


Review

Unveiling the Role of Hydrolytic Enzymes from Soil Biocontrol Bacteria in Sustainable Phytopathogen Management

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Abstract

Background: Phytopathogens, encompassing fungi, bacteria, viruses, and nematodes, pose a significant threat to the agricultural industry by causing substantial economic losses through severe plant diseases. The excessive use of synthetic fungicides to combat phytopathogens has raised environmental and human health concerns. **Results:** Consequently, there is an increasing demand for safe and environmentally friendly biopesticides to align with consumer preferences for uncontaminated food. One particularly promising alternative to synthetic fungicides involves harnessing biocontrol bacteria that produce extracellular hydrolytic enzymes. These enzymes serve to effectively manage phytopathogens while concurrently fostering sustainable plant protection. Among the pivotal hydrolytic enzymes generated by biocontrol bacteria are chitinase, cellulase, protease, lipase, glucanase, and amylase. These enzymes exert their influence by breaking down the cell wall, proteins, and DNA of phytopathogens, thereby establishing a dependable method of biocontrol. **Conclusions:** Recognizing the critical role of these hydrolytic enzymes in sustainable biocontrol, this review seeks to delve into their primary functions, contribution to sustainable plant protection, and mechanisms of action. Through an exploration of the potential presented by biocontrol bacteria and their enzymatic mechanisms, we can discern effective and environmentally conscious strategies for managing phytopathogens in agriculture.

Keywords: phytopathogens; extracellular hydrolytic enzymes; chitinase; cellulase; protease; lipase; biocontrol

1. Introduction

Plant diseases have profoundly influenced the course of food production and the development of human civilizations over decades [1]. The ultimate consequence of these plant pathogens is reducing food quantity, quality, and security, exerting significant pressures on agricultural systems, and prompting adaptations and innovations to ensure sustainable food production [2,3]. The severity of plant diseases can vary from mild to severe, depending on various factors such as environmental conditions, host resistance, pathogen aggressiveness, and the duration of infection [4]. Soil-borne phytopathogens pose a particularly severe threat as they cause extensive damage, resulting in a 30% loss across a wide range of plants. This not only leads to economic disasters for producers but also contributes to the risk of starvation, particularly in underdeveloped countries with limited access to disease management methods [5]. For instance, the devastating prevalence of potato late blight, caused by *Phytophthora infestans*, led to famine, starvation, death, and mass migration throughout history [6]. It is worth noting that the impact of phytopathogens on plants has been exacerbated by two key factors: global climate change and the globalization of markets. These factors have accelerated the spread of phytopathogens, in-

creasing the likelihood of emerging diseases affecting crops [7]. Among plant phytopathogens, soilborne pathogens pose a significant challenge to plant protection [8,9]. Soil-borne plant pathogenic fungi, such as *Fusarium* sp., *Sclerotinia* sp., *Phytophthora* sp., *Verticillium* sp., *Rhizoctonia* sp., and *Pythium* sp. are reported to cause 50 to 75% yield loss for various horticultural and agricultural products [10]. In addition to soilborne phytopathogenic fungi, *Ralstonia solani*, which probably is the most destructive plant pathogenic bacterium globally, as well as *Meloidogyne* spp. and *Heterodera* spp., as the most damaging nematodes, have a tremendous effect on economic, political and cultural development [11–13]. Regardless of damages and losses caused by phytopathogens, another key challenge is developing efficient strategies that rapidly manage plant pathogens [14]. Synthetic pesticides have been the primary method for managing plant diseases for several decades because of their high effectiveness and ease of application [15]. However, the intensive and indiscriminate use of synthetic pesticides has led to several issues in modern plant protection. These include the emergence of pesticide-resistant strains, new disease outbreaks, and mounting concerns about the impact on health, environment, and contamination of soil and water [16]. As a re-



sult, there has been a revolution in plant protection to develop more sustainable and environmentally-friendly alternatives [15,17–19]. Therefore, some eco-friendly management methods include soil solarization, crop rotation, soil steam sterilization, anaerobic soil disinfestation, resistant cultivars or grafted plants, biofumigants, soil fertility, and soil fertility biopesticides, have been developed to mitigate soilborne phytopathogens while maintaining the environment safe [20,21]. Currently, sustainable agriculture is experiencing emerging opportunities such as the utilization of biological agents [22–26], integration of nanoscience [25,27], advancement of resistant plants, and implementation of biopolymers [28–39]. Using soil microbial communities for biological control has emerged as a promising strategy for suppressing soilborne plant pathogens [40–42]. Biocontrol bacteria utilize diverse antagonistic strategies against phytopathogens, encompassing the synthesis of lytic enzymes, antibiotics, volatile organic compounds, siderophores, nutrient and spatial competition, as well as the initiation of host resistance [43]. Among these mechanisms, the extracellular enzymes, commonly referred to as hydrolytic enzymes, synthesized by diverse biocontrol bacteria, have a direct impact on phytopathogens by breaking down the structural components of their cell walls [44,45]. Soil biocontrol bacteria can effectively manage plant diseases caused by soilborne pathogens by producing extracellular enzymes, including chitinase, cellulase, protease, amylase, and lipase. This process helps to break down organic matter in the soil, leading to the suppression of pathogenic microorganisms and promoting plant growth. Regardless of the indirect effect of bacterial biocontrol hydrolytic enzymes on the plant, some detected enzymes, including pectinases, chitinases, lipases, cellulases, and amylases, can directly affect plant growth by providing better colonization. The production of these enzymes is reported to be upregulated in the bacterial interaction with the host plant, involved in the recognition, attachment, and movement of beneficial bacteria through plant tissues which leads to the induction of the plant immune system against biotic stresses [46]. This review considers one of the primary biocontrol mechanisms employed by antagonistic bacteria in sustainable agriculture to manage various plant pathogens. This mechanism involves the production of cell-wall degrading enzymes and is crucial in meeting the increasing demand for safe and pathogen-free food for the world's growing population.

2. How Biocontrol Bacteria Control Plant Diseases?

Recently, antagonistic microorganisms, especially biocontrol bacteria, have been extensively reported as the most promising strategies to guarantee plant health, quality and safety of fruits and vegetables [40,47]. Several bacterial genera, including *Bacillus*, *Pseudomonas*, *Serratia*, *Rhizobium*, *Xanthomonas*, *Streptomyces*, *Enterobacter*,

Agrobacterium, *Erwinia*, *Alcaligenes*, *Stenotrophomonas*, and *Arthrobacter* have demonstrated antagonistic activity in the biocontrol of various plant pathogens [3,48–51]. These bacteria suppress the development of plant pathogens through multiple mechanisms of action, which can be divided into direct and indirect mechanisms (Fig. 1).

Indirect modes of action include colonization of the infection site followed by competition for nutrients and space and, more importantly, induction of host defense systems [52]. *Pseudomonas* spp. are among the most reported beneficial bacteria used as biopesticides due to several relevant properties, including their potential capability to trigger plant defense responses, strong biocontrol activity against a wide range of phytopathogens and their high ecological fitness [53]. Fluorescent pseudomonads have the potential to colonize not only the rhizosphere but also the phyllosphere and endosphere, outcompete other microorganisms for nutrients and space, and contribute to plant growth promotion, disease suppression and nutrient cycling [54]. For instance, better nutrient utilization and growth rate of *P. fluorescens* EPS62e compared to *Erwinia amylovora* reduced bacterial infection [55]. Under nutrient deficiency, especially the limitation of iron, *Pseudomonas* spp. suppress pathogenic microorganisms through a siderophore-mediated competition mechanism [56]. In addition, *Pseudomonas* spp. are known as dominant bioactive metabolites producers like enzymes, antibiotics, and cyclic peptides, playing significant antagonistic roles [57]. The induction of plant systemic resistance (ISR) is one of the most important indirect mechanisms activated by *Pseudomonas* spp., which confers plants with resistance to multiple pathogens via the stimulation of induced systemic resistance. ISR activates the plants' defense responses and primes them for a more effective defense response. For instance, *Pseudomonas fluorescens* PTA-CT2 activated the ISR mechanism in grapevines. As a result, the plants developed increased resistance against *Botrytis cinerea* and *Plasmopara viticola*, two common pathogens [58]. Also, a relevant trait of *Bacillus* species is their capability to elicit ISR, enhancing plant defense mechanisms against a variety of pathogens [59]. Besides these two important genera, species of *Lactobacillus* spp., *Pantoea* spp. and *Streptomyces* spp. are among the most studied bacteria with biological control activity through a wide variety of mechanisms [60–62].

The direct mechanisms are based on liberating antioxidants, lipopeptides, antibiotics, hormones, biosurfactants, volatile compounds, and cell wall degrading enzymes, reducing pathogens' growth or metabolic activity [60–62]. Further, the production of various highly active antimicrobial metabolites, such as bacteriocins, pyrrolnitrin, pyoluteorin, dialkylresorcinols, and phloroglucinols have been reported to be contributed directly to the biological control of plant pathogens [63]. Flury *et al.* [64] reported the involvement of pyoluteorin and hydrogen cyanide produced by *Pseudomonas* spp. in the biocontrol of some phy-

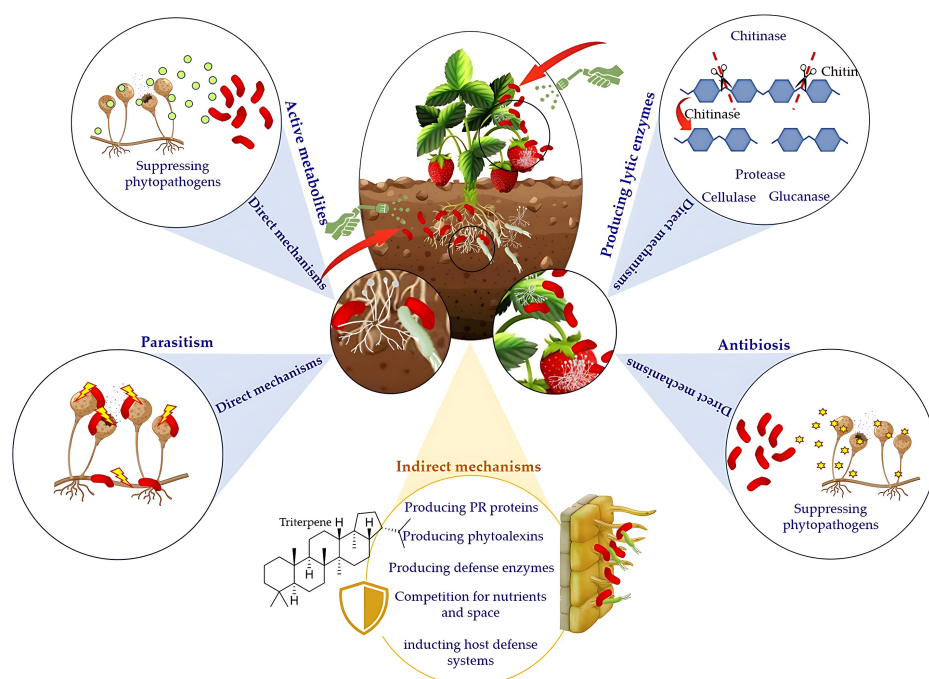


Fig. 1. Multiple modes of action of biocontrol bacteria against phytopathogens.

topathogens. *Pseudomonas* spp. produce cyclic lipopeptides, which are antimicrobial compounds that can harm plant pathogens by disrupting their cell membranes. This disruption can result in cytolysis and leakage, ultimately leading to the death of the pathogen [63]. For example, plant pathogens such as *Pythium*, *Phytophthora*, and *Rhizoctonia* have been managed using orfamides produced by *P. protegens* [65]. Lytic extracellular enzymes, such as cellulase, β -1,3 glucanases, and chitinase play important roles in the biocontrol activity of *Pseudomonads* by degrading the cell wall compounds, such as glucan, chitin, and glycosidic bridges [66].

The second most exploited antagonistic bacteria as biopesticides are *Bacillus* species. Their wide distribution in different habitats, such as plant surface and soil, endospore forming ability and the production of a wide variety of antimicrobial compounds, and the stimulation of plant immune system are considerable traits for their application in plant protection [67]. Several bacteriocins, such as subtilin A, subtilin B, subtilin, amysin, thuricin, amylocyclicin, and amylolysin produced by *Bacillus* spp. exhibit antimicrobial activity by forming spores in the cell membrane or preventing the cell wall synthesis [68]. More than that, many *Bacillus* species produce cyclic lipopeptides like surfactins, fengicins, and iturins, which are key factors in suppressing fungal phytopathogens [69]. *Bacillus* spp. strains can also liberate extracellular enzymes such as protease, lipase, chitinase, glucanase, cellulase, and chitosanase, that important factors in the biocontrol of bacterial and fungal pathogens [59].

3. Diversity of Enzyme-Producing Bacteria

Among these modes of action, extracellular enzymes, also known as hydrolytic enzymes, produced by various biocontrol bacteria directly affect phytopathogens via the degradation of cell wall structural compounds of most pathogens [44]. In fact, Hydrolytic enzymes play a crucial role in breaking down fungal pathogen spores and mycelia [70]. Bacterial lytic enzymes, such as chitinase, β -1,3-glucanase, catalase, cellulase, and proteases, break down polymeric compounds like chitin, glucan, cellulose, proteins, DNA, and hemicellulose which are the main compounds in the cell wall structure of phytopathogens [71]. Fig. 2 depicts the effects of hydrolysis enzymes on the degradation of cell membranes and cell walls of phytopathogenic fungi.

A wide variety of plant biocontrol bacteria can remarkably represent a mutually helpful interaction with microbial microorganisms by synthesizing various extracellular enzymes that can change their environment in a self-beneficial manner. The production of cell wall degrading enzymes has been reported in different groups of bacteria isolated from the rhizosphere and phyllosphere of different plant species. For instance, Bibi *et al.* [72] reported the isolation of amylase, lipase, protease, and cellulase-producing bacterial strains of various genera from the leaves, roots, and soil of mangroves.

In addition to producing extracellular enzymes, biocontrol bacteria can also disrupt the quorum-sensing system of pathogens by producing inhibitor enzymes, such as chitinase, pectinase, cellulase, and lactonase. These inhibitors prevent the synthesis or degradation of signal molecules re-

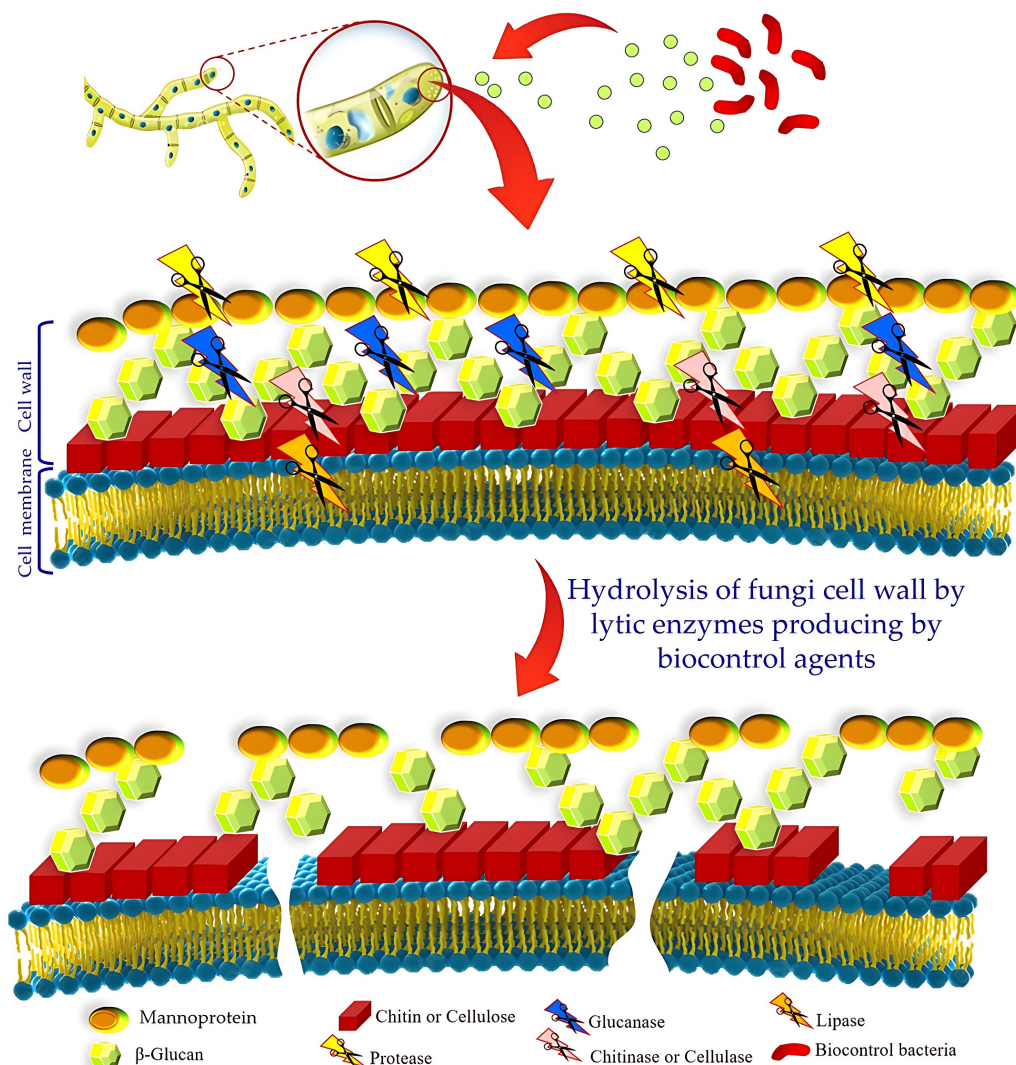


Fig. 2. The effects of hydrolysis enzymes on the degradation of the cell membrane and cell walls of phytopathogenic fungi.

quired for the pathogens to infect their host plants. This interference with the quorum-sensing system can reduce the virulence of the pathogens and limit the damage they cause to the plants [73].

The most dominant bacteria belong to the genera *Vibrio*, *Halomonas*, *Alteromonas*, *Marinobacter*, *Erwinia*, *Microbulbifer*, *Chromohalobacter*, *Psychrobacter*, *Aidingimonas*, *Isoptericola*, and *Bacillus*. Some of them, including *Bacillus*, followed by *Halomonas*, *Marinobacter*, and *Microbulbifer* species, were also active against fungal pathogens, such as *P. capsica*, *P. ultimum*, *F. oxysporum*, and *A. mali*. Evaluating the potential of the bacterial flora associated with maize in Brazil's main maize-producing regions for producing hydrolytic enzymes indicated that these bacterial strains belong to the phyla Proteobacteria, Firmicutes, and Actinobacteria. Moreover, *Pantoea dispersa* and *Massilia timonae* were the new producers of lipase and amylase, respectively [74]. While

conducting a study across three distinct regions of Tamil Nadu in India, numerous bacterial strains displaying hydrolytic enzyme production were successfully isolated. Out of 72 bacterial isolates, 20.83% were found to produce amylase, cellulase, and inulinase simultaneously. Most isolates exhibiting enzyme activities were identified as *Bacillus cereus*, *B. thuringiensis*, and *B. anthracis* [75]. Many strains of *B. subtilis* depict the capability to suppress several plant pathogens through the secretion of extracellular enzymes such as β -glucanases, cellulases, and proteases [76]. Bhutani *et al.* [77] conducted a study in which they isolated endophytic bacteria from *Cajanus cajan* and *Vigna radiata*. These bacteria were found to secrete various enzymes, including cellulase, amylase, pectinase, and protease. The identification results revealed that the isolates belonged to different species of *Bacillus* or *Bacillus*-derived genera, specifically *B. licheniformis*, *B. panaciumi*, *B. cereus*, *B. megaterium*, and *B. subtilis*. *B. licheni-*

formis B307 produced chitinase, and this enzyme's production and its properties can be modified under optimal conditions [78]. Regardless of *Bacillus* genera, various other bacterial strains such as *Serratia marcescens*, *S. plymuthica*, *P. putida*, *Enterobacter agglomerans*, *Aeromonas caviae*, *Streptomyces* spp., *Geobacillus thermodenitrificans*, *P. fluorescens*, *Paenibacillus ehimensis*, *P. cepacian*, *P. ehimensis*, *P. stutzeri*, *S. viridodlasticus*, *Paenibacillus polymyxa*, and *Stenotrophomonas maltophilia* have been reported to have biocontrol activity against phytopathogens through the production of several cell-wall degrading enzymes, such as protease, serine protease, β -1,3- glucanase, and chitinase [44]. Recently, Admassie *et al.* [79] reported that bacterial isolates obtained from the pepper plants with the high production of lytic enzymes like cellulase, protease, lipase and chitinase were identified as *Enterobacter cloacae* and *P. fluorescens*.

4. Unlocking the Potential of Hydrolytic Enzymes Produced by Biocontrol Bacteria

Extracellular hydrolytic enzymes are a highly heterogeneous group of enzymes, including lyases, esterases, glycosyl-hydrolases, and oxidoreductases. Microorganisms with degrading activities toward plant cell wall polysaccharides are the most source of hydrolytic enzymes for industrial applications. Although, large-scale industrial production of microbial enzymes as biopesticides in the management of phytopathogens has been considered by many researchers. Among rhizosphere microbes, various bacterial strains produce cell wall degrading enzymes, including chitinase, cellulase, proteases, lipases, and amylases, in response to phytopathogen attacks, which are fully discussed in the following sections (Table 1, Ref. [40,79–107]). These enzymes can either be applied indirectly by manipulating genes coding enzymes, purified enzyme proteins, or directly applying on phytopathogens.

4.1 Bacterial Chitinase in the Biocontrol of Phytopathogens

Chitinase enzymes, which can be classified as exochitinases, endochitinases, β -N-acetylglucosaminidases, and chitobiasis are capable of hydrolyzing glycoside bonds in chitin, a β -1,4 linked biopolymer of N-Acetylglucosamine [108]. The presence of chitin polymer in the cell walls of fungal phytopathogens represents chitinase as a vital mean in the biocontrol of many plant diseases as its degradation lyses fungal cell wall and induces plant immune system [80]. Various microorganisms, such as crustaceans, insects, fungi, yeasts, vertebrates, higher plants, and bacteria, have been reported as chitinase producers. Biocontrol bacteria with chitinolytic activity have been reported to be effective against fungal phytopathogens [109]. Loss of biocontrol activity in antagonistic bacteria through the inactivation of gene-coding chitinase exhibited the importance of chitinase activity in mitigating

phytopathogens [81]. *Streptomyces* spp. has been broadly studied as a chitinase-production microorganism among antagonistic bacteria. For instance, Umar *et al.* [82] reported that extracellular crude chitinase produced by *Streptomyces* isolate CT02 showed antagonistic activity against *Aspergillus niger* and *A. oryzae*. In another study, among seven *Streptomyces* species isolated from grassland soils, *S. flavogriseus*, *S. albus*, and *S. fumosus* exhibited chitinolytic activity although *S. albus* produced the highest amount of chitinase. The chitinase produced by these species inhibited the growth of *F. graminearum*, *Magnaporthe oryzae*, *Rhizoctonia solani*, *Botrytis cinerea*, and *Puccinia* species [83]. *Streptomyces cellulosae* Actino 48 revealed the highest chitinase generation and the strongest suppression of *Sclerotium rolfii* by malformation, abnormalities, and hyphal injuries, resulting in a considerable loss of mycelia density and mass [84]. Several *Pseudomonas* and *Bacillus* species with chitinolytic activity have also been reported as antagonistic agents against phytopathogens. Sharma *et al.* [80] found that chitinase generated by *Pseudomonas putida* and *B. subtilis* protected mug bean plants against *M. phaseolina*. *Magnaporthe grisea*, the causal agent of rice blast disease. *Magnaporthe grisea*, the causal agent of blast disease infecting ragi, was suppressed by chitinase-producing *Pseudomonas* spp. Although, the isolate with maximum efficacy and chitinase generation was identified as *P. fluorescens* [85]. The biocontrol activity of *Enterobacter cloacae* and *P. fluorescens* against *Phytophthora capsici* was associated with the high potential of hydrolytic enzymes such as chitinase [79]. Dhouib *et al.* [86] indicated that chitinase production by *Bacillus velezensis* is one of the most important mechanisms in managing *Verticillium* wilt disease caused by *V. dahliae*. Similarly, *Alternaria alternata*, *Botrytis cinerea*, *Fusarium oxysporum*, *F. graminearum*, *Ustilaginoidea virens*, and *Fulvia fulva* were grown significantly decreased by a chitinase producer bacteria called *B. velezensis* NGK-2 [87]. The extracellular chitinase produced by *Paenibacillus elgii* HOA73 inhibited the spore germination of *B. cinerea* under *in vitro* conditions [81]. Jangir *et al.* [88] reported the role of extracellular chitinase produced by different *Bacillus* isolates in suppressing *F. oxysporum* f. sp. *lycopersici*. Chitinase production also improved the biocontrol potential of *Bacillus* isolates against *M. phaseolina* and *R. solani* [89]. Chitinase coding genes in *B. cereus* were implicated in root colonization and managing the maize pathogenic fungus *F. verticillioides* [90]. Chitinase produced by *B. aerius* and *Geobacillus thermodenitrificans* is reported as a biocontrol aspect involved in the management of *Phytophthora capsica* [91]. Another important chitinase producer bacteria, *Serratia plymuthica*, effectively protected ginger against *Pythium myriotylum* via swelling, vacuolation, distortion and lysis of fungal mycelia [92]. Recently, Malik *et al.* [93] observed the inhibitory effect of chitinase synthesized by *B. subtilis* TD11 against fungi containing chitin in their hyphal walls such as *Col-*

Table 1. Extracellular lytic enzymes in the biocontrol of phytopathogens.

Biocontrol bacteria	Hydrolytic enzyme	Target pathogen	Reference
<i>Streptomyces</i> isolate CT02	Chitinase	<i>Aspergillus niger</i> , <i>A. oryzae</i>	[82]
<i>Streptomyces albus</i> , <i>S. flavo-griseus</i> , <i>S. fumosus</i>	Chitinase	<i>Fusarium. graminearum</i> , <i>Magnaporthe oryzae</i> , <i>Rhizoctonia solani</i> , <i>Botrytis cinerea</i> , <i>Puccinia</i> species	[83]
<i>Streptomyces cellulosae</i>	Chitinase	<i>Sclerotium rolfsii</i>	[84]
<i>Pseudomonas putida</i> , <i>B. subtilis</i>	Chitinase	<i>M. phaseolina</i>	[80]
<i>Pseudomonas fluorescens</i>	Chitinase	<i>Magnaporthe grisea</i>	[85]
<i>Pseudomonas fluorescens</i> , <i>Enterobacter cloacae</i>	Chitinase, cellulase, lipase, protease	<i>Phytophthora capsici</i>	[79]
<i>Bacillus velezensis</i>	Chitinase, protease, β -Glucanase	<i>Verticillium daliae</i>	[86]
<i>Bacillus velezensis</i> NKG-2	Protease, Lipase	<i>Gaeumannomyces graminis</i> Var. <i>tritici</i> , <i>Gaeumannomyces graminis</i> var. <i>tritici</i>	[40]
<i>Paenibacillus elgii</i> HOA73	Chitinase	<i>B. cinerea</i>	[81]
<i>B. subtilis</i> TD11	Chitinase, cellulase	<i>Colletotrichum</i> , <i>Aspergillus</i> , <i>Fusarium</i> , <i>Rhizoctonia</i> .	[93]
<i>Bacillus velezensis</i> NKG-2	Chitinase, β -Glucanase, cellulase, amylase	<i>Alternaria alternata</i> , <i>Botrytis cinerea</i> , <i>Fusarium oxysporum</i> , <i>F. graminearum</i> , <i>Ustilagoideae virens</i> , <i>Fulvia fulva</i>	[87]
<i>Bacillus</i> spp.	Chitinase, protease, glucanase	<i>Rhizoctonia solani</i> , <i>M. phaseolina</i>	[89]
<i>Bacillus</i> spp.	Chitinase, β -1,3-glucanase, protease	<i>F. oxysporum</i> f. sp. <i>lycopersici</i>	[88]
<i>B. cereus</i>	Chitinase	<i>F. verticillioides</i>	[90]
<i>Serratia plymuthica</i>	Chitinase	<i>Pythium myriotylum</i>	[92]
<i>B. aerius</i> , <i>Geobacillus</i> , <i>Thermodenitrificans</i>	Chitinase	<i>P. capsici</i>	[91]
<i>B. cereus</i> , <i>B. subtilis</i> , <i>Pantoea agglomerans</i>	Chitinase	<i>Colletotrichum</i> , <i>Rhizoctonia</i> , <i>Aspergillus</i> , <i>Fusarium</i>	[93]
<i>Bacillus simplex</i> , <i>B. subtilis</i>	Cellulase, chitinase, pectinase, xylanase	<i>Fusarium</i> spp.	[94]
<i>B. velenzensis</i> TSA32-1	Cellulase, protease	<i>F. fujikuroi</i> , <i>F. graminearum</i> , <i>Diaporthe actinidiae</i> , <i>A. alternata</i> , <i>Pythium ultimum</i>	[95]
<i>B. subtilis</i>	Cellulase, chitinase, glucanase	<i>Colletotrichum gloeosporioides</i> OGC1	[96]
<i>Pseudomonas</i> spp.	Cellulase, glucanase, xylanase	<i>Verticillium dahliae</i>	[97]
<i>Bacillus pumilus</i>	Protease, cellulase	<i>Fusicoccum aesculli</i> , <i>Phomopsis macrospora</i> , <i>Cytospora chrysosperma</i> .	[98]
<i>B. cereus</i>	Protease	<i>Bursaphelenchus xylophilus</i>	[100]
<i>B. cereus</i> BCM2	Protease, chitinase	<i>Meloidogyne incognita</i>	[99]
<i>P. aeruginosa</i> FG106	Protease, lipase	<i>Xanthomonas euvesicatoria</i> pv. <i>perforans</i> , <i>R. solani</i> , <i>P. infestans</i> , <i>A. alternata</i> , <i>B. cinerea</i> , <i>Clavibacter michiganensis</i> subsp. <i>Michiganensis</i> , <i>P. colocasiae</i>	[101]
<i>P. putida</i> ASU15	Lipase, protease, chitinase	<i>Uromyces appendiculatus</i>	[102]
<i>B. cereus</i>	α - amylase	<i>Rhizoctonia cerealis</i>	[103]
<i>B. cereus</i> SCB-1	α - amylase, cellulase, protease	<i>Fusarium</i> , <i>Alternaria</i> , <i>Curvularia</i> , <i>Neodeighonia</i> , <i>Saccharicola</i> , <i>Cochliobolus</i> , <i>Phomopsis</i>	[104]

Table 1. Continued.

Biocontrol bacteria	Hydrolytic enzyme	Target pathogen	Reference
<i>Staphylococcus warneri</i> , <i>B. velezensis</i> , <i>B. megaterium</i> , <i>Caballeronia glebae</i> , <i>B. licheniformis</i>	Amylase	<i>Ralstonia solanacearum</i>	[105]
One <i>Bacillus</i> and one <i>Pseudomonas</i> isolate	Amylase, protease	<i>R. solanacearum</i>	[106]
<i>P. syringae</i> , <i>P. fluorescens</i> , <i>P. aeruginosa</i>	α - amylase, protease	<i>R. solanacearum</i>	[107]

letotrichum, *Aspergillus*, *Fusarium*, and *Rhizoctonia*. Similarly, *B. subtilis*, *B. cereus*, and *Patoea agglomerans* isolated from the rhizosphere of tomato plants were found to liberate extracellular hydrolytic chitinase with antagonistic activity against *Colletotrichum*, *Rhizoctonia*, *Aspergillus*, and *Fusarium* [93]. It can be concluded from this section that chitinase plays an essential role in the biocontrol of many phytopathogens through the degradation of chitin polymers in the cell wall structure.

4.2 Bacterial Cellulase in the Biocontrol of Phytopathogens

Cellulase extracellular enzymes are glycoside hydrolases that cleavage β -1,4-D glucan bond present in the cellulose structure as an important cell wall component of certain fungi, bacteria, and all plants. Cellulase causes cell wall degradation and produces cellobiose, glucose, and cello-oligosaccharide. This enzyme is categorized into three major kinds, including endo- β -1,4 glucanase, exoglucanase, and β -glucosidase, all taking part in cellulase hydrolysis [110]. Cellulase has been reported as a potential biocontrol mechanism of some fungi, bacteria, and actinomycetes [44]. For instance, cellulase from *Bacillus velezensis* NKG-2 was found to show antagonistic activity against some major plant fungal pathogens *Alternaria alternata*, *Botrytis cinerea*, *Fusarium oxysporum*, *F. graminearum*, *Ustilago violacea*, and *Fulvia fulva* [87]. The bacteria *P. fluorescens* and *E. cloacae* have been successfully used in the biocontrol of *Phytophthora capsici* by producing cellulolytic enzymes [79]. Cellulase produced by *B. subtilis* TD11 was found to show antifungal activity against *Colletotrichum*, *Aspergillus*, *Fusarium*, and *Rhizoctonia* [93]. Khan *et al.* [94] indicated that *Bacillus simplex* and *B. subtilis* could liberate extracellular cellulase, which acts against *Fusarium* spp. in infected soils. The cellulase enzyme from *B. velezensis* TSA32-1 has been characterized and was found to exert antifungal action against *F. fujikuroi*, *F. graminearum*, *Diaporthe actinidiae*, *A. alternata*, and *Pythium ultimum* [95]. Ashwini & Srividya [96] observed the excretion of cellulase by *B. subtilis*, which effectively reduced *C. gloeosporioides* mycelia in liquid culture. Cellulase of two strains of *B. velezensis* showed efficacy in biocontrol of grey mold disease caused by *B.*

cinerea [111]. In a study by Yanti *et al.* [112], the cellulase of *B. cereus* and *B. pseudomycoides* were reported in the biocontrol of tomato phytopathogens. The investigation of biocontrol agents for managing *Verticillium* wilt of olive caused by *V. dahliae* resulted in the characterization of some *Pseudomonas* strains with the cellulase production activity [97]. Cellulase producing endophytic *B. pumilus* JK-SX001 showed antifungal activity on *Fusicoccum aesculli*, *Phomopsis macrospora* and *cytospora chrysosperma*, the casual agents of canker disease of poplar [98]. According to above-mentioned studies, cellulase produced by biocontrol bacteria is a key step in the suppression of plant pathogens especially fungal phytopathogens.

4.3 Bacterial Proteases in the Biocontrol of Phytopathogens

Proteases are enzymes that break down proteins and are vital in biological control processes and in protecting plants from disease-causing microorganisms. Proteases degrade proteins into peptide chains and amino acids, resulting in the breakdown of the cell wall. This occurs because the fibrils of β -Glucanase and chitin are incorporated into the protein matrix [113]. The protease generated by bacteria is mainly extracellular, easy to obtain, and active under various environmental conditions, disrupting the action of pathogenic proteins on plant cells [114]. Several bacterial genera have been reported to mitigate plant pathogens by producing extracellular protease enzymes. For example, tomato phytopathogen was inhibited by the protease liberated from *B. cereus* and *B. pseudomycoides* [112]. Protease production by *Pseudomonas fluorescens*, and *Enterobacter cloacae* limited the growth of *Phytophthora capsici* [79]. According to Dhouib *et al.* [86], *Bacillus velezensis* produce protease that can suppress the growth of *V. dahliae*. One of the important hydrolytic enzymes in controlling phytopathogens like *F. fujikuroi*, *F. graminearum*, *Diaporthe actinidiae*, *A. alternata*, and *Pythium ultimum* was protease produced by *B. velezensis* TSA32-1 [95]. Also, protease from *Bacillus* spp. conferred the protection against *Rhizoctonia solani*, *M. phaseolina*, and *F. oxysporum* f. sp. *lycopersici* [88,89]. Ren *et al.* [98] reported an endophytic *B. pumilus* strain as a protease producer, which conferred protection against poplar canker disease caused by *Fusicoccum aesculli*, *Phomopsis macrospora*, and *cytospora*

chrysosperma. The investigation of an alkaline protease of *B. amyloliquefaciens* SP1 showed its involvement in the efficient biocontrol of *F. oxysporum* [115]. Serine protease extracted from *B. licheniformis* W10 exhibited its antifungal potential against *B. cinerea* [116]. Hu *et al.* [99] reported that one of the potential mechanisms employed by *B. cereus* BCM2 in the infection and death of *Meloidogyne incognita*, which causes sever root-knot disease in crops, is the production of extracellular hydrolytic enzymes, especially protease and chitinase. Recently, the pathogenicity of an alkaline protease secreted from *B. cereus* NJSZ-13 to prevent pine wood nematode, *Bursaphelenchus xylophilus* was suggested by Li *et al.* [100]. Many researchers have proved the great fungicidal and nematicidal potential of protease produced by antagonistic bacteria.

4.4 Bacterial Lipases in the Biocontrol of Phytopathogens

Lipases are vital lipolytic enzymes many microorganisms produce, from procaryotes to eucaryotes. These enzymes belong to the alpha and beta hydrolase superfamily with many catalytic characteristics, such as alcoholysis, transesterification, decarboxylation, and aminolysis [117]. Their mechanism of action catalyzes the hydrolysis of different lipid substrates. Various bacterial strains representing lipase production can be considered as biological control agents. The lipases produced by these bacteria affect phytopathogens directly and induce plant defense mechanisms by liberating lipids [71]. Lipases produced by *P. aeruginosa* FG106, isolated from the rhizosphere of tomato plants, improved its biocontrol activity in managing *Xanthomonas euvesicatoria* pv. *perforans*, *R. solani*, *P. infestans*, *A. alternata*, *B. cinerea*, *Clavibacter michiganensis* subsp. *Michiganensis*, and *P. colocasiae* [101]. Admassie *et al.* [79] reported lipases as one of the most important antagonistic compounds liberated by *Pseudomonas fluorescens* and *Enterobacter cloacae* in the control of *P. capsici*. The *P. putida* strain AUS15, isolated from fresh beans, represented direct biocontrol efficacy against *Uromyces appendiculatus* through lipolytic, chitinolytic, and proteolytic activities [102]. *Streptomyces puniceus* with strong lipase activity exhibited significant inhibition to the growth of *Verticillium dahliae*, and *Valsa mali* [118]. Evaluating the ability of several isolates of *Bacillus* (*B. subtilis*, *B. licheniformis*, *B. firmus*, *B. lentus*, *B. circulans*, and *B. aeruginosa*) and *Pseudomonas* (*P. fluorescens*, *P. luteola*, and *P. aeruginosa*) to inhibit the mycelia growth of *F. oxysporum* f. sp. *ciceris* showed different rates of inhibition due to the excretion of different hydrolytic enzymes including lipase [119]. A study by Mota *et al.* [120] isolated bacteria from different plant species and soils which were identified as *B. cereus*, *B. subtilis*, *B. thuringiensis*, *Paenobacillus polymyxa*, *Pseudomonas poae*, *Pseudochrobactrum saccharolyticum*, *P. putida*, *B. amyloliquefaciens*, *Bacillus* spp. and *Pseudomonas* spp. killed juveniles of *Mesocriconema xenoplax* by the production of

extracellular lytic enzymes such as lipases. Similarly, lipase production activity was observed in bacteria isolated from different sources, which were identified as *Bacillus* sp., *Pantoea* sp., *Pantoea vegans*, *Burkholderia cepacian*, *Acinetobacter* sp., *P. putida*, *Staphylococcus warneri*, *B. licheniformis*, *B. amyloliquefaciens*, *Paenibacillus cineris* and *Oceanobacillus oncorhynchi*. These bacteria exhibited antagonistic activity against *Xanthomonas oryzae* pv. *oryzae*, the causal agent of bacterial leaf blight of paddy [121]. Consequently, lipases play a vital role as an important lytic enzyme in the plant protection mechanism employed by many biocontrol bacteria.

4.5 Bacterial Amylase in the Biocontrol of Phytopathogens

Amylases are classified into three main groups including, β -amylases which are exo-hydrolases, hydrolyzing α -1,4-glucan binds into maltose units, α -amylases, producing maltose and glucose by catalyzing the hydrolysis of α -1,4- glycosidic linkages and γ -amylases, producing glucose via breaking down the α -1-6 and α -1-4 glycosidic bonds [122]. These enzymes tolerate acidic conditions, and calcium is needed to stabilize their conformation. They are found in various microorganisms, including bacteria, fungi, and oomycetes. Many researchers have proved the antimicrobial capability of amylase produced by several biocontrol bacteria. For instance, Huang *et al.* [103] observed the secretion of an α -amylase by *B. cereus*, inhibiting the growth of *R. cerealis*. Moreover, α - amylase produced by *B. subtilis* SCB-1 contributed to its antifungal potential against diverse fungal pathogens, including *Fusarium*, *Alternaria*, *Curvularia*, *Neodeightonia*, *Saccharicola*, *Cochliobolus* and *Phomopsis* [104]. Myo *et al.* [87] discovered that *B. velezensis* NKG-2 exhibited antifungal activity against *F. graminearum*, *B. cinerea*, *F. oxysporum*, *Fulvia fulva*, *U. virens*, and *A. alternata* through the production of amylase. Endophytic beneficial bacteria, such as *Staphylococcus warneri*, *B. velezensis*, *B. megaterium*, *Caballeronia glebae*, *B. licheniformis* with high antagonistic activity against *Ralstonia solanacearum*, the causal agent of bacterial wilt, was positive for amylase production [105]. In a separate investigation, bacterial wilt in tomatoes, induced by *R. solanasearum*, was effectively managed using a single *Bacillus* isolate and one *Pseudomonas* isolate, both of which exhibited the capacity to produce amylase under *in vitro* conditions [106]. Three *Pseudomonas* isolates, including *P. syringae*, *P. fluorescens* and *P. aeruginosa*, could produce α - amylase, protease, and lipase, making them potential in the growth inhibition of *R. solanacearum* [107]. Among 73 endophytic bacteria isolated from different tissues of *Clerodendrum colebrookianum*, 84.6% of them exhibited remarkable amylase production and antifungal activity against *F. oxysporum*, *F. graminearum*, *Colletotrichum capsici*, *F. proliferatum* and *R. solani* [123]. Therefore, amylase-producing bacteria are potential biocontrol agents for several phytopathogens.

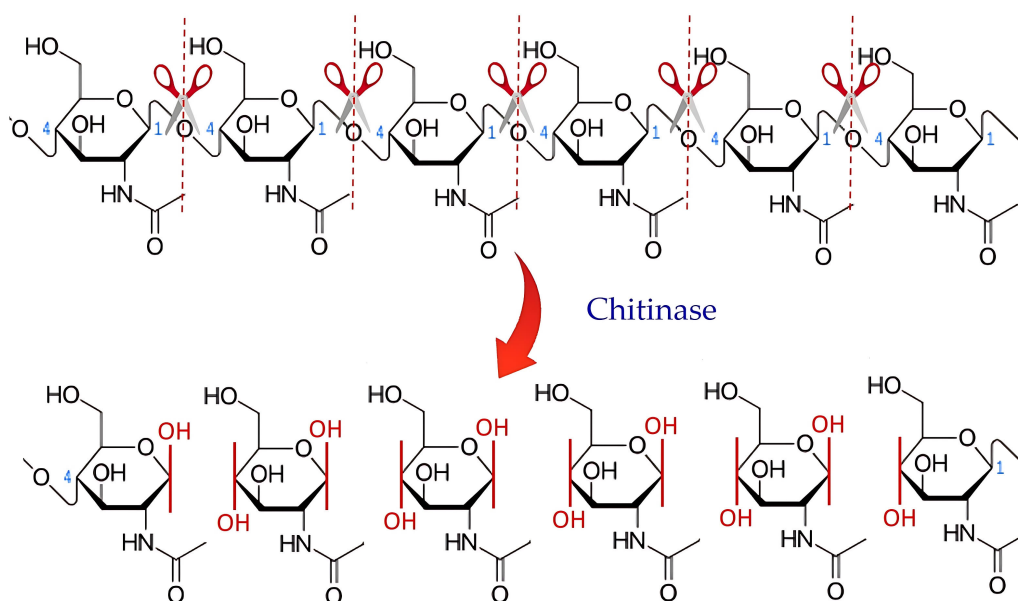


Fig. 3. The action mechanism of chitinase.

5. Deciphering the Mechanisms of Hydrolytic Enzymes in Phytopathogen Biocontrol

The main action mechanism of different extracellular enzymes liberated by biocontrol bacteria catalyzes the hydrolysis of phytopathogens' cell wall, proteins, and DNA, leading to the outflow of intracellular materials and cell death [124]. The cell wall of pathogenic microorganisms maintains their cells' physical integrity, composed of proteins, different carbohydrates, chitin, β -1,3-glucan, and lipids. Different cell wall parts can be affected depending on the target pathogen and biocontrol bacteria. For example, chitinase degrades the polymer chitin presented in the cell wall of nematodes and fungi. However, it is divided into two types based on the mode of action: (1) Endochitinases, degrading internal sites of chitin microfibril over the whole length and producing multimer N-acetyl glucosamine such as chitotetraose and chititriose and dimer diacetyl-chitobiose, and (2) Exochitinases, which are classified into (a) β -1,4-glucosaminidases, breaking down oligomers obtained by Endochitinases into N-acetyl glucosamine monomer, and (b) chitotriosidase which produce diacetylchitobiose via breaking the non-reducing end of chitin [44]. Fig. 3 depicts the degradation of chitin by chitinase.

The second hydrolytic enzyme discussed in this article is cellulase, hydrolyzing 1,4- β -D-glycosidic bonds of cellulose as a major polysaccharide compound in the pathogens' cell wall. These enzymes produce glucose, cellobiose, and cello-oligosaccharide after breaking cellulose down. Different cellulolytic enzymes, including cellulose (endo-glucanases), β -glucosidases, and exocellobiohydrolase (exo-glucanases), are required for the

synergistic conversion of cellulose to glucose [125]. Fig. 4 describes the degradation of cellulose by cellulase. The third bacterial hydrolysis enzyme called protease not only lyses the protein matrix in the cell wall but also degrades the major phytopathogens proteins into peptide chains and amino acids, disrupting their action on plant cells. Proteases based on their site of action are classified into (1) Exopeptidases, removing amino acids from the carboxy-terminal (carboxypeptidases) or amino-terminal (aminopeptidases) end of the proteins, and (2) Endopeptidases break down the internal amino acids of the polypeptide chain [126]. The lipase's mode of action is hydrolyzing different lipid substrates by breaking ester bonds down and producing glycerol, fatty acids, and other alcohols. These enzymes can also induce the plant immune system by liberating lipids [102]. The last discussed extracellular hydrolytic enzyme, amylase, breaks down starch into maltose and glucose sugars. According to the action site, amylases are classified as α -amylases, β -amylases, and γ -amylases, lysing α -1-6 and α -1-4 glycosidic linkages in starch structure [71]. It can be concluded that hydrolytic enzymes secreted from biocontrol bacteria act on different parts of the phytopathogenic cell wall, and all of them lead to the outflow of intercellular materials and cell death.

6. Conclusion and Prospects

With the increasing global population and growing demand for agricultural products, finding alternatives to synthetic pesticides has become a top global priority. Antagonistic microorganisms, especially biocontrol bacteria, have emerged as promising strategies to ensure plant health, food safety, and sustainable agriculture. These biocontrol bacte-

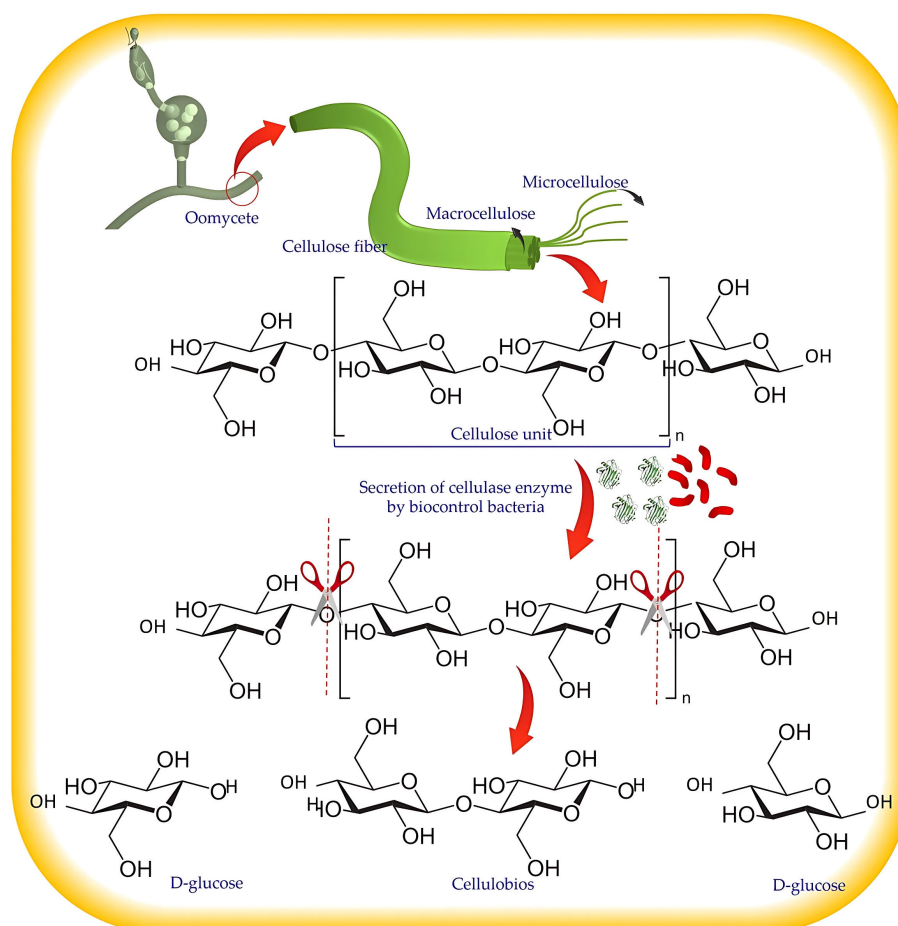


Fig. 4. The action mechanism of cellulase.

ria, belonging to genera like *Bacillus*, *Pseudomonas*, *Streptomyces*, and others, exhibit antagonistic activity against various plant pathogens through multiple modes of action, particularly those producing hydrolytic enzymes. Hydrolytic enzymes, such as chitinase, cellulase, protease, lipase, and amylase, play a critical role in breaking down components of phytopathogens' cell walls, leading to their degradation. Moreover, some of these enzymes can directly affect plant growth and promote colonization by beneficial bacteria, triggering the plant's immune system against biotic stresses. This mechanism of action not only combats pathogens, but also enhances plant defense responses and overall health. Looking forward, the perspective of harnessing hydrolytic enzymes as a cornerstone of plant protection strategies is highly promising, with ongoing research on identifying novel and potent hydrolytic enzymes to efficiently degrade a wide range of pathogenic organisms, ultimately enhancing the effectiveness of biocontrol agents. Additionally, integrating these enzymes into various formulations, such as sprays or coatings, could facilitate easy application. As these enzymes work through a fundamentally different mechanism from chemical pesticides, it significantly reduces the likelihood of pathogens developing resistance, ensuring a sustainable and long-term so-

lution. Scaling up production processes for these enzymes using advanced biotechnological methods is another avenue that holds great potential. However, challenges include maintaining the stability and activity of enzymes under different conditions, as well as ensuring their safe use without any adverse effects on non-target organisms or the environment. Continued research, technological innovation, and field trials will be instrumental in realizing the full scope of benefits that hydrolytic enzymes can offer in sustainable agriculture and disease management.

Author Contributions

RSR, and MH, conceptualization; MV, MH, and EAB, data collection and analysis; RSR, and MH, visualization; EAB, format analysis; MV, MH, and EAB, original draft preparation; MV, MH, and EAB, review and editing; RSR, supervision. All authors contributed to editorial changes in the manuscript. All authors read and approved the final manuscript. All authors have participated sufficiently in the work and agreed to be accountable for all aspects of the work.

Ethics Approval and Consent to Participate

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Conflict of Interest

The authors declare no conflict of interest.

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