

Review

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

Roohallah Saberi Riseh<sup>1,\*</sup>, Masoumeh Vatankhah<sup>1</sup>, Mohadeseh Hassanisaadi<sup>1</sup> ,  
Essaid Ait Barka<sup>2</sup><sup>1</sup>Department of Plant Protection, Faculty of Agriculture, Vali-e-Asr University of Rafsanjan, 7718897111 Rafsanjan, Iran<sup>2</sup>Université de Reims Champagne-Ardenne, Unité de Recherche Résistance Induite et Bio-Protection des Plantes-EA 4707-USC INRAE1488, 51100 Reims, France\*Correspondence: [r.saberi@vru.ac.ir](mailto:r.saberi@vru.ac.ir) (Roohallah Saberi Riseh)

Academic Editors: Renato Fani, Giovanni Emiliani and Giulia Semenzato

Submitted: 25 October 2023 Revised: 26 December 2023 Accepted: 30 December 2023 Published: 15 March 2024

## 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]. Soilborne 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.

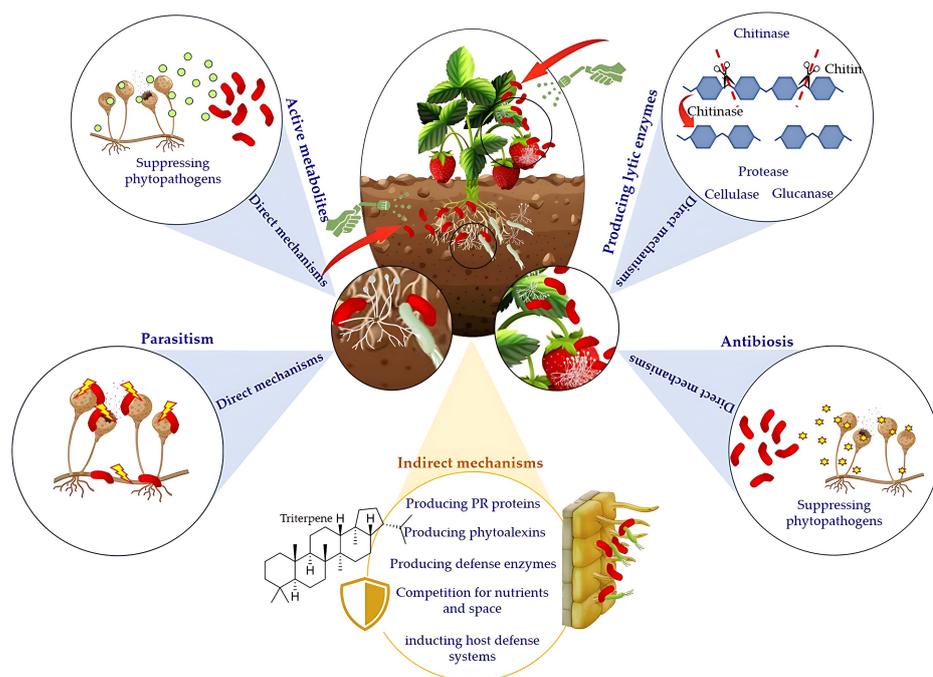
## 2. How Biocontrol Bacteria Control Plant Diseases?

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,  $\beta$ -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].

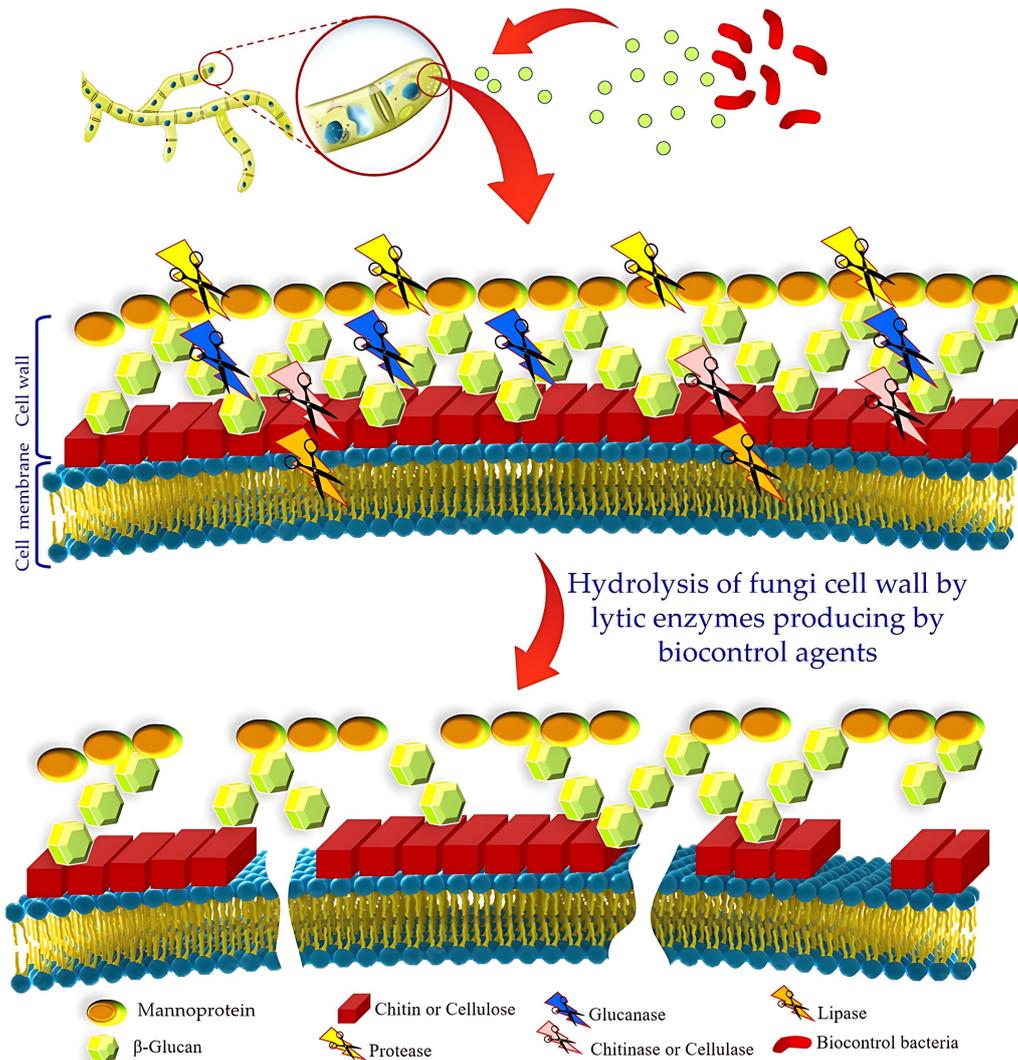
The second most exploited antagonistic bacteria as biopesticides are *Bacillus* species. Their wide distribution in different habitats, such as plant surface and soil, endospore forming ability and the production of a wide variety of antimicrobial compounds, and the stimulation of plant immune system 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,  $\beta$ -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  $\beta$ -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. viridodiasticus*, *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,  $\beta$ -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,  $\beta$ -N-acetylglucosaminidases, and chitobiasis are capable of hydrolyzing glycoside bonds in chitin, a  $\beta$ -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 cellulosa* Actino 48 revealed the highest chitinase generation and the strongest suppression of *Sclerotium rolfsii* 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, $\beta$ -Glucanase	<i>Verticillium daliae</i>	[86]
<i>Bacillus velezensis</i> NKG-2	Protease, Lipase	<i>Gaeumanomyces 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, $\beta$ -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, $\beta$ -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>	$\alpha$ - amylase	<i>Rhizoctonia cerealis</i>	[103]
<i>B. cereus</i> SCB-1	$\alpha$ - amylase, cellulase, protease	<i>Fusarium</i> , <i>Alternaria</i> , <i>Curvularia</i> , <i>Neodeighntonia</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>	$\alpha$ -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  $\beta$ -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 cellobiosaccharide. This enzyme is categorized into three major kinds, including endo-  $\beta$ -1,4 glucanase, exoglucanase, and  $\beta$ -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. pseudomyces* 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  $\beta$ -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. pseudomyces* [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*

*chrysoferma*. 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 severe 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 nematocidal 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 prokaryotes to eukaryotes. 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 cepacia*, *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,  $\beta$ -amylases which are exo-hydrolases, hydrolyzing  $\alpha$ -1,4-glucan binds into maltose units,  $\alpha$ -amylases, producing maltose and glucose by catalyzing the hydrolysis of  $\alpha$ -1,4-glycosidic linkages and  $\gamma$ -amylases, producing glucose via breaking down the  $\alpha$ -1-6 and  $\alpha$ -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  $\alpha$ -amylase by *B. cereus*, inhibiting the growth of *R. cerealis*. Moreover,  $\alpha$ -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. solanacearum*, 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  $\alpha$ -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.

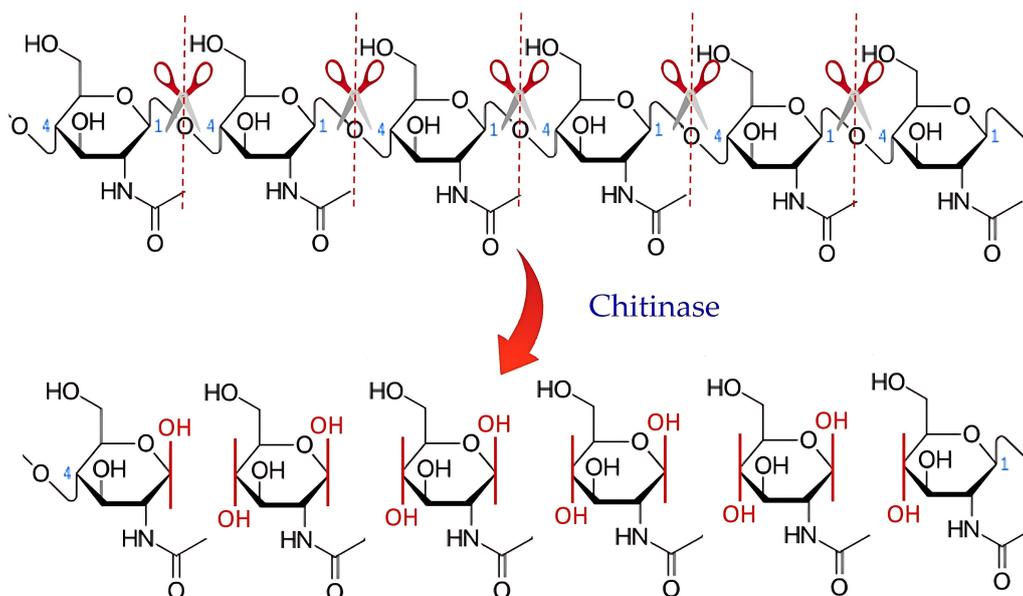


Fig. 3. The action mechanism of chitinase.

## 5. Deciphering the Mechanisms of Hydrolytic Enzymes in Phytopathogen Biocontrol

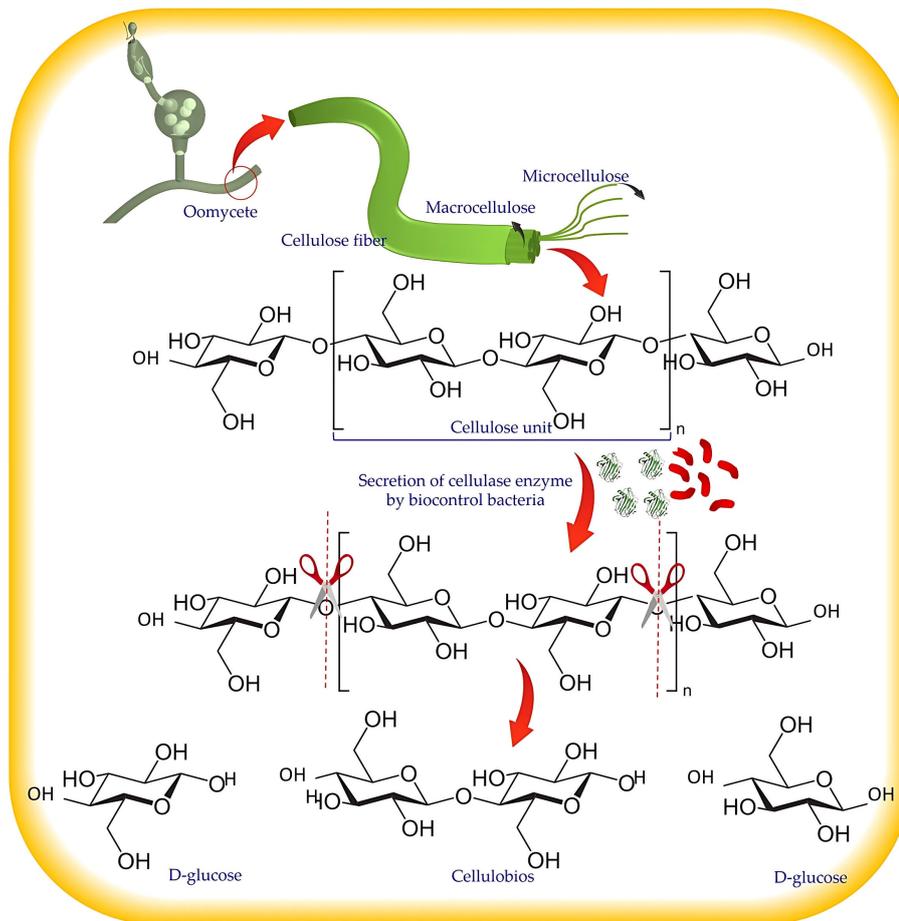
The main action mechanism of different extracellular lytic enzymes liberated by biocontrol bacteria catalyzes the hydrolysis of phytopathogens' cell wall, proteins, and DNA, leading to the outflow of intracellular materials and cell death [124]. The cell wall of pathogenic microorganisms maintains their cells' physical integrity, composed of proteins, different carbohydrates, chitin,  $\beta$ -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)  $\beta$ -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- $\beta$ -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),  $\beta$ -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  $\alpha$ -amylases,  $\beta$ -amylases, and  $\gamma$ -amylases, lysing  $\alpha$ -1-6 and  $\alpha$ -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

Not applicable.

## Acknowledgment

Not applicable.

## Funding

This research received no external funding.

## Conflict of Interest

The authors declare no conflict of interest.

## References

- [1] Peng Y, Li SJ, Yan J, Tang Y, Cheng JP, Gao AJ, *et al.* Research Progress on Phytopathogenic Fungi and Their Role as Biocontrol Agents. *Frontiers in Microbiology*. 2021; 12: 670135.
- [2] Rizzo DM, Lichtveld M, Mazet JAK, Togami E, Miller SA. Plant health and its effects on food safety and security in a One Health framework: four case studies. *One Health Outlook*. 2021; 3: 6.
- [3] Saberi-Riseh R, Hajieghrari B, Rouhani H, Sharifi-Tehrani A. Effects of inoculum density and substrate type on saprophytic survival of *Phytophthora drechsleri*, the causal agent of gummosis (crown and root rot) on pistachio in Rafsanjan, Iran. *Communications in Agricultural and Applied Biological Sciences*. 2004; 69: 653–656.
- [4] Velásquez AC, Castroverde CDM, He SY. Plant-Pathogen Warfare under Changing Climate Conditions. *Current Biology: CB*. 2018; 28: R619–R634.
- [5] Katan J. Diseases caused by soilborne pathogens: biology, management and challenges. *Journal of Plant Pathology*. 2017; 305–315.
- [6] Ristaino JB, Anderson PK, Bebbler DP, Brauman KA, Cunniffe NJ, Fedoroff NV, *et al.* The persistent threat of emerging plant disease pandemics to global food security. *Proceedings of the National Academy of Sciences of the United States of America*. 2021; 118: e2022239118.
- [7] Kumar L, Chhogyel N, Gopalakrishnan T, Hasan MK, Jayasinghe SL, Kariyawasam CS, *et al.* Climate change and future of agri-food production. In Rajeev, B (ed.) *Future Foods* (pp. 49–79). Elsevier. 2022.
- [8] Jamali F, Sharifi-Tehrani A, Okhovvat M, Zakeri Z, Saberi-Riseh R. Biological control of chickpea Fusarium wilt by antagonistic bacteria under greenhouse condition. *Communications in Agricultural and Applied Biological Sciences*. 2004; 69: 649–651.
- [9] Saberi-Riseh R, Javan-Nikkhah M, Heidarian R, Hosseini S, Soleimani P. Detection of fungal infectious agent of wheat grains in store-pits of Markazi province, Iran. *Communications in Agricultural and Applied Biological Sciences*. 2004; 69: 541–544.
- [10] Dignam BE, Marshall SD, Wall AJ, Mtandavari YF, Gerard EM, Hicks E, *et al.* Impacts of soil-borne disease on plant yield and farm profit in dairying soils. *Journal of Sustainable Agriculture and Environment*. 2022; 1: 16–29.
- [11] Mansfield J, Genin S, Magori S, Citovsky V, Sriariyanum M, Ronald P, *et al.* Top 10 plant pathogenic bacteria in molecular plant pathology. *Molecular Plant Pathology*. 2012; 13: 614–629.
- [12] Jones JT, Haegeman A, Danchin EGJ, Gaur HS, Helder J, Jones MGK, *et al.* Top 10 plant-parasitic nematodes in molecular plant pathology. *Molecular Plant Pathology*. 2013; 14: 946–961.
- [13] Zeynadini-Riseh A, Mahdikhani-Moghadam E, Rouhani H, Moradi M, Saberi-Riseh R, Mohammadi A. Effect of some probiotic bacteria as biocontrol agents of *Meloidogyne incognita* and evaluation of biochemical changes of plant defense enzymes on two cultivars of Pistachio. *Journal of Agricultural Science and Technology*. 2018; 20: 179–191.
- [14] Jeger M, Beresford R, Bock C, Brown N, Fox A, Newton A, *et al.* Global challenges facing plant pathology: multidisciplinary approaches to meet the food security and environmental challenges in the mid-twenty-first century. *CABI Agriculture and Bioscience*. 2021; 2: 1–18.
- [15] Okey-Onyesolu CF, Hassanisaadi M, Bilal M, Barani M, Rahdar A, Iqbal J, *et al.* Nanomaterials as nanofertilizers and nanopesticides: An overview. *ChemistrySelect*. 2021; 6: 8645–8663.
- [16] Kalyabina VP, Esimbekova EN, Kopylova KV, Kratasyuk VA. Pesticides: formulants, distribution pathways and effects on human health - a review. *Toxicology Reports*. 2021; 8: 1179–1192.
- [17] Kumar P, Gupta VK, Tiwari AK, Kamle M. *Current trends in plant disease diagnostics and management practices*. Springer: New York City. 2016.
- [18] Hassanisaadi M, Bonjar AHS, Rahdar A, Varma RS, Ajalli N, Pandey S. Eco-friendly biosynthesis of silver nanoparticles using *Aloysia citrodora* leaf extract and evaluations of their bioactivities. *Materials Today Communications*. 2022; 33: 104183.
- [19] Hassanisaadi M, Barani M, Rahdar A, Heidary M, Thysiadou A, Kyzas GZ. Role of agrochemical-based nanomaterials in plants: Biotic and abiotic stress with germination improvement of seeds. *Plant Growth Regulation*. 2022; 97: 375–418.
- [20] Panth M, Hassler SC, Baysal-Gurel F. *Methods for management of soilborne diseases in crop production*. Agriculture. 2020; 10: 16.
- [21] Riseh RS, Hassanisaadi M, Vatankhah M, Babaki SA, Barka EA. Chitosan as a potential natural compound to manage plant diseases. *International Journal of Biological Macromolecules*. 2022; 220: 998–1009.
- [22] Saberi Riseh R, Moradi Pour M, Ait Barka E. A Novel route for double-layered encapsulation of *Streptomyces fulvissimus* Uts22 by alginate–Arabic gum for controlling of *Pythium aphanidermatum* in Cucumber. *Agronomy*. 2022; 12: 655.
- [23] Saberi-Riseh R, Moradi-Pour M. The effect of *Bacillus subtilis* Vru1 encapsulated in alginate - bentonite coating enriched with titanium nanoparticles against *Rhizoctonia solani* on bean. *International Journal of Biological Macromolecules*. 2020; 152: 1089–1097.
- [24] Saberi-Riseh R, Moradi-Pour M. A novel encapsulation of *Streptomyces fulvissimus* Uts22 by spray drying and its biocontrol efficiency against *Gaeumannomyces graminis*, the causal agent of take-all disease in wheat. *Pest Management Science*. 2021; 77: 4357–4364.
- [25] Moradi Pour M, Saberi Riseh R, Skorik YA. Sodium Alginate-Gelatin Nanoformulations for Encapsulation of *Bacillus velezensis* and Their Use for Biological Control of Pistachio Gummosis. *Materials (Basel, Switzerland)*. 2022; 15: 2114.
- [26] Saberi-Riseh R, Fathi F, Moradzadeh-Eskandari M. Effect of some *Pseudomonas fluorescens* and *Bacillus subtilis* strains on osmolytes and antioxidants of cucumber under salinity stress. *Journal of Crop Protection*. 2020; 9: 1–16.
- [27] Hassanisaadi M, Bonjar GHS, Rahdar A, Pandey S, Hosseinipour A, Abdolshahi R. Environmentally Safe Biosynthesis of Gold Nanoparticles Using Plant Water Extracts. *Nanomaterials (Basel, Switzerland)*. 2021; 11: 2033.
- [28] Hassanisaadi M, Saberi Riseh R, Rabiei A, Varma RS, Kennedy JF. Corrigendum to “Nano/micro-cellulose-based materials as adsorbents for the remediation of chemical pollutants from agricultural resources” [Int. J. Biol. Macromol. 246 (2023) published online/125763]. *International Journal of Biological Macromolecules*. 2023; 250: 126128.
- [29] Saberi Riseh R, Vatankhah M, Hassanisaadi M, Kennedy JF. Increasing the efficiency of agricultural fertilizers using cellulose nanofibrils: A review. *Carbohydrate Polymers*. 2023; 321: 121313.
- [30] Riseh RS, Vazvani MG, Kennedy JF. The application of chitosan as a carrier for fertilizer: A review. *International Journal of Biological Macromolecules*. 2023; 252: 126483.

- [31] Saberi Riseh R, Vatankhah M, Hassanisaadi M, Kennedy JF. Chitosan/silica: A hybrid formulation to mitigate phytopathogens. *International Journal of Biological Macromolecules*. 2023; 239: 124192.
- [32] Saberi Riseh R, Vatankhah M, Hassanisaadi M, Kennedy JF. Chitosan-based nanocomposites as coatings and packaging materials for the postharvest improvement of agricultural product: A review. *Carbohydrate Polymers*. 2023; 309: 120666.
- [33] Saberi Riseh R, Gholizadeh Vazvani M, Hassanisaadi M, Skorik YA. Micro-/Nano-Carboxymethyl Cellulose as a Promising Biopolymer with Prospects in the Agriculture Sector: A Review. *Polymers*. 2023; 15: 440.
- [34] Saberi Riseh R, Hassanisaadi M, Vatankhah M, Soroush F, Varma RS. Nano/microencapsulation of plant biocontrol agents by chitosan, alginate, and other important biopolymers as a novel strategy for alleviating plant biotic stresses. *International Journal of Biological Macromolecules*. 2022; 222: 1589–1604.
- [35] Riseh RS, Vatankhah M, Hassanisaadi M, Varma RS. A review of chitosan nanoparticles: Nature's gift for transforming agriculture through smart and effective delivery mechanisms. *International Journal of Biological Macromolecules*. 2024. (online ahead of print)
- [36] Riseh RS, Vazvani MG, Kennedy JF.  $\beta$ -glucan-induced disease resistance in plants: A review. *International Journal of Biological Macromolecules*. 2023; 253: 127043.
- [37] Saberi-Riseh R, Moradi-Pour M, Mohammadinejad R, Thakur VK. Biopolymers for Biological Control of Plant Pathogens: Advances in Microencapsulation of Beneficial Microorganisms. *Polymers*. 2021; 13: 1938.
- [38] Saberi Riseh R, Skorik YA, Thakur VK, Moradi Pour M, Tamanadar E, Noghabi SS. Encapsulation of Plant Biocontrol Bacteria with Alginate as a Main Polymer Material. *International Journal of Molecular Sciences*. 2021; 22: 11165.
- [39] Saberi Riseh R, Tamanadar E, Hajabdollahi N, Vatankhah M, Thakur VK, Skorik YA. Chitosan microencapsulation of rhizobacteria for biological control of plant pests and diseases: Recent advances and applications. *Rhizosphere*. 2022; 23: 100565.
- [40] Pour MM, Riseh RS, Ranjbar-Karimi R, Hassanisaadi M, Rahdar A, Bains F. Microencapsulation of *Bacillus velezensis* Using Alginate-Gum Polymers Enriched with TiO<sub>2</sub> and SiO<sub>2</sub> Nanoparticles. *Micromachines*. 2022; 13: 1423.
- [41] Saberi Riseh R, Gholizadeh Vazvani M, Hassanisaadi M, Thakur VK, Kennedy JF. Use of whey protein as a natural polymer for the encapsulation of plant biocontrol bacteria: A review. *International Journal of Biological Macromolecules*. 2023; 234: 123708.
- [42] Saberi Riseh R, Hassanisaadi M, Vatankhah M, Kennedy JF. Encapsulating biocontrol bacteria with starch as a safe and edible biopolymer to alleviate plant diseases: A review. *Carbohydrate Polymers*. 2023; 302: 120384.
- [43] Köhl J, Kolnaar R, Ravensberg WJ. Mode of Action of Microbial Biological Control Agents Against Plant Diseases: Relevance Beyond Efficacy. *Frontiers in Plant Science*. 2019; 10: 845.
- [44] Mishra P, Mishra J, Dwivedi S, Arora NK. Microbial enzymes in biocontrol of phytopathogens. *Microbial Enzymes: Roles and Applications in Industries*. 2020; 259–285.
- [45] Saberi Riseh R, Dashti H, Gholizadeh Vazvani M, Dini A. Changes in the activity of enzymes phenylalanine ammonia-lyase, polyphenol oxidase, and peroxidase in some wheat genotypes against take-all disease. *Journal of Agricultural Science and Technology*. 2021; 23: 929–942.
- [46] Oukala N, Aissat K, Pastor V. Bacterial Endophytes: The Hidden Actor in Plant Immune Responses against Biotic Stress. *Plants (Basel, Switzerland)*. 2021; 10: 1012.
- [47] El-Saadony MT, Saad AM, Soliman SM, Salem HM, Ahmed AI, Mahmood M, *et al.* Plant growth-promoting microorganisms as biocontrol agents of plant diseases: Mechanisms, challenges and future perspectives. *Frontiers in Plant Science*. 2022; 13: 923880.
- [48] Bonaterra A, Badosa E, Daranas N, Francés J, Roselló G, Montesinos E. Bacteria as Biological Control Agents of Plant Diseases. *Microorganisms*. 2022; 10: 1759.
- [49] Pour MM, Saberi-Riseh R, Mohammadinejad R, Hosseini A. Investigating the formulation of alginate-gelatin encapsulated *Pseudomonas fluorescens* (VUPF5 and T17-4 strains) for controlling *Fusarium solani* on potato. *International Journal of Biological Macromolecules*. 2019; 133: 603–613.
- [50] Hassanisaadi M, Shahidi Bonjar GH, Hosseini-pour A, Abdolshahi R, Ait Barka E, Saadoun I. Biological control of *Pythium aphanidermatum*, the causal agent of tomato root rot by two *Streptomyces* root symbionts. *Agronomy*. 2021; 11: 846.
- [51] Ebrahimi-Zarandi M, Saberi Riseh R, Tarkka MT. Actinobacteria as Effective Biocontrol Agents against Plant Pathogens, an Overview on Their Role in Eliciting Plant Defense. *Microorganisms*. 2022; 10: 1739.
- [52] Lahlali R, Ezrari S, Radouane N, Kenfaoui J, Esmael Q, El Hamss H, *et al.* Biological Control of Plant Pathogens: A Global Perspective. *Microorganisms*. 2022; 10: 596.
- [53] Jan AT, Azam M, Ali A, Haq QMR. Novel approaches of beneficial *Pseudomonas* in mitigation of plant diseases—an appraisal. *Journal of Plant Interactions*. 2011; 6: 195–205.
- [54] Oso S, Walters M, Schlechter RO, Remus-Emsermann MNP. Utilisation of hydrocarbons and production of surfactants by bacteria isolated from plant leaf surfaces. *FEMS Microbiology Letters*. 2019; 366: fnz061.
- [55] Cabrefiga J, Bonaterra A, Montesinos E. Mechanisms of antagonism of *Pseudomonas fluorescens* EPS62e against *Erwinia amylovora*, the causal agent of fire blight. *International Microbiology: the Official Journal of the Spanish Society for Microbiology*. 2007; 10: 123–132.
- [56] Schiessl KT, Janssen EML, Kraemer SM, McNeill K, Ackermann M. Magnitude and Mechanism of Siderophore-Mediated Competition at Low Iron Solubility in the *Pseudomonas aeruginosa* Pyochelin System. *Frontiers in Microbiology*. 2017; 8: 1964.
- [57] Shahid I, Han J, Hardie D, Baig DN, Malik KA, Borchers CH, *et al.* Profiling of antimicrobial metabolites of plant growth promoting *Pseudomonas* spp. isolated from different plant hosts. *3 Biotech*. 2021; 11: 48.
- [58] Lakkis S, Trotel-Aziz P, Rabenoelina F, Schwarzenberg A, Nguema-Ona E, Clément C, *et al.* Strengthening Grapevine Resistance by *Pseudomonas fluorescens* PTA-CT2 Relies on Distinct Defense Pathways in Susceptible and Partially Resistant Genotypes to Downy Mildew and Gray Mold Diseases. *Frontiers in Plant Science*. 2019; 10: 1112.
- [59] Miljković D, Marinković J, Balešević-Tubić S. The Significance of *Bacillus* spp. in Disease Suppression and Growth Promotion of Field and Vegetable Crops. *Microorganisms*. 2020; 8: 1037.
- [60] Hirozawa MT, Ono MA, Suguiura IMDS, Bordini JG, Ono EYS. Lactic acid bacteria and *Bacillus* spp. as fungal biological control agents. *Journal of Applied Microbiology*. 2023; 134: lxac083.
- [61] Smits THM, Duffy B, Blom J, Ishimaru CA, Stockwell VO. Pantocin A, a peptide-derived antibiotic involved in biological control by plant-associated *Pantoea* species. *Archives of Microbiology*. 2019; 201: 713–722.
- [62] Kaari M, Joseph J, Manikkam R, Sreenivasan A, Venugopal G. Biological control of *Streptomyces* sp. UT4A49 to suppress tomato bacterial wilt disease and its metabolite profiling. *Journal of King Saud University-Science*. 2022; 34: 101688.
- [63] Höfte M. The use of *Pseudomonas* spp. as bacterial biocontrol agents to control plant disease. In Jürgen, K. and Willem, J.R (eds.) *Microbial bioprotectants for plant disease management*. Burleigh Dodds: Cambridgeshire. 2021.

- [64] Flury P, Vesga P, Péchy-Tarr M, Aellen N, Dennert F, Hofer N, *et al.* Antimicrobial and Insecticidal: Cyclic Lipopeptides and Hydrogen Cyanide Produced by Plant-Beneficial *Pseudomonas* Strains CHA0, CMR12a, and PCL1391 Contribute to Insect Killing. *Frontiers in Microbiology*. 2017; 8: 100.
- [65] Ma Z, Geudens N, Kieu NP, Sinnaeve D, Ongena M, Martins JC, *et al.* Biosynthesis, Chemical Structure, and Structure-Activity Relationship of Orfamide Lipopeptides Produced by *Pseudomonas* protegens and Related Species. *Frontiers in Microbiology*. 2016; 7: 382.
- [66] Omoboye OO, Oni FE, Batoool H, Yimer HZ, De Mot R, Höfte M. *Pseudomonas* Cyclic Lipopeptides Suppress the Rice Blast Fungus *Magnaporthe oryzae* by Induced Resistance and Direct Antagonism. *Frontiers in Plant Science*. 2019; 10: 901.
- [67] Caulier S, Nannan C, Gillis A, Licciardi F, Bragard C, Mahillon J. Overview of the Antimicrobial Compounds Produced by Members of the *Bacillus subtilis* Group. *Frontiers in Microbiology*. 2019; 10: 302.
- [68] Lajis AFB. Biomanufacturing process for the production of bacteriocins from Bacillaceae family. *Bioresources and Bioprocessing*. 2020; 7: 1–26.
- [69] Malviya D, Sahu PK, Singh UB, Paul S, Gupta A, Gupta AR, *et al.* Lesson from Ecotoxicity: Revisiting the Microbial Lipopeptides for the Management of Emerging Diseases for Crop Protection. *International Journal of Environmental Research and Public Health*. 2020; 17: 1434.
- [70] Lübeck M, Lübeck PS. Fungal Cell Factories for Efficient and Sustainable Production of Proteins and Peptides. *Microorganisms*. 2022; 10: 753.
- [71] Carro L, Menéndez E. Knock, knock-let the bacteria in: Enzymatic potential of plant associated bacteria. In Vivek, S., Richa S. and Laith K.T.A (eds.) *Molecular Aspects of Plant Beneficial Microbes in Agriculture* (pp. 169–178). Elsevier: Cambridge. 2020.
- [72] Bibi F, Ullah I, Alvi SA, Bakhsh SA, Yasir M, Al-Ghamdi AAK, *et al.* Isolation, diversity, and biotechnological potential of rhizo- and endophytic bacteria associated with mangrove plants from Saudi Arabia. *Genetics and Molecular Research: GMR*. 2017; 16.
- [73] Kalia VC, Patel SKS, Kang YC, Lee JK. Quorum sensing inhibitors as antipathogens: biotechnological applications. *Biotechnology Advances*. 2019; 37: 68–90.
- [74] dos Santos F, de Castro F, Apolonio T, Yoshida L, Martim D, Tessmann D, *et al.* Isolation, diversity, and biotechnological potential of maize (*Zea mays*) grains bacteria. *Genetics and Molecular Research*. 2019; 18.
- [75] Aarti C, Khusro A, Agastian P, Darwish NM, Al Farraj DA. Molecular diversity and hydrolytic enzymes production abilities of soil bacteria. *Saudi Journal of Biological Sciences*. 2020; 27: 3235–3248.
- [76] Hashem A, Tabassum B, Fathi Abd Allah E. *Bacillus subtilis*: A plant-growth promoting rhizobacterium that also impacts biotic stress. *Saudi Journal of Biological Sciences*. 2019; 26: 1291–1297.
- [77] Bhutani N, Maheshwari R, Kumar P, Dahiya R, Suneja P. Bio-prospecting for extracellular enzymes from endophytic bacteria isolated from *Vigna radiata* and *Cajanus cajan*. *Journal of Applied Biology & Biotechnology*. 2021; 9: 26–34.
- [78] Akeed Y, Atrash F, Naffaa W. Partial purification and characterization of chitinase produced by *Bacillus licheniformis* B307. *Heliyon*. 2020; 6: e03858.
- [79] Admassie M, Woldehawariat Y, Alemu T. In Vitro Evaluation of Extracellular Enzyme Activity and Its Biocontrol Efficacy of Bacterial Isolates from Pepper Plants for the Management of *Phytophthora capsici*. *BioMed Research International*. 2022; 2022: 6778352.
- [80] Sharma CK, Vishnoi VK, Dubey R, Maheshwari D. A twin rhizospheric bacterial consortium induces systemic resistance to a phytopathogen *Macrophomina phaseolina* in mung bean. *Rhizosphere*. 2018; 5: 71–75.
- [81] Kim YH, Park SK, Hur JY, Kim YC. Purification and Characterization of a Major Extracellular Chitinase from a Biocontrol Bacterium, *Paenibacillus elgii* HOA73. *The Plant Pathology Journal*. 2017; 33: 318–328.
- [82] Umar AA, Hussaini AB, Yahayya J, Sani I, Aminu H. Chitinolytic and Antagonistic Activity of *Streptomyces* Isolated from Fadama Soil against Phytopathogenic Fungi. *Tropical Life Sciences Research*. 2021; 32: 25–38.
- [83] Ekundayo FO, Folorunsho AE, Ibisani TA, Olabanji OB. Antifungal activity of chitinase produced by *Streptomyces* species isolated from grassland soils in Futa Area, Akure. *Bulletin of the National Research Centre*. 2022; 46: 1–14.
- [84] Abo-Zaid G, Abdelkhalek A, Matar S, Darwish M, Abdel-Gayed M. Application of Bio-Friendly Formulations of Chitinase-Producing *Streptomyces cellulosa* Actino 48 for Controlling Peanut Soil-Borne Diseases Caused by *Sclerotium rolfsii*. *Journal of Fungi (Basel, Switzerland)*. 2021; 7: 167.
- [85] Negi YK, Prabha D, Garg SK, Kumar J. Biological control of ragi blast disease by chitinase producing fluorescent *Pseudomonas* isolates. *Organic Agriculture*. 2017; 7: 63–71.
- [86] Dhoub H, Zouari I, Abdallah DB, Belbahri L, Taktak W, Triki MA, *et al.* Potential of a novel endophytic *Bacillus velezensis* in tomato growth promotion and protection against *Verticillium* wilt disease. *Biological Control*. 2019; 139: 104092.
- [87] Myo EM, Liu B, Ma J, Shi L, Jiang M, Zhang K, *et al.* Evaluation of *Bacillus velezensis* NKG-2 for bio-control activities against fungal diseases and potential plant growth promotion. *Biological Control*. 2019; 134: 23–31.
- [88] Jangir M, Pathak R, Sharma S, Sharma S. Biocontrol mechanisms of *Bacillus* sp., isolated from tomato rhizosphere, against *Fusarium oxysporum* f. sp. *lycopersici*. *Biological Control*. 2018; 123: 60–70.
- [89] El-Bendary MA, Hamed HA, Moharam ME. Potential of *Bacillus* isolates as bio-control agents against some fungal phytopathogens. *Biocatalysis and Agricultural Biotechnology*. 2016; 5: 173–178.
- [90] Douriet-Gámez NR, Maldonado-Mendoza IE, Ibarra-Laclette E, Blom J, Calderón-Vázquez CL. Genomic Analysis of *Bacillus* sp. Strain B25, a Biocontrol Agent of Maize Pathogen *Fusarium verticillioides*. *Current Microbiology*. 2018; 75: 247–255.
- [91] San Fulgencio NS, Suárez-Estrella F, López M, Jurado M, López-González J, Moreno J. Biotic aspects involved in the control of damping-off producing agents: the role of the thermotolerant microbiota isolated from composting of plant waste. *Biological Control*. 2018; 124: 82–91.
- [92] John CJ, Radhakrishnan E. Chemicobiological insight into anti-phytopathogenic properties of rhizospheric *Serratia plymuthica* R51. *Proceedings of the National Academy of Sciences, India Section B: Biological Sciences*. 2018; 88: 1629–1635.
- [93] Malik MS, Haider S, Rehman A, Rehman SU, Jamil M, Naz I, *et al.* Biological control of fungal pathogens of tomato (*Lycopersicon esculentum*) by chitinolytic bacterial strains. *Journal of Basic Microbiology*. 2022; 62: 48–62.
- [94] Khan N, Martínez-Hidalgo P, Ice TA, Maymon M, Humm EA, Nejat N, *et al.* Antifungal Activity of *Bacillus* Species Against *Fusarium* and Analysis of the Potential Mechanisms Used in Biocontrol. *Frontiers in Microbiology*. 2018; 9: 2363.
- [95] Kim JA, Song JS, Kim PI, Kim DH, Kim Y. *Bacillus velezensis* TSA32-1 as a Promising Agent for Biocontrol of Plant Pathogenic Fungi. *Journal of Fungi (Basel, Switzerland)*. 2022; 8: 1053.
- [96] Ashwini N, Srividya S. Potentiality of *Bacillus subtilis* as bio-control agent for management of anthracnose disease of chilli caused by *Colletotrichum gloeosporioides* OGC1. *3 Biotech*. 2014; 4: 127–136.

- [97] Gómez-Lama Cabanás C, Legarda G, Ruano-Rosa D, Pizarro-Tobías P, Valverde-Corredor A, Niqui JL, *et al.* Indigenous *Pseudomonas* spp. Strains from the Olive (*Olea europaea* L.) Rhizosphere as Effective Biocontrol Agents against *Verticillium dahliae*: From the Host Roots to the Bacterial Genomes. *Frontiers in Microbiology*. 2018; 9: 277.
- [98] Ren JH, Li H, Wang YF, Ye JR, Yan AQ, Wu XQ. Biocontrol potential of an endophytic *Bacillus pumilus* JK-SX001 against poplar canker. *Biological Control*. 2013; 67: 421–430.
- [99] Hu H, Gao Y, Li X, Chen S, Yan S, Tian X. Identification and Nematicidal Characterization of Proteases Secreted by Endophytic Bacteria *Bacillus cereus* BCM2. *Phytopathology*. 2020; 110: 336–344.
- [100] Li L, Sun Y, Chen F, Hao D, Tan J. An alkaline protease from *Bacillus cereus* NJSZ-13 can act as a pathogenicity factor in infection of pinewood nematode. *BMC Microbiology*. 2023; 23: 10.
- [101] Ghadamgahi F, Tarighi S, Taheri P, Saripella GV, Anzalone A, Kalyandurg PB, *et al.* Plant Growth-Promoting Activity of *Pseudomonas aeruginosa* FG106 and Its Ability to Act as a Biocontrol Agent against Potato, Tomato and Taro Pathogens. *Biology*. 2022; 11: 140.
- [102] Abo-Elyousr KAM, Abdel-Rahim IR, Almasoudi NM, Alghamdi SA. Native Endophytic *Pseudomonas putida* as a Biocontrol Agent against Common Bean Rust Caused by *Uromyces appendiculatus*. *Journal of Fungi (Basel, Switzerland)*. 2021; 7: 745.
- [103] Huang Q, Liu H, Zhang J, Wang S, Liu F, Li C, *et al.* Production of extracellular amylase contributes to the colonization of *Bacillus cereus* 0-9 in wheat roots. *BMC Microbiology*. 2022; 22: 205.
- [104] Hazarika DJ, Goswami G, Gautom T, Parveen A, Das P, Barooah M, *et al.* Lipopeptide mediated biocontrol activity of endophytic *Bacillus subtilis* against fungal phytopathogens. *BMC Microbiology*. 2019; 19: 71.
- [105] Agarwal H, Dowarah B, Baruah PM, Bordoloi KS, Krishnatreya DB, Agarwala N. Endophytes from *Gnetum gnemon* L. can protect seedlings against the infection of phytopathogenic bacterium *Ralstonia solanacearum* as well as promote plant growth in tomato. *Microbiological Research*. 2020; 238: 126503.
- [106] Mekonnen H, Kibret M, Assefa F. Plant Growth Promoting Rhizobacteria for Biocontrol of Tomato Bacterial Wilt Caused by *Ralstonia solanacearum*. *International Journal of Agronomy*. 2022.
- [107] Mohammed AF, Oloyede AR, Odeseye AO. Biological control of bacterial wilt of tomato caused by *Ralstonia solanacearum* using *Pseudomonas* species isolated from the rhizosphere of tomato plants. *Archives of Phytopathology and Plant Protection*. 2020; 53: 1–16.
- [108] Tran TN, Doan CT, Nguyen MT, Nguyen VB, Vo TPK, Nguyen AD, *et al.* An Exochitinase with *N*-Acetyl- $\beta$ -Glucosaminidase-Like Activity from Shrimp Head Conversion by *Streptomyces speibonae* and Its Application in Hydrolyzing  $\beta$ -Chitin Powder to Produce *N*-Acetyl-d-Glucosamine. *Polymers*. 2019; 11: 1600.
- [109] Gasmí M, Kitouni M, Carro L, Pujic P, Normand P, Boubakri H. Chitinolytic actinobacteria isolated from an Algerian semi-arid soil: development of an antifungal chitinase-dependent assay and GH18 chitinase gene identification. *Annals of Microbiology*. 2019; 69: 395–405.
- [110] Jayasekara S, Ratnayake R. Microbial cellulases: an overview and applications. *Cellulose*. 2019; 22: 92.
- [111] Jiang CH, Liao MJ, Wang HK, Zheng MZ, Xu JJ, Guo JH. *Bacillus velezensis*, a potential and efficient biocontrol agent in control of pepper gray mold caused by *Botrytis cinerea*. *Biological Control*. 2018; 126: 147–157.
- [112] Yanti Y, Hamid H. Biochemical characterizations of selected indigenous endophytic bacteria potential as growth promoters and biocontrol agents on Tomato. In *IOP Conference Series: Earth and Environmental Science*. IOP Publishing. 2021; 757: 012002.
- [113] Solanki P, Putatunda C, Kumar A, Bhatia R, Walia A. Microbial proteases: ubiquitous enzymes with innumerable uses. *3 Biotech*. 2021; 11: 428.
- [114] Bhatia RK, Ullah S, Hoque MZ, Ahmad I, Yang YH, Bhatt AK, *et al.* Psychrophiles: a source of cold-adapted enzymes for energy efficient biotechnological industrial processes. *Journal of Environmental Chemical Engineering*. 2021; 9: 104607.
- [115] Guleria S, Walia A, Chauhan A, Shirkot CK. Molecular characterization of alkaline protease of *Bacillus amyloliquefaciens* SP1 involved in biocontrol of *Fusarium oxysporum*. *International Journal of Food Microbiology*. 2016; 232: 134–143.
- [116] Ji ZL, Peng S, Chen LL, Liu Y, Yan C, Zhu F. Identification and characterization of a serine protease from *Bacillus licheniformis* W10: A potential antifungal agent. *International Journal of Biological Macromolecules*. 2020; 145: 594–603.
- [117] Agobo K, Arazu V, Uzo K, Igwe C. Microbial lipases: a prospect for biotechnological industrial catalysis for green products: a review. *Journal of Fermentation Technology*. 2017; 6: 2.
- [118] Gao L, Ma J, Liu Y, Huang Y, Mohamad OAA, Jiang H, *et al.* Diversity and Biocontrol Potential of Cultivable Endophytic Bacteria Associated with Halophytes from the West Aral Sea Basin. *Microorganisms*. 2021; 9: 1448.
- [119] Abed H, Rouag N, Mouatassef D, Rouabhi A. Screening for *Pseudomonas* and *Bacillus* antagonistic rhizobacteria strains for the biocontrol of *Fusarium* wilt of chickpea. *Eurasian Journal of Soil Science*. 2016; 5: 182–191.
- [120] Mota MS, Gomes CB, Souza Júnior IT, Moura AB. Bacterial selection for biological control of plant disease: criterion determination and validation. *Brazilian Journal of Microbiology: [publication of the Brazilian Society for Microbiology]*. 2017; 48: 62–70.
- [121] Azman NA, Sijam K, Hata EM, Othman R, Saud HM. Screening of bacteria as antagonist against *Xanthomonas oryzae* pv. *oryzae*, the causal agent of bacterial leaf blight of paddy and as plant growth promoter. *Journal of Experimental Agriculture International*. 2017; 16: 1–15.
- [122] Anbu P, Gopinath SCB, Chaulagain BP, Lakshmi Priya T. *Microbial Enzymes and Their Applications in Industries and Medicine* 2016. *BioMed Research International*. 2017; 2017: 2195808.
- [123] Passari AK, Mishra VK, Leo VV, Gupta VK, Singh BP. Phytohormone production endowed with antagonistic potential and plant growth promoting abilities of culturable endophytic bacteria isolated from *Clerodendrum colebrookianum* Walp. *Microbiological Research*. 2016; 193: 57–73.
- [124] Jadhav H, Shaikh S, Sayyed R. Role of hydrolytic enzymes of rhizoflora in biocontrol of fungal phytopathogens: an overview. *Rhizotrophs: Plant growth promotion to bioremediation*. 2017; 183–203.
- [125] Wang BT, Hu S, Yu XY, Jin L, Zhu YJ, Jin FJ. Studies of Cellulose and Starch Utilization and the Regulatory Mechanisms of Related Enzymes in Fungi. *Polymers*. 2020; 12: 530.
- [126] Akbarian M, Khani A, Eghbalpour S, Uversky VN. Bioactive Peptides: Synthesis, Sources, Applications, and Proposed Mechanisms of Action. *International Journal of Molecular Sciences*. 2022; 23: 1445.