isolated from soil and this bacterium inhibiting the growth of *Rhizoctonia solani* (Hilber-Bodmer et al. 2017). *Jeotgalicoccus aerolatus*, *Moraxella osloensis*, *Sulftobacter dubius* and *Staphylococcus epidermidis* from *Halodule uninervis* were reported as antagonists of *Pyricularia oryzae*, *Phytophthora capsici* and *Pythium ultimum* (Bibi et al. 2018). *Paenibacillus jamilae* from cucumber was reported for inhibiting the growth soilborne pathogen *Bipolaris sorokiniana* (Wang et al. 2019). In an investigation, *Bacillus velezensis* from maize was reported inhibiting the pathogenic fungi including *Fusarium verticillioides*, *Penicillium oxalicum*, and *Talaromyces funiculosus* (Yang et al. 2020). *Bacillus paralicheniformis* and *Trichoderma asperellum* from rice rhizosphere were reported as growth inhibitors of *Xanthomonas oryzae* (Kannan et al. 2021). In another report, *Lysinabacillus fusiformis* and *Paenibacillus alvei* from *Nasutitermes* were found to inhibit the growth of *Phytophthora capsici* (Fitriana et al. 2022). *Serratia*

marcescens from cabbage was reported for inhibiting the growth of pathogen *Pythium aphanidermatum* (Al-Daghari et al. 2023).

Interkingdom signaling and interconnections of the plant microbiome

It is thought that the numerous signaling molecules used by prokaryotes and eukaryotes to communicate with one another influence both partners' gene expression. The process of interkingdom signaling involves the creation and release of small chemicals by the contacted species, which establishes communication pathways between two kingdoms. The pathogenic or beneficial microbiomes frequently communicate with their host plants across kingdoms, with variable results depending on the precise chemical-triggered signaling pathways. Major present hurdles in this area include figuring out how it works and decoding the indications or language of this communication between kingdoms. A variety of signaling molecules can be generated by or obtained from bacteria and plants in the processes of the signaling pathways. Instead of eradicating the hazardous bacteria directly, the investigation of such experiments will encourage the creation of methods to enhance plant disease resistance through managing interkingdom communication.

Plant reactions and bacterial QS signals

Bacterial communication known as quorum sensing (QS) organizes bacterial behavior in a population density-dependent way by creating and detecting signal molecules. First discovered in *Vibrio fischeri* cells, population density dependent phenomena activate light generation when the cell population surpassed a threshold density. *N*-acyl homoserine lactone (AHL), sometimes known as the first QS signal or autoinducer was discovered in *Photobacterium fischeri luciferase* (Eberhard et al. 1981). The discovery of QS made it possible to see that, like multicellular creatures, individual microbial cells can coordinate their behavior to better adapt to complicated nutrition or environmental niches. The most extensively researched QS signals to date are AHLs, which are often employed signals by different group of bacteria (Kan et al. 2017). The LuxR and LuxI proteins serve as AHL synthase and

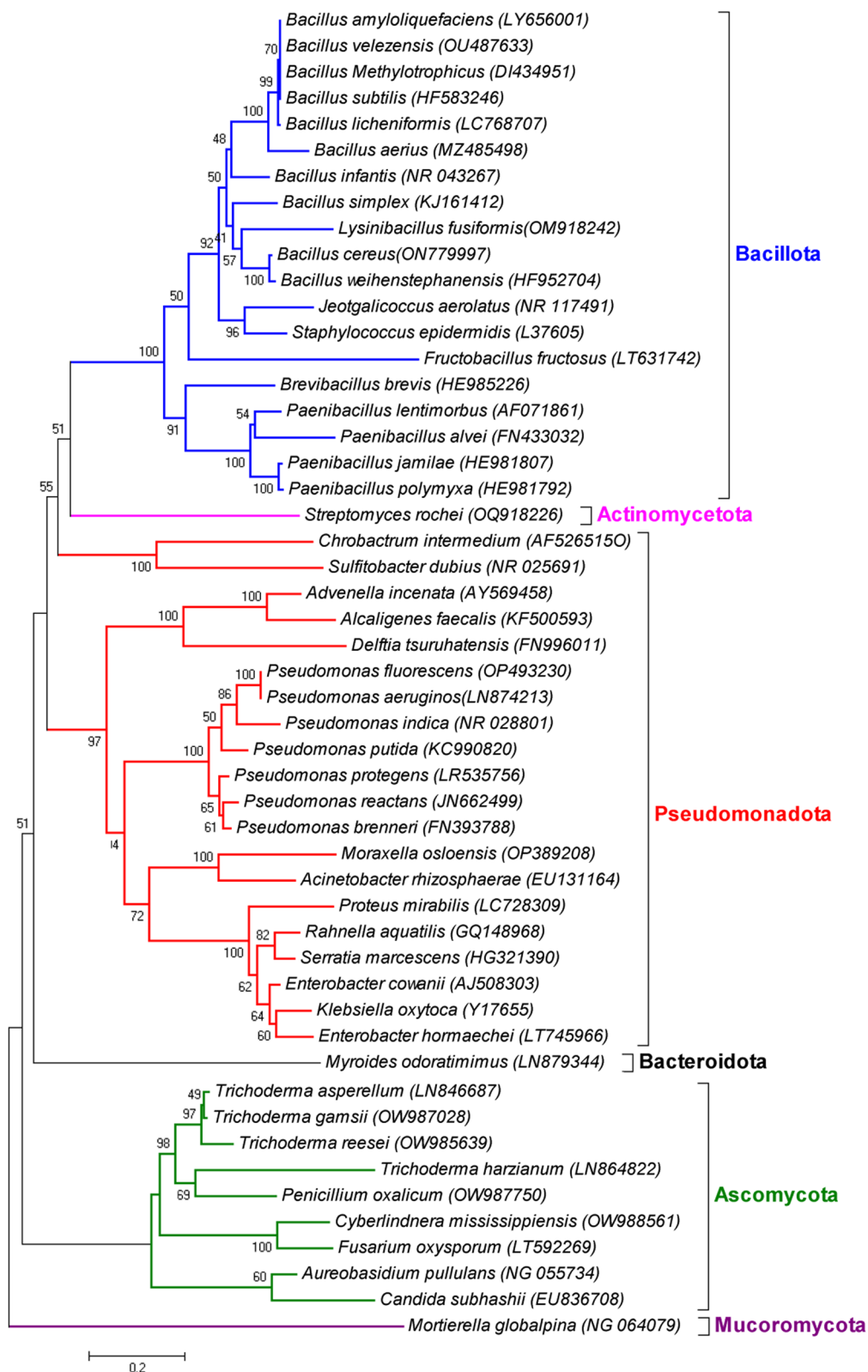


Fig. 1 Phylogenetic tree showing the relationship among different antagonistic microbes isolated from host worldwide

signal receptor, respectively, in a typical AHL-QS system (Fuqua et al. 1994).

Cross-kingdom signaling plays a variety of roles in interactions between plants and bacteria and considerably expands the functional spectrum of QS signals. Bacterial AHLs influenced plant growth, immunity, and development (Shrestha et al. 2020). A homoserine lactone (HSL), 3-oxo-C₁₄-HSL from bacterium *Sinorhizobium meliloti*, via an ethylene-dependent mechanism was shown to significantly increase the nodule counts in *Medicago truncatula* (Veliz-Vallejos et al. 2014). In barley, glutathione S-transferase and dehydroascorbate reductase were affected by 3-HSLs (C₆-, C₈-, and C₁₀-HSLs), but these enzymes were unaffected in yam beans, with the exception that C₁₀-HSL treatment resulted in a decrease the amount of content of chlorophyll (Götz-Rösch et al. 2015). The short-chain C₄- and C₆-HSLs that accumulated in biological films can induce the release of carpospores from the different group of algae (Singh et al. 2015). In *Arabidopsis*, AHLs containing acyl chains, between 4 and 14C in length, have been reported to influences the growth of the roots. *N*-decanoyl-HSL (C₁₀-HSL) was the most active AHL in changing the structural makeup of the root system. Although the other evaluated AHLs affected the expression- of genes that control the division and differentiation of cells without requiring auxin signaling (Ortiz-Castro et al. 2008). C₄-HSL treatment caused a brief and quick rise in cytosolic Ca²⁺ levels, while C₆-HSL treatment caused a rise in calmodulin levels (Zhao et al. 2015). The 3-oxo-C₆-HSL enhanced cell division in the meristematic zone and cell elongation in the elongation zone in *Arabidopsis* by activating the transcription factor AtMYB44 and mediating primary root growth through the regulation of cytokinin- and auxin-related genes (Zhao et al. 2016).

As a result of local induction by microorganisms, plants can develop strengthened defense mechanism against an assortment of pathogens known as induced systemic resistance (Pieterse et al. 2014). In addition, number AHLs bacterial factors are also involved in triggering ISR (Kan et al. 2017). Using rhizobacteria that produce AHL to prime plants for systemic resistance is one method of biocontrol. ISR became activated in AHL-producing plants and protected against infections when *S. marcescens* AHL-producing and degrading genes were introduced in tobacco (*Nicotiana tabacum*) plants, whereas due to a lack of ISR, the AHL-degrading plant was unable to provide a defense mechanism against pathogen invasion (Ryu et al. 2013). According to study, treatment with oxo-C₁₄-HSL also caused physiological changes in plant, such as oxylipin levels, phenolic compound accumulation, cellulose deposition, cell wall lignification, and SA-induced stomatal closure in response to

P. syringae infection (Schenk et al. 2014). *S. meliloti* generated oxo-C₁₄-HSL, was used to inoculate host plants, and these plants displayed improved resistance to fungi (Hernández-Reyes et al. 2014). The bryophyte moss *Physcomitrella patens*, an example of the first plants to grow on land, exhibits altered spore germination in response to AHLs, showing that number of bacteria change spore germination in the environment via the generation of AHL signal molecules (Vesty et al. 2020). Therefore, one potential crop protection method would be to use bacteria that produce AHL to enhance plant resistance and reduce production losses.

Another distinctive QS signal is the diffusible signal factor (DSF), which has been recognized as *cis*-11-methyl-2-dodecenoic acid. First discovered in the phytopathogenic bacterium *Xanthomonas campestris* pv. *campestris* (Xcc), this new unsaturated fatty acid has been linked to bacterial virulence, toxin tolerance and biological film formation (He et al. 2006). Glucose is the substrate which supplies carbon and carbon drives the production of the DSF-family signals in Xcc (Deng et al. 2015). However, structurally comparable compounds have been discovered in two unrelated bacteria, *Burkholderia cenocepacia* and *P. aeruginosa*, indicating that DSF synthesis is not just limited to Xanthomonads (Deng et al. 2010). More than one type of DSF-family signal can be produced by a single bacterial strain, and many bacteria can each produce a single type of signal (He et al. 2010). In interspecies and interkingdom signaling, DSF-family signals have a role (Ryan et al. 2015). *P. aeruginosa*'s production of *cis*-2-decenoic acid caused *C. albicans* and other microorganisms to disperse from biofilms that they had formed together (Jennings et al. 2012). It has also been demonstrated that the DSF-family signals influence plant immunity. However, it was found that in certain plants, the opposite effect that elicits innate immunity (Kakkar et al. 2015).

Many Proteobacteria include unpaired QS LuxRs (called LuxR solos or orphans) that lack matching LuxI homologs (Kan et al. 2017). The LuxR solos' modular design is identical to that of a standard LuxR protein, featuring a DNA-binding helix-turn-helix (HTH) domain at the C-terminus and an AHL-binding domain at the N-terminus. LuxR soloists, however, substitute a few preserved residues within the AHL-binding domain (González and Venturi 2013). The regulating repertory of the usual LuxI/LuxR QS systems is widened by these LuxR solos. Using "eavesdropping" on signals generated by nearby bacteria or eukaryotic signals created via interkingdom signaling, they react to endogenous or exogenous AHLs (Kan et al. 2017). In contrast to AHLs, a subfamily of LuxR solos in plant-associated bacteria (Palazzini et al.) act to low molecular weight compounds

generated by plants. These bacteria are important in biocontrol, symbiosis and virulence in plants (Patel et al. 2013). Interkingdom signaling that is mediated by LuxR alone has received a lot of interest, particularly with regard to understanding the communications' chemical code.

In plant-associated Proteobacteria, like *Pseudomonas*, *Dickeya*, and *Xanthomonas* from the α -proteobacteria group and *Rhizobium*, *Agrobacterium*, *Sinorhizobium*, *Citricella*, and *Rhodospirillum* from the γ -proteobacteria group, LuxR solos were common (González and Venturi 2013). Quorum quenching, an interference with QS signaling, hinders the QS-controlled mechanisms that are frequently essential for fruitful bacterial-host interactions. There are numerous methods for quenching QS. For instance, to stop the expression of bacterial target genes, plants synthesize and secrete a variety of natural chemicals that imitate QS signal. Therefore, symbiosis and pathogenicity are influenced by interkingdom signaling between plants and bacteria, with bacterial QS playing a role. AHLs and DSFs impact plant development and immunology. Both plants and bacteria live in the same environment, with low molecular weight compounds influencing their processes. LuxRs, including LuxR solos, use conserved DNA binding and auto-inducer domains as signal switches, responding more specifically to specific plants than classical QS ligands. Understanding the intra- and inter-communication between microorganisms and plants is therefore urgently needed.

Mode of action of antagonistic microbes for the management of pest–pathogens

Hydrolytic enzymes

Microorganisms offer promise as a biocontrol agent because they may eliminate phytopathogens without threatening the environment or other organisms that are not target. Compared to synthetic pesticides, this is unquestionably advantageous (Khamna et al. 2009). The studies of antagonistic microbiomes are gaining attention in order to manage plant diseases attracting more focus. Biological control agents (BCAs) typically increases the growth of plants via antibiosis, hyperparasitism, enzyme synthesis, competition for vital space and nutrients, plant resistance mechanisms, and production of plant resistance mechanisms (Babbal et al. 2017).

The search for alternative pest control techniques was sparked by rising anxiety and awareness regarding the increasing use of pesticides and their negative effects on the human being and environment, biological accumulation in food chain, insect resistance, and the ongoing presence of harmful chemicals in the environment. Hydrolytic enzymes are essential biochemical elements of insect metabolism and life cycles and include chitinases,

lipases, proteases, cellulases, and glucanases, have emerged as a novel tool for management of pest. There have been reports of numerous entomopathogenic fungi, bacteria, and viruses releasing hydrolytic enzymes to kill pests. The potential usage of hydrolytic enzymes, as well as their mode of action and virulence, could therefore be useful for creating insecticides that are stronger and safer. The control of pests and the achievement of IPM objectives will be aided by a thorough understanding of the chemistry, regulation, and metabolism of chitin, a part of the insect pest that is more vulnerable to extra-cellular hydrolytic enzymes, as well as insect stages and life cycle.

Chitinase

Chitin is an insoluble linear homopolymer of *N*-acetylglucosamine (GlcNAc) that is hydrolyzed by chitinases (Berini et al. 2018). The *N*-acetylglucosamine polymer, that makes up chitin is the second most common polysaccharide on the planet, and it is connected by β -(1,4) linkages (Adrangi and Faramarzi 2013). It is widely distributed in nature and serves as functions polysaccharide in the exoskeleton of arthropods, the cell wall of fungi, the shells of crustaceans, and the cuticle of nematodes. Chitin is found in three polymorphic forms and is arranged in an antiparallel manner: α -, β -, and γ -chitins (Dahiya et al. 2006). The primary type of chitin found in nature is β -chitin, which is primarily used as a structural component in invertebrate exoskeletons and fungal cell walls (Van Dyken and Locksley 2018). These are the primary chitin degraders in nature and participate in the hydrolysis-based recycling of nitrogen and carbon (Hartl et al. 2012). Plants, insects, and animals all produce these enzymes for various reasons, including morphogenesis, nourishment, and defense (Adrangi and Faramarzi 2013).

Large families of chitinases with specific roles in digestion, cell differentiation, and cuticle turnover are found in bacteria, plants, and insects. However, many animals, plants, and insects also express genes that produce lectins that resemble chitinases, but do not contain the catalytic site (Arakane and Muthukrishnan 2010). They retain the capacity to bind chitin despite lacking chitinolytic activity (Adrangi and Faramarzi 2013). Endochitinases (3.2.1.14) and exochitinases (3.2.1.52) are two categories of chitinolytic enzymes based on how they function (Van Dyken and Locksley 2018). The glycosyl hydrolase family (GH) can be used to classify chitinases on the basis of similarities in their amino acid sequences (Khoushab and Yamabhai 2010). Exochitinases are found in GH families 3, 18, 20, and 84, whereas endochitinases are primarily found in GH families 18, 19, 23, and 48 (Khan and Ahmad 2019).

According to Farag et al. (2016), the *Aspergillus terreus* purified chitinolytic enzyme has the ability to inhibit the

growth of *A. niger*, *A. oryzae*, *Penicillium oxysporium*, *Rhizoctonia solani*, *Candida albicans*, and *Fusarium solani*. *Streptomyces rimosus* purified chitinase shown antifungal activity against *Fusarium solani* and *Alternaria alternata* in vitro (Brzezinska et al. 2013). *Paenibacillus* sp. D1, a high chitinase producer, was discovered by Singh et al. to be effective in the management of *Helicoverpa armigera*. This strain caused 40% mortality rate in the larvae, and when it was paired with the insecticide acephate, a synergistic effect was seen (Singh et al. 2016).

Though chemical pesticides will continue to be utilized for a very long time, it is imperative that it was find environmentally acceptable solutions if it want to prevent additional harm to the Earth's ecosystems. As they are already a part of the earth's soil and endophytic microbiome and would therefore only slightly modify the environment, chitinolytic bacteria are a potential substitute for these chemicals. In numerous different situations, they have also been shown to offer protection against diseases, and in other cases, simply adding chitin to the soil causes the pathogen population to drop. Although the results so far are encouraging, this line of study continues to be not adequately developed, so further research in this area should be conducted in order to gather enough information to effectively address the issues affecting food production and harvest.

Cellulase

Cellulolytic enzymes are classified primarily into three main groups: endoglucanases (EC 3.2.1.4) (1,4- β -D-glucan-4-glucanohydrolase or carboxymethyl cellulose), exoglucanases [Cellobiohydrolase (EC 3.2.1.91) cellodextrinase (EC 3.2.1.74)], and β -glucosidases (EC 3.2.1.2.1) (Hasunuma et al. 2013). According to the classification of the CAZy database, the three cellulase groups are made up of individuals from different GH families (Lombard et al. 2014). The targeting substrate's depolymerization stage determines how cellulases are categorized. Endoglucanases randomly hydrolyze the glycosidic linkages found in crystalline and amorphous cellulose, producing oligomers with different levels of polymerization (Sharma et al. 2016). The lytic enzyme, including cellulases, chitinases, chitosanases, glucanases, and proteases produced by the antagonists, disintegrate the fungal cell wall, which is made up of chitin and glucan in addition to wall proteins, and this contributes to the biocontrol activity (Spadaro and Droby 2016). The β -1,3-glucanase isolated from *T. harzianum* CECT 2413 has been reported to cause morphological changes in plants such as cytoplasm leakage, hyphal tip swelling, formation of numerous septae, as well as inhibition of plant disease by preventing the development of pathogenic *Rhizopus solani* and *Fusarium* sp. (Behera et al. 2017). *Pythium* is a plant pathogen

that affected cucumber seedlings, was said to be less harmful in hypercellulolytic *T. longibrachiatum* mutants because they produced more β -1,4-endoglucanase than the wild type (Chet et al. 1998). Cellulase could therefore be employed as a biocontrol agent to shield seeds and plants from plant diseases (Bahera et al. 2017).

Protease

Proteases (EC. 3.4) are hydrolytic enzymes that break down proteins into smaller chains of peptides and amino acid groups (E.C. 3.4). Exopeptidases (EC 3.4.11–19), which cleave peptide bonds close to the amino or carboxy termini of the substrate, and endopeptidases (EC 3.4.21–25), which rupture peptide bonds far from the termini of the substrate, are the two primary categories into which proteases are commonly categorized (Rao et al. 1998). Proteases are further divided into four functional group found at the active site: aspartic, cysteine, serine, and metallo proteases (Khan and Ahmad 2019). These enzymes, which are physiologically essential for living and can be found in a variety of sources including microbes animals and plants, play numerous roles in literally all cellular processes (Yadav et al. 2016). Due to their metabolic diversity, quick development, and genetic modification susceptibility, which are all desired properties for biotechnological applications, microbes make an ideal source of proteases (Khan and Ahmad 2019). Insects are poisonous to proteases from a various species, such as fungi, bacteria, plants, insects, and viruses. Since proteins make up between 55 and 80 percent of an insect's cuticle, the activity of chitinases and lipases follows a protease attack (Petrisor and Stoian 2017). The two most important proteins found in cuticle are collagen and the elastic tissue known as resilin that is peculiar to invertebrates (Khan and Ahmad 2019).

According to the report, *Metarhizium anisopliae* has been extensively explored as a model study, in pathogenicity and virulence processes against insect pests (Rosas-García et al. 2014). In similar report, *Beauveria bassiana*, an entomopathogenic fungus, has demonstrated potential as a biological pest management agent (Valero-Jiménez et al. 2016). *Galleria mellonella* produces proteinase inhibitors and antifungal peptides, which *Metarhizium robertsii* can detect and respond to by selectively expressing metalloproteases and proteases that target and degrade the insect defense molecules (Mukherjee and Vilcinskis 2018). An extracellular cuticle-degrading protease released by the soil-isolated *Saccharomonospora viridis* displayed exceptional nematotoxic action against *Panagrellus redivivus* (Darwesh et al. 2019).

In terms of a collection of varied and mostly unknown agents for the control of pests pathogens proteases stand

out. Target specificity is a crucial concern before such proteases are widely used for pest management. The pest specificity is highly desired for reduced risk allied with any pest control approach. The future development of insect resistant transgenic plants shows special potential with the applications of proteases in plant defense against herbivory. The identification of potential proteases for use in pest management may be made easier in the genomes and transcriptomics era with a more efficiently understanding of the biology of virulence factors.

Glucanase

The most prevalent class of polysaccharides is β -glucans and made by microbes and higher plants as extracellular compounds, storage substances, and structural elements of the cell wall. Various microbes produce enzymes that can hydrolyze β -glucans (Bielecki and Galas 1991). Four different β -glucanases have been identified that catalyze the hydrolysis of β -glucan: lichenase (EC 3.2.1.73), cellulase (EC 3.2.1.4), laminarinase (EC 3.2.1.39), and β -1,3(4)-glucanase (EC 3.2.1.6) (Luo et al. 2010).

In plant tissues, β -glucanases take role in the breakdown of glucans like callose, which is one of the wall changes implicated in resistance responses. Although investigations of β -glucanase I deficient mutants made via antisense transformation reveal that these enzymes play a critical role in viral pathogenesis, antifungal β -glucanase I appears to be optimized for defense against fungi, according to previous research (Prasannath 2017). While the exotype β -1,3-glucanase is involved in the further hydrolysis of released oligosaccharides, the endotype β -1,3-glucanase enzyme appears to be more crucial for the breakdown of the callosic walls. According to one theory, these glucanohydrolases function in at least two separate ways: directly by destroying the pathogen's cell walls and indirectly by encouraging the release of substances produced from the pathogen's cell walls that can trigger immune responses (Prasannath 2017; Veliz et al. 2017).

The anti-pathogenic effects of *Trichoderma asperellum* were sorted out from plantations damaged by banana wilt, by number of mechanisms. One of them is antibiosis, a pathogenic fungus from the *Fusarium* genus that is utilized by *T. asperellum* which inhibits spore germination by 30–75% and reduces phytopathogen development by 65–74%. The mycolytic enzymes β -1,3 glucanase and chitinase that *T. asperellum* releases may also be able to demolish phytopathogen cell walls. Enzymes β -1,3 glucanase and chitinase both had significantly increased transcript accumulation and enzymatic activity in pathogen-induced cells (Win et al. 2021). The genes were induced by chitinase and glucanase activity, while genes encoding antioxidant enzymes were regulated, when the

plant immune system was stimulated by biocontrol fungal communities against RKNs, ET- and SA-responsive (Molinari and Leonetti 2019).

In mangoes infected with *Colletotrichum gloeosporioides*, the yeast *Debaryomyces nepalensis* generated β -1,3-glucanases. This hydrolytic enzyme's production, along with the creation of other beneficial substances such volatile chemicals, assisted in controlling the spread of the fungus infection (Zhou et al. 2018). An intriguing BCA against *Magnaporthe oryzae*, the rice blast, is *Paenibacillus terrae* NK3-4. It was claimed that the 1,3- β -glucanase this bacterium produces may be almost liable for its antagonistic action (Yu et al. 2019). Promising BCAs for pepper grey mold, which is brought on by *Botrytis cinerea*, include the *Bacillus velezensis* strains 5YN8 and DSN012. According to the report, these strains of *bacillus* produced significant levels of glucanases enzymes (Jiang et al. 2018). It is interesting to note that plants' β -1,3 can be activated by volatile substances produced by bacteria. In another report, tobacco leaves harmed by *R. solani* and the oomycete *Phytophthora nicotianae*, volatiles of *Bacillus* sp. JS led to the up-regulation of PR-2 encoding β -1,3-glucanase (Kim et al. 2015).

Phytohormones production

Small substances known as plant hormones play a substantial role in a numerous physiological functions throughout stress and growth responses (Ma and Ma 2016). Through the manipulation of plant hormonal pathways, pathogens can also gain an advantage through two different mechanisms: firstly they can inhibit defense responses controlled by “stress” hormones in order to colonize plant tissues; and then they can interfere with nutrient allocation and plant development processes controlled by “growth” hormones in order to promote long-lasting colonization and dissemination. The “classical five”—commonly recognized classes of Phytohormones including abscisic acid, auxins, cytokinins, ethylene and gibberellins. Brassinosteroid, oligosaccharides, bioamines, salicylates-salicylic acid, and jasmonic acid are a few more new phytohormones or hormone-like compounds that have been identified (Tsavkelova et al. 2006).

A good example of this in pest–pathogen management is the ability of the bacterium *P. fluorescens* G20-18 to produce plant hormones (cytokinins), which improve the defenses of plants or crops against bacterial infections. On cultivated thale cress (*Arabidopsis thaliana*), this effect has been successfully proven (Großkinsky et al. 2016). In a report, virulent sugarcane aphid can initially start feeding on seedlings of both lines, according to a comparison of the two sorghum genotypes BTx623 and, Tx2783 but only Tx2783 showed to be resistant and able to protect against SCA. A complex molecular

defense system like phytohormone-mediated defense is one of many internal defenses that resistant plants have to withstand unanticipated attacks (Huang et al. 2022). Therefore, metabolomic technique used to evaluate phytohormone expression profiles in plants with aphid infestations revealed that seven phytohormones expressed differently in resistant and vulnerable plants, supporting the critical function of phytohormones jasmonic acid, salicylic acid, and Auxin in sugarcane plant defense.

Durum wheat is more prone to *Fusarium* head blight. Antagonizing microbes can stimulate the biosynthesis of phytohormones, which are essential components of the plant defense system. The inoculation of *B. velezensis* RC 218 and *S. albidoflavus* RC 87B increase the level of salicylic acid (SA) and jasmonic acid (JA) under green house condition to control *Fusarium* blight infection in durum wheat increases the likelihood that these BCAs will become commercially successful products (Palazzini et al. 2018). The biocontrol of the anthracnose disease and better sorghum plant development have both been linked to *T. harzianum*'s generation of IAA (Saber et al. 2017). Thus, a deeper understanding of the mechanism and action of phytohormones will help to uncover new strategies for managing pest pathogens.

Secondary metabolites production

Antibiotics, anticancer drugs, growth hormones, pigments, and other microbial secondary metabolites are necessary for the development and growth of microorganisms, but they showed a great deal of potential for improving the well-being of humans, plants and animals (Ruiz et al. 2010). A numerous bioactive molecules produced by microbes, including Actinobacteria, and fungi among the microorganisms that create the aforementioned chemicals have a great potential for use in various fields (O'Brien and Wright 2011). Accordingly, the expression of these clusters would be useful in taking advantage of the biodiversity of microbes. These bioactive molecules are mostly created by the activation of cryptic gene clusters, which are inactive under normal circumstances (Xu et al. 2019).

Crop protection has become a necessity in modern agriculture in order to maintain production. Chemical pesticides are thought to be a great solution for any pest issue, but using them excessively led to other environmental issues in addition to the fact that resistance developed, rendering them worthless. Microbial pest-pathogen management had at this point become a viable alternative technique because of its high ecological safety and target specificity. Although many different microorganisms including, bacteria, fungi, and nematodes are commercially accessible and being developed as well, their metabolites actually cause pathogenicity and host

killing. It follows that choosing a particular strain of microbe for pest management depends on the pesticide metabolites, it produce and their bioactivity against target pest (Subbanna et al. 2020).

There are numerous secondary metabolites that have been shown to have pesticidal activity in field usage. These include the fungicides like kasugamycin, strobilurin A and B, validamycin, mildiomycin, blastidicin S, and polyoxin, the miticide as tetranactin, and the insecticides as avermectin and spinosyn (Maharana et al. 2022). Numerous investigations have recently revealed novel bioactive compounds from a wide range of microbial agents in pest management (Maharana et al. 2022). *Sphaeropsidins* belong to class of natural compound pimarane diterpene produced by fungi *Diplodia* spp. exhibit antibacterial antimycotic, and insecticidal activity (Ingels et al. 2017). *Photorhabdus luminescens* and *Xenorhabdus nematophila* produces secondary metabolites like p-hydroxyphenylpropionic acid (PHPP), Benzylideneacetone (BZA), 2-oxindole, acetylated phenylalanine-glycine- valine (Ac-FGV), 4-hydroxyphenylacetic acid (HPA), proline tyrosine (PY), cyclo-proline tyrosine (cPY) against insect pest that Inhibited phospholipase A2 (PLA2) and shut down eicosanoid biosynthesis (Mollah et al. 2020). *P. chlororaphis*, *P. fluorescens*, and *P. aeruginosa* produces Phenazine-1-carboxylate that has broad antifungal and antibacterial activity against plant pathogens (Shahid et al. 2017).

The majority of investigations used traditional activity monitoring and additional characterization utilizing fundamental molecular methods to examine the metabolites from known and established microbial pathogens. Additionally, the use of various media, fermentation methods, and screening approaches may result in a significant amount of bioactive secondary metabolites. Purification of products and the commercialization of powerful metabolites benefit greatly from developments in organic and synthetic chemistry. Additionally, conventional genetic techniques like recombination and mutation can be used to enhance the bioactivity and efficacy of metabolites. Thus, microbial pest-pathogen management has become a viable alternative to chemical pesticides due to its high ecological safety and target specificity. The commercial availability of biological pesticides with metabolites of microbial origin has been made possible by the isolation and characterization of secondary metabolites genes and their products of microbial origin.

Microbial pesticides in the new scenario of crop protection

The microbial pesticides are also known as biological control agent. In this group, the active substance is microbiomes that are either occur naturally or is

genetically modified (Nega 2014). The bio based pesticides offer the advantages of high accuracy and no harmful effect in comparison to chemical pesticides (Hernandez et al. 2005). The biopesticides contain living organism (bacteria, fungus, virus, protozoan or alga, rickettsia, Mycoplasma and nematodes) which are toxic for the targeted pest including, *Bacillus thuringiensis*, bioherbicides (phytophthora) and biofungicides (*Trichoderma*, *Pseudomonas*, and *Bacillus*) (Gupta and Dikshit 2010). They suppress pest and pathogen by causing disease, producing pathogenic metabolites and preventing by other microorganism through numerous mode of action (Clemson 2007).

Bacteria

Bacteria are unicellular, prokaryotic microorganism varied from less than 1 μm to divergent length. Most of the pathogenic microbes belong to family Enterobacteriaceae, Micrococcaceae, Pseudomonadaceae, Streptococcaceae and Bacillaceae, in which member of Bacillaceae particularly *Bacillus* spp. showed maximum recognition as biocontrol agent (Kachhawa 2017). Bacteria biopesticides are used for the management to control the growth of harmful pathogenic bacteria. They are generally specific to the individual species of butterflies and moths or species of mosquitoes, flies and beetles (Kausar 2018). In insect, bacteria disrupt the digestive system by colonize the interior part of plant and producing endotoxin that is constantly specific to targeted insect pest (O'Brien et al. 2009). The most commonly used biopesticides are strain of *Bacillus thuringiensis* (*Bt*), accounting around 90% of the biopesticides in the market of USA (Chattopadhyay et al. 2004). *Bt* has been most widely used to control insect pest and pathogen in agriculture, medicine and forestry (Mazid et al. 2011). During synthesis of *Bt* sporulation of crystalline containing Cry protein showed insecticidal properties (Federici et al. 2006). Although their high attentiveness and security in the environment, *Bt* and Cry protein are effective, safe and sustainable substitute to chemical pesticides for management of insect pest (Kumar et al. 2008).

Fungi

Entomopathogenic fungi play an important role as biocontrol agent of insect population (Sharma and Malik 2012). A diverse group of fungal species is found in various infected insect and infecting capability including, facultative and obligate pathogens (Pucheta et al. 2016). In 1980s, the first insect pathogenicity was carried out and their main focus was to detect the method of disease management of silkworm (Steinhaus 1975). A diverse group of fungi belongs to phylum Ascomycota, Chytridiomycota, Deuteromycota, Oomycota and Zygomycota

(Samson et al. 1988). The entrance point of entomopathogen is through integument and they also infect the insect by through wounds or trachea or ingestion method (Holder and Keyhani 2005). The entomopathogenic fungi had the most relevant biocontrol agent, as they represent a group with approx 750 species and when disseminate in the environment and produce fungal infection in insect community. They begin their infective process when the spore of fungi is employ on integument surface, where the formation of germinative tube inaugurates. The fungi also produce enzyme such as chitinases, lipoxigenases, proteases, Upases and quitobias (Vaghasiya et al. 2021). These enzymes deteriorate the insect cuticle and help in penetration by mechanical pressure that is begin by appressorium (Zhang et al. 2010). After that fungi flourish as hyphal bodies that promulgate hemocoel and infect diverse group of fatty bodies, malpighian tubes, muscle tissues, hemocytes and mitochondria, cause the death of insect after 3 to 14 days of infection (Woldemelak 2020). Once the insect dies a large number of nutrient are consume, fungi start micelles growth and occupy the entire organ in the host cell. Ultimately, hyphae penetrate the cuticle in interior of insect and make an appearance at the surface where they start spore formation under the adequate environmental conditions (Henrik et al. 2023).

Viruses

Insect virus are considered as beneficial and environmentally friendly which may contribute to attain sustainable agriculture through providing an appropriate replacement of chemical pesticides which have negative impact on the environment (Riyaz et al. 2022). A virus is an assembly of one or more nucleic acid template molecules that are generally covered in a protein or lipoprotein protective shell and are able to coordinate their own replication in specific kinds of host cells. The virus has been sorted out from more than 1000 species of insect from nearly 13 different insect orders (Käfer et al. 2019). Entomogenous viruses are categories into two, viz. inclusion viruses producing inclusion bodies in the host cell and another is non-inclusion viruses, which do not produce inclusion bodies. The insect virus belonging to the family of Baculoviridae was considered for the development and commercialization of viral biopesticides (Moore et al. 1987). Baculoviruses contain enveloped viruses that only infect insects. They have circular, supercoiled double-stranded DNA genomes that range in size from 80 to 180 kbp (Chambers et al. 2018). A large number of baculoviruses have been sorted out from butterflies, moths, sawflies and mosquitoes (Blissard et al. 2000).

The name baculovirus are derived from Latin, which are approximately 230–385 nm in length and 40–60 nm in diameter. These viruses are transmissible by mouth

and reveal via horizontal transmission. When the occlusion bodies (OBs) are digested by insect and release the virions particles into the lumen (Derksen and Granados 1988). These virions entered into nucleus, at the point in which virus replicate within the nucleus of susceptible tissue and tissue susceptibility varied between virus and nuclear polyhedrosis viruses being capable of infecting all the tissue and granulosis viruses (GVs) being specific for tissue replication (Adams and McClintock 1991). The budded virus starts infection to other tissue such as hemocytes, nerve cells and fat bodies. However, cell infected in the second round of virus replicate in the insect larva and produce budded virus but particles of occlude virus within polyhedral in the nucleus (Godfray et al. 1997). The accretion of polyhedral within the insect profits until the host incorporates almost completely of a bag of virus. At the last stage of infection insect liquefies and release polyhedral, which can infect other insect and targeted pest killed 3–7 days but when the condition is not ideal the death may take 3–4 weeks (Kalha et al. 2014). The viruses are used as biopesticides against insect pest, but the main drawback is the requirement for in vivo conditions and this high sensitivity to ultraviolet radiation.

Development and commercialization of microbial pesticides

The use of pesticides to protect plants from viruses, pests, and weeds has steadily evolved from a therapeutic strategy to a pragmatic one those priorities protecting human health and the environment over any form of productivity or commercialization. Currently, number of beneficial microbiomes are among the vigorous ingredients in a new generation of bacterial pesticides or serve as the basis for numerous naturally occurring chemicals obtained by microbial extraction. The development of microbial pesticides involves number of steps such as the isolation of pure culture in form of single distinct archaea, bacteria, fungi, and screening of isolated microbes for biocontrol attributes (Fig. 2). To be commercially delivered, a microbial pesticide, industrial-scale production is important, followed by preservation and formulation with biocompatible additives to enhance the survival and improving applications and stability of the final product (Montesinos 2003).

Formulation and production

India has the greatest potential for microbial-based insecticide because agriculture is foundation of our economy. The researchers should look into all of the limitations and popularization prospects in this emerging field. Excessive and incorrect use of insecticide has led to the emergence of secondary pests, the rise of pesticide

resistance to main classes of pesticides, high levels of pesticide residue in product, and the extinction of natural enemies. The excessive utilization of the pesticides has led to the adverse effect on humans and the environment. Biopesticides are an environmental friendly alternative to the biopesticides. Biopesticides have been categorized into microbial, biochemical, and plant-incorporated protectants (PIPs). The most commonly utilized biological pesticides are microbes which possess a pathogenic effect on pest of interest. These consist of bioinsecticides which include *Bacillus thuringiensis* and *Bacillus sphaericus*; biofungicides including *Trichoderma*; bioherbicides including *Phytophthora*.

Antinsect compounds such as thiolutin, aminolevulinic acid, thuringiensin, xenorhabdins, actinomycin A, aplasmomycin, citromycin, piericidins, spinosyns and nikkomycin derived from actinomycetes, fungi and non-filamentous bacteria are well known to produce toxic effects and are able to act as antifeedants, growth inhibitors and physiological disrupters against the pests (Kirst 2010). Some of these compounds such as spinosyns and avermectins have been commercialized. The superior characteristics of microbial pesticides have gained much attention and also have made them a hot spot of research in biotechnology and numerous companies.

Fermentation provides a source of bioactivity against agriculturally important target organisms. The development of a biopesticide is a lengthy process with several stages such as discovery, product, production, efficacy testing, development, registration, and finally commercialization. Formulation technology must be account at all stages from concept to final action on the target. The method of production frequently dictates subsequent formulation activities, which may result in changes to the production process. The method of manufacturing frequently dictates subsequent formulation activities, which may changes in production process. Formulation serves four main function: stabilizing the organism during production, distribution, and storage; assisting with product handling and application so that it can be delivered to the target easily; protecting the agent from harmful environmental factors at the target site; and enhancing the activity of the organism at the location of the target through boosting its activity, development, connection, and interaction with the target (Jones and Burges 1998).

Microbial pesticides can be found in a number of formulations, including suspensions, wettable powders, oil suspensions, suspended seed coatings, and water dispersible granules. Microbial pesticide production is a complex and complicated process as compared to the chemical pesticides. Microbial pesticides are more susceptible to external environmental factors during the process of preparation (Lin et al. 2023).

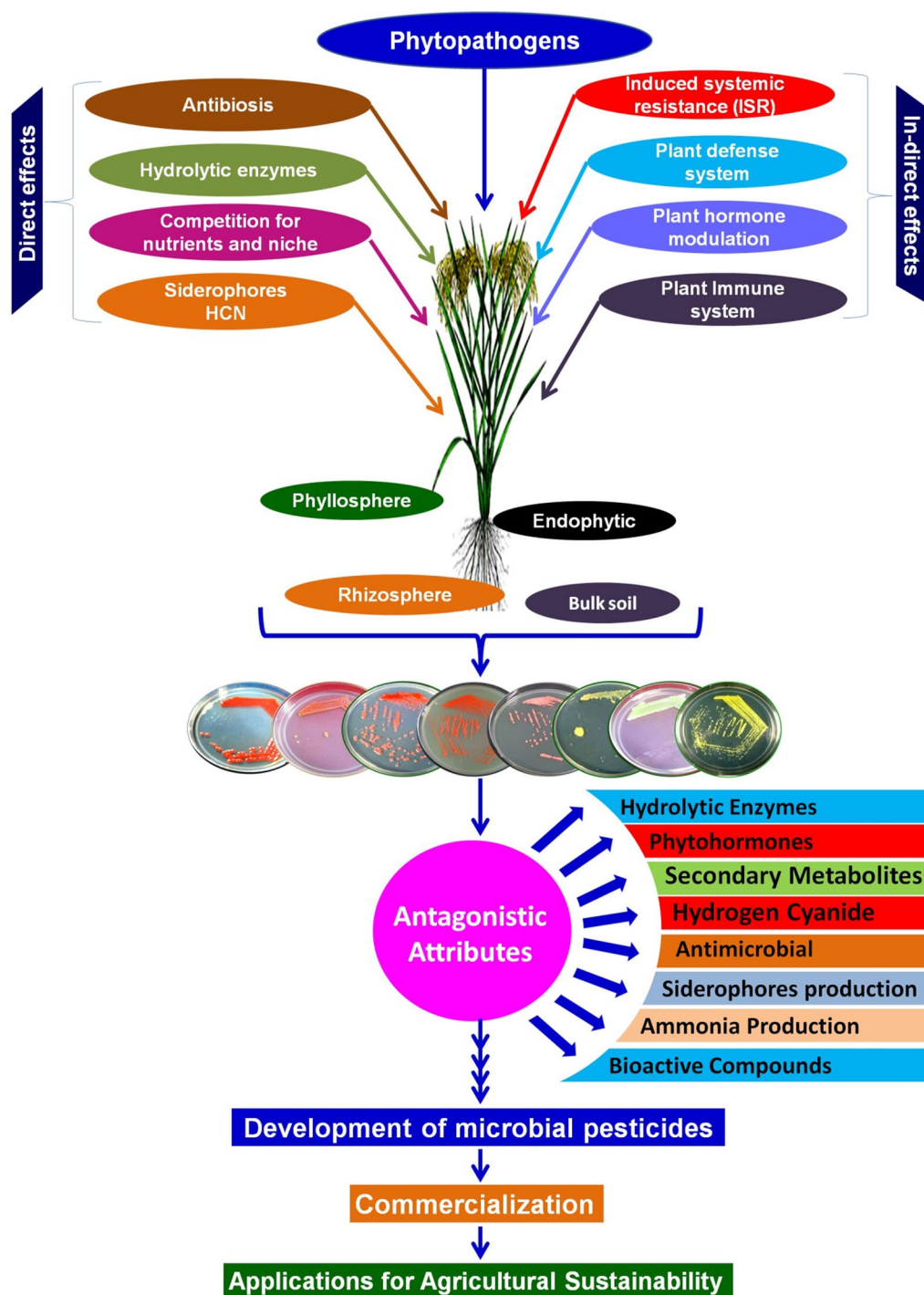


Fig. 2 A schematic representation of isolation, characterization and applications of antagonistic microbes for agricultural sustainability

Microorganisms directly affected physical properties of pesticide preparations such as wettability, suspension, and dispersibility. Microbial pesticides are produced using adjuvants, which are primarily divided into transporters, protecting agents, surfactants, and nutritive

adjuvants. Surfactants play an essential role for enhancing the potency, efficiency, and cost-effectiveness of the synthesis of microbial pesticides as well as conserving energy and raw materials. They improve biological functions and maintain physical stability of the product

(Castro et al. 2014). The main function of a carrier is to encapsulate or dilute the active components of microbial pesticides. (Borger et al. 2013). Attapulgit, bentonite, diatomite, and silica are examples of carriers that can be employed to create wettable powders, granules, or high concentration powders (Kashyap et al. 2015).

Microbial pesticides are passivation degraded, or damaged by UV radiation (Jarzębski et al. 2019). The majority of UV protection compounds employed in the formation of microbial pesticides grouped into two categories UV ray absorption materials and antioxidant UV protection substances. UV ray absorbers can absorb the UV ray and fluorescent light sources without changing itself (Jadhav et al. 2022). Strong antioxidant properties of anti-oxidative UV protection compounds assist in the prevention of microbial pesticides being easily oxidized and converted into additional compounds that are useless against potentially dangerous organisms when exposed to UV radiation. Protective substances can extend the shelf lives and enhance the control effect of microbial pesticides when used in the field (Pershakova et al. 2021). The dietary requirements of the microbes in microbial pesticides are met by nutritional adjuvants, which improved their ability to reproduce and encourage their proliferation and expansion in the field.

The active ingredient used in bio-pesticide formulations is the most important factor in their production. The active compound influences the composition of bio-pesticides. The microbial formulation technique is governed by the active ingredient, which differs in each of them. In the case of microbial bio-based pesticides, the active ingredient is microbiomes that are useful in controlling crop damage which is caused by insect pests. In order to make this formulation, these microorganisms must be utilized in a specific method. The microorganisms are biogenetically altered in a way that restricts the range of applications for their action spectrum (Meena and Mishra 2020).

Microbial pesticides contain active ingredients that are specific to their target pests (Kawalekar 2013). These pesticides are therefore safe for non-target beneficial pests and maintained ecological balance. The use of bio-pesticides is increasing at a rate of about 10% per year (Bailey and Mupondwa 2006). However, due to increased resistance of pest to chemical pesticides and increasing awareness about the use of non-toxic and safe substances in agriculture, this rate has been increasing in recent years. The USA uses the biopesticides (45%), followed by the European Union (20%) and the rest by other countries (Bailey et al. 2010). Depending on the preparation and retention of the microorganisms, the shelf life of bacterial pesticides might range from a few days to several months.

Commercialization

Currently, the biopesticides market enjoys an annual expansion of 15%, and the prospect for growth seems bright. But, efforts are still required to achieve a successful commercialization. It is crucial to focus on customer satisfaction based on sustained product performance in respect to prices and usability. There are number of factors that determine success or failure of a product. In 1938, France, with Sporeine, a living organism, was used commercially for the first time in agriculture. *Bt* was used as a biopesticide for controlling the caterpillars. Products based on nematodes fungi, and bacteria gradually entered the market at beginning in the 1960s, and the range of pest and disease control products has grown ever since. Today, the worldwide turnover of bio-based pesticides is approximately 1.8 billion US\$. Annual growth for the last decade has been approximately 15% (Ravensberg 2015).

Microbial biopesticides are the most common broad-spectrum biopesticides used today, accounting for the majority of pest-specific bio-pesticides. At the least 1500 naturally occurring insect specific microorganisms exist, with 100 of them being insecticidal. Over 200 microbial biopesticides are available in 30 Organizations for Economic Cooperation and Development member countries (OECD). There are 22 registered microbial biopesticides in Canada, 53 in USA and 21 in the European Union. Overall microbial biopesticides registration are increased globally, the expansion of numerous technology has increased the scope of more product and the trends toward development of microbial product is definitely changed (Opender Koul 2012).

The development and use of microbial pesticides is gradually replacing the highly harmful and chemical pesticides in the market. The production of microbial-based pesticides increases at the rate of 20% annually, while the production of chemical-based pesticides has declined by 2% every year (Cheng et al. 2010). Pest Management Regulatory Agency accepted registration of 24 microbial active substances in 83 formulations in Canada in 1972–2008 (Bailey et al. 2010). The majority of the registrations (55/83) occurred up to 2000, and in 2008 alone, there were ten new products under regulatory evaluation. Commercially, there are some biopesticides available to farmers. There are about 175 registered bio-based pesticides globally, with 700 active substances available for use.

In India, 194 compounds have been registered as chemical pesticides and 12 biopesticides by the year 2006. The number of newly created and approved microbial pesticides is rising at a rate of 4% annually, but the overall market share of biopesticides has increased to 30% (Gupta 2006). Presently, about 75% of biopesticide use consists of *Bt*-based products. *Bt* has been used to

control lepidopteran, dipteran and coleopteran insects for more than three decades. As an effective microbial pesticide, mostly biochemical biopesticides worldwide are the purified toxin from this strain. Metabolites from *Photorhabdus luminescens* are a promising alternative to synthetic fungicides. They are effective against pecan scab because of the bioactive compound trans-cinnamic acid that showed antifungal (Bock et al. 2014). *Beauveria bassiana* can be used as a biopesticide in the management of crop pests (Samada and Tambunan 2020).

New microbial insecticides containing pathogenic or inhibiting microorganisms must follow guidelines for safety testing and registration. These guidelines provide interested businesses and government agencies. They are the outcome of recent, vigorous involvement with this field and more than a decade of experience. The identity, biological characteristics, production, formulation, quality control, application, and efficacy of the novel bacteria are all necessary for the registration of a new microbial product. The current recommendations include a list of required tests for new bacterial pesticides. The standards for registering a novel bacterial pesticide should generally be the same, although guidelines may differ according to the national pesticide registration protocols of other nations (Burgess et al. 1982).

Role of microbial pesticides in agriculture

Environmental challenges and threats to sustainable agriculture are presently causing an increasing amount of concern (Gomiero et al. 2011). The farmers are increasing used chemical pesticides to control the pest and pathogen for improvement of crop production. Chemical pesticides are made from chemical such as polymer which is specific to targeted host (Rakhimol et al. 2020). The over application of pesticides and excess discharge into water bodies during rainfall can cause death of fishes and other marine life. The consumption of fishes by human may cause disease including cardiovascular, diabetes, kidney failure, skin, cancer, liver dysfunction, eczema and neurological destruction (Manfo et al. 2020). In agriculture use of chemical pesticides harm beneficial soil microbes, plant and soil texture (Riedo et al. 2021). In light of all of these considerations, using biopesticides over the long run appears to be more cost-effective, environmentally friendly, productive, and accessible to marginal and small farmers than chemical insecticides. This makes crops more susceptible to insect pest attacks, which severely decreases crop yield. Natural product is eco-friendly in nature and also easily biodegradable. In response to the demand for food grown organically and changing consumer tastes and preferences, biopesticides are appropriate substitutes for synthetic pesticides (Okunlola and Akinrinola 2014). As a result of their short pre-harvest

intervals, biopesticides are safe to use on fresh fruits and vegetables (Khater 2012). They are efficient in small amounts, and their use stimulates viable pest control, which helps contribute to sustainable agriculture (Nawaz et al. 2016). In order to reduce the amount of chemical pesticides used in the management of crop pests, biopesticides can therefore be effectively included into integrated pest management (IPM) (Sesan et al. 2015). Additionally, biopesticides have been used for cleaning up agricultural soils by introducing significant microbial populations (Javaid et al. 2016).

Limitations and challenges

Although microbial inoculants offer a potential alternative to chemical fertilizers, there are a number of restrictions and difficulties that come with their use as biopesticides. They only have a short shelf life, and if they are not utilized promptly or stored properly, they may lose their potency (Qiu et al. 2019). New biotechnological techniques should be developed in order to provide formulations with extended shelf life. Additionally, there are certain restrictions on the usage of microbial inoculants, such as the need to monitor their consistency, consistency of their quality, application methods, compatibility with chemical fertilizers, and environmental conditions including temperature, moisture, and pH (Shahwar et al. 2023). The ability to enhance or protect yield is the most crucial component for a successful product. In addition to the other aspects, this is undoubtedly the most crucial and essential factor for the success of the entire product. However, success in the laboratory or greenhouse does not always equate to success in the field. The use of an inoculants or biocontrol product by both the manufacturer and the consumer is a crucial component in determining its success. The product should ideally have a low adoption barrier and be compatible with the farmer's equipment and production practices (Parnell et al. 2016).

Conclusions

The challenge of pest control for sustainable agriculture has been of great concern. Efficient, low-risk and eco-friendly pest control solutions to meet manufacturer, consumer and regulatory needs are of major importance. The research on microbes-based biopesticides is emerging as an important alternative for chemicals used for pest control for many years. Biopesticides control the plant pathogens, pests and weeds by diverse mechanisms. In fact, the biopesticides are becoming an integral part of pest management systems due to their advantages of environmental safety, biodegradability, effectiveness and suitability in the integrated pest management (IPM) programs. Further research on biopesticides and their development is important on priority basis. It is important to

make awareness and educate general people, farmers, agriculturists, government agencies and policy makers about the use and handling of microbial pesticides. The popularization of the biopesticides is another challenge which can be met with through training programs on production and quality control to manufacturers. The adoption of this technology also requires organizational training to extension workers and farmers. The search for new biocontrol agents for future use in different habitats and climates should continue. Development of novel methods for manufacturing, formulation, storage and utilization to improve efficiency and cost effectiveness will also open way for adoption of microbes-based biopesticides. Changes in political and social attitudes have though increased the opportunities for microbial pesticides still further research on pest pathogen ecology and exploration of diversity is required. All this will lead to a more comprehensive understanding of the benefits of biopesticides as a green and sustainable alternative.

Abbreviations

AHL	<i>N</i> -acyl homoserine lactone
AMPs	Antimicrobial peptides
BCAs	Biological control agents
BZA	Benzylideneacetone
cPY	Cyclo-proline tyrosine
DSF	Diffusible signal factor
EOs	Essential oils
GlcNAc	<i>N</i> -acetylglucosamine
GVs	Granulosis viruses
HPA	4-Hydroxyphenylacetic acid
HSL	Homoserine lactone
IPM	Integrated pest management
NPs	Natural products
OBs	Occlusion bodies
pHPP	<i>p</i> -hydroxyphenylpropionic acid
PY	Proline tyrosine
QS	Quorum sensing

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Declarations

Ethics approval and consent to participate

All procedures performed in studies are in accordance with the ethical standards of the institutional and/or national research committee. We further declare that no animal was harmed during this study.

Consent for publication

Informed consent was obtained from all individual participants included in the study.

Competing interests

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