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Review article

Can we control potato fungal and bacterial diseases? — microbial regulation

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ABSTRACT

The potato plant is one of the main crops in the world. However, relatively little is known about key virulence factors of major fungal and bacterial diseases in potatoes, biocontrol measures to improve activity and stability, and the core driving forces in the control process. Here, we focus on analyzing the mechanisms by which genes, proteins, or (and) metabolites of potato pathogens as key virulence factors. Then, the single strain biocontrol agents, synthetic microbial communities, microbial microcapsule strategies were introduced, and the latter two strategies can improve stability and activity in biocontrol. Meanwhile, summarized the defense mechanisms of biocontrol and their specific issues in practical applications. Furthermore, explore how potato crop management, soil management, and climate effects, as crucial driving forces affect potato biocontrol in the system. Dynamic and systematic research, excavation of biocontrol strain resources, find the causes of regional disease resistance and exploration of biocontrol mechanism will provide promising solutions for biotic stress faced by potato in the future.

1. Introduction

Potato (*Solanum tuberosum* L.) is an important food crop planted worldwide and provides food for more than 1 billion people. However, more and more microbial diseases attack potatoes [1]. Among them, 9 diseases occur globally and are also the main factors that damage the decline in potato quality (Table 1). In addition, relying heavily on fungicides to effectively control diseases will cause unpredictable risks to the environment and lead to resistance of pathogens [2,3]. Pathogens have faster regeneration time, different metabolic pathways and higher resistance. People support using plant protection products and other interventions only at an ecologically reasonable level and need to minimize risks to human health and the environment [4]. As an environment-friendly alternative to disease control, biocontrol has aroused people's interest [5].

Many studies have reported that soil rhizome microbial communities play a vital role in host plants' health and stress resistance [19]. Meanwhile, many beneficial microorganisms have been isolated and used to control potato fungal and bacterial diseases. For

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example, *Bacillus subtilis* V26 can control dry potato rot and potato fusarium wilt [8]. On the other hand, the metabolites secreted by microorganisms are also of great significance to potato fungal and bacterial diseases. For example, The volatile organic compounds released by *Trichoderma* strains can inhibit the mycelial growth of *Phytophthora infestans* [20]. Furthermore, lipopeptide iturin A and fengycin A produced by *Bacillus* spp. can inhibit the growth of hyphae infected with *Phytophthora infestans* in vitro reduce the incidence rate of potato late blight [21]. However, there is currently limited description of the virulence factors of key fungal and bacterial diseases in potatoes. In addition, many current biocontrol methods are prone to losing their activity and stability in complex situations, and we urgently need to find measures to solve this problem. Meanwhile, there is insufficient understanding of the practical applications and driving forces of dynamic changes in biocontrol.

Herein, we summarized the 6 major fungal and bacterial diseases suffered by potatoes. Analysis is mainly conducted using the genes, proteins, or (and) metabolites of pathogens as virulence factors when infecting the host. In addition, we also discussed synthetic microbial communities and microbial microencapsulation technology as complementary strategies to enhance biocontrol activity and stability. Meanwhile, the treatment time and methods, safety, cost of biocontrol are key issues in practical applications. Furthermore, the relevant driving forces in the biocontrol process were discussed in detail, which will improve the efficiency of biocontrol in a systematic and dynamic manner. Finally, we propose that 1) dynamic systematic research, 2) mining biocontrol resources, 3) searching for reasons for regional disease resistance, and 4) further exploration of biocontrol mechanisms are goals and challenges for future development (Fig. 1).

2. The challenges of potato planting—biotic stress

2.1. Fungal pathogens as biotic stress

2.1.1. Late blight

Late blight is one of the most devastating plant diseases [4]. Potatoes infected with late blight initially cause water-soaked lesions on leaves that are small, light to dark green, and round to irregular in shape. Finally, symptoms extend to petioles and stalks, leading to plant death (Fig. 2a,b,c,d) [6]. *Phytophthora infestans* is a devastating pathogen causing late potato blight. It has a sporangia structure that can survive in harsh environments [22].

Understanding the molecular pathogenicity of *Phytophthora infestans* is a key point in managing diseases. *Phytophthora infestans* secrete a large number of pathogenic related molecules to degrade plant cells, overcome host defense, and promote successful invasion. These molecules can play roles both inside and outside the host plant cells [26,27]. For example, *Phytophthora infestans* RXLR effector factors PITG20303 and PITG20300 inhibit potato PAMP (pathogen-associated molecular patterns) triggered immunity (PTI) and promote pathogen colonization by targeting and stabilizing the potato MAPK (mitogen-activated protein kinase) cascade protein StMKK1 [28]. In addition, two effector proteins of *P. infestans*, PexRD2 and Pi22926, have been reported to promote *P. infestans* colonization [29].

Furthermore, it has been found that certain genes in *Phytophthora infestans* are related to their virulence. For example, the predicted 54 amino acid/auxin permease genes in the *P. infestans* genome exhibit activity during tuber infection. However, how amino acid/auxin permease genes are regulated in eukaryotes remains to be elucidated. What's more, the small RNAs encoded by *Phytophthora infestans* can affect potato mRNA, thereby promoting disease occurrence. For example, a single miRNA encoded by *Phytophthora infestans* (miR8788) was found to target a potato lipase-like membrane protein-encoding gene (*StLL1*) localized to the tonoplast. And the miR8788-knockout strain had reduced growth on potatoes compared to the wild-type strain 88,069 [30]. In addition, the emergence of new *Phytophthora infestans* has avoided the detection of the main effector *R* gene in potatoes. Further exploration of the pathogenic mechanism is needed for corresponding biocontrol measures.

Table 1
Types of potato fungal and bacterial diseases infections and related information.

Disease	Pathogens	Bacteria or fungi	References
Late blight	*Phytophthora infestans*	Fungi	[6]
Early blight	*Phytophthora infestans, Alternaria solani, A. grandis, A. alternata*	Fungi	[2,3,7]
Fusarium wilt and Fusarium dry rot	*Fusarium ambucaine, F. solani, F. graminearum, F. oxysporum*	Fungi	[8]
Verticillium wilt	*Verticillium* spp.	Fungi	[5]
Powdery scab	*Spongospora subterranean*, *Streptomyces* spp.	Fungi	[6,9]
Bacterial wilt	*Ralstonia solanacearum*	Bacteria	[10,11]
Soft rot/blackleg disease complex	*Pectobacterium, Pectobacterium Brasiliense, Dickeya, R. solanacearum*	Bacteria	[6]
Common Scab	*Streptomyces scabiei, S. acidiscabiei, S. turgidiscabiei*	Bacteria	[1,12–15]
Zebra chip disease	*Candidatus Liberibacter solanacearum*	Bacteria	[6,16–18]

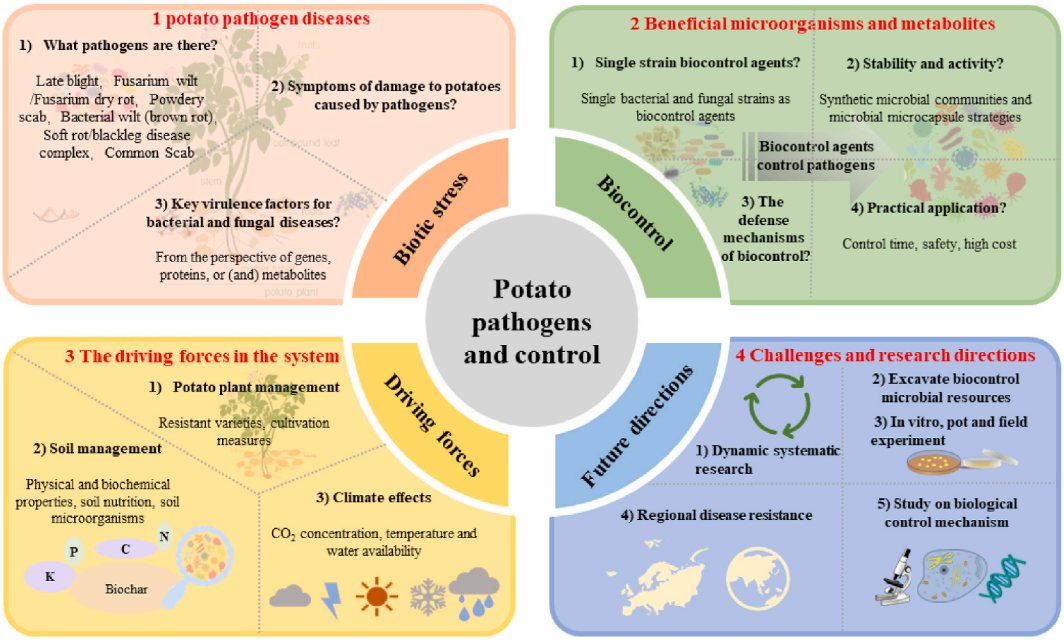

Fig. 1. The main discussion content of this review.

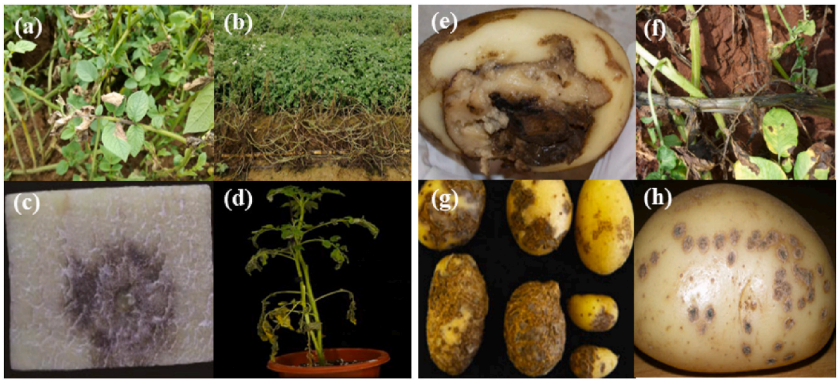

Fig. 2. Symptoms of infection of potato pathogenic diseases. (a) (b) represent late blight infections in the field, (c) represents late blight infection in potato tubers, (d) represents late blight infection in pots, (e) represents soft rot infection in potatoes tubers, (f) represents blackleg infection in the field, (g) represents common scab infection in potato tubers, (h) represents powder scab infection in potato tubers [6,23–25].

2.1.2. Fusarium wilt and fusarium dry rot

Fusarium disease persists worldwide and is prevalent in most potato-growing areas, causing 30–50 % yield loss and reduced tuber quality [31]. Several *Fusarium* species have been implicated in potato crop diseases, including *Fusarium sambucinum*, *F. solani*, *F. graminearum*, *F. proliferatum* and *F. oxysporum* [8]. *Fusarium* enters plants from the root tips and can survive in the soil for up to 30 years. The *Fusarium* mycelium grows in the xylem vessels, cutting off the water supply and causing the plant to wilt. *Fusarium* can also invade the parenchyma of plants, eventually reaching the surface of dead tissue and forming large spores. In addition, vascular wilt pathogens meet their nutritional needs by efficiently acquiring scarce nutrients available in xylem sap, by enzymatic digestion of host cell walls, by invading adjacent cells, or by inducing nutrient leakage from surrounding tissues [32].

The effector proteins secreted by *Fusarium* are virulent factors during the infection process [33]. *Fusarium* regulates host innate immunity and induces host cell death by transmitting effector proteins. For example, the FGL1 lipase secreted by *Fusarium graminearum*, an effector protein, can induce the release of free fatty acids, inhibit the formation of plant immune related callose, and thus promote infection. In addition, the deletion of ribonuclease Fg12 (an effector protein) secreted by *Fusarium graminearum* reduced its virulence. Fg12 has ribonuclease activity and can degrade total RNA. Therefore, Fg12 not only contributes to the virulence of pathogens, but also induces plant cell death [34]. Furthermore, ECM33 is a glycosylphosphatidylinositol (GPI)-anchored protein essential for fungal development and infection by regulating fungal cell wall integrity. For example, FocECM33, is required for vegetative growth and virulence in *Fusarium oxysporum*. FocECM33 appears to promote the virulence of *Fusarium oxysporum* by regulating hyphal

growth, reactive oxygen species production and chitin synthesis [35].

Fusarium also produces depolymerizing enzymes and mycotoxins as virulence factors during the infection process. For example, *Fusarium graminearum* enhances its penetration and proliferation in the host by producing pectinase, amylase, cellulase, xylanase, protease, and lipase. Furthermore, *Fusarium* produces mycotoxins as virulence factors. For example, trichothecene causes various host defense reactions, including hydrogen peroxide production and programmed cell death [36]. The *Tri5* gene encodes trichodiene synthase, which converts farnesyl diphosphate into trichodiene. Mutants lacking the *Tri5* gene, due to their inability to produce trichothecene, significantly reduce their infection rate against wheat [37]. And different isolates of *Fusarium* have different trichothecene profiles [38].

From the perspective of pathogenic genes of *Fusarium*, the pathogenic genes of *Fusarium* can be divided into two categories: one is the basic pathogenic genes shared by *Fusarium* and other pathogenic fungi, the other is the special pathogenic genes. In most cases, the pathogenic genes of *Fusarium* are unique to a single *Fusarium* species on a specific host. Research has found that over 100 genes can specifically alter the virulence of *Fusarium graminearum*. These include *Secreted In Xylem* (*SIX*) genes, which encodes small effector proteins secreted by *F. oxysporum* during tomato plant infection [38].

Further revealing the host process targeted by effector factors is a key issue for future research. In addition, due to the high genetic variability and wide host specificity of *Fusarium*, detailed molecular mechanisms of pathogenicity at different species and strain levels need to be studied, especially in the current lack of relevant research on *Fusarium solani* and *Fusarium proliferatum*.

2.1.3. Powdery scab

Powdery scab symptoms include lesions on the tuber surface and root galling (Fig. 2h). The symptoms of common potato scab and powdery scab are indistinguishable. Therefore, accurate identification of symptoms is critical for disease management and control [6]. Powdery scab caused by *Spongiospora subterranean*. The life cycle of *Spongospora subterranea* involves the germination of dormant spores that first overwinter to release zoospores. Subsequently, the zoospores swim to the roots, penetrate and infect the epidermal cells or root hairs, producing the multinucleated spore *Plasmodium*, which develops within the root and is enclosed in multinucleated compartments, eventually forming the zoosporangium. Zoospores are confined to the soil and only infect nearby hosts. Therefore, potato tubers are the primary source of inoculation leading to the long-distance spread of pathogens to new areas [9].

Spongospora subterranea is a soil borne pathogen, its key is to dormant propagules to continuously germinate in the soil environment. Further research has found that cell wall cytoskeleton, host root exudates, water retention capacity, and ions are key factors in the germination of propagules. For example, both actin and beta tubulin proteins are downregulated in germinating spores, indicating that changes in the cell wall cytoskeleton may be a necessary condition for morphological changes during the germination process of resting spores [39]. However, how proteins participate in the subsequent steps of spore germination is another important issue that needs to be addressed. Furthermore, the migration of *Spongospora subterranea* zoospores to the roots of susceptible hosts may be triggered by chemotactic attraction of root exudates. Various compounds were detected in potato root exudates, including L-glutamine, tyramine, *N*-acetylcysteine, L-serine, citrulline, L-rhamnose, cellobiose, L-aspartic acid, piperazine, glucuronic acid, succinic acid and citric acid. They can stimulate the *Spongospora subterranea* germination [40,41]. In addition, the incidence rate of tuber disease will increase in soil with high water retention capacity, because the movement of zoospores to host roots will also increase in the presence of abundant water. Meanwhile, the influx and signal transmission of ions play an important role in the convergence and encapsulation of zoospores. Therefore, understanding the effects of ion influx and signal transduction on *Spongospora subterranea* can further control its disease occurrence [42].

Further research is needed on the factors that affect the movement or attraction of zoospores towards the host. In addition, the study of the characteristics of root exudates that stimulate static spore germination and/or attract zoospores to host roots will provide important biological knowledge of host pathogen interactions.

2.2. Bacterial pathogens as biotic stress

2.2.1. Bacterial wilt (brown rot)

Bacterial wilt (or brown rot) is a severe disease of potatoes that can result in substantial yield losses [6]. Bacterial wilt is caused by members of the *Ralstonia solanacearum* species complex. *Ralstonia solanacearum* species complex has a broad geographic distribution and host range. Members of the global *Ralstonia solanacearum* species complex were previously assigned to four phylotypes, each of which was primarily associated with a geographical region (phylotype I strain from Asia, phylotype IIA and IIB strain from the Americas, phylotype III strains from Africa and Mayotte Island, and phylotype IV strains from Australia, Indonesia and Japan) [43]. The IIB1 type strain is highly destructive, hardy and persistent, causing latent infection in tubers [6].

The main virulence factor of *R. solanacearum* is the Type III Secretory System (T3SS), which can transmit effector proteins (T3Es) within plant cells. T3Es cause disease in multiple ways. T3Es can interfere with the basic immunity of plants, interfere with different metabolic processes of hosts, trigger plant immune responses, and prevent other effectors from being recognized by plants [44]. In addition, *R. Solanacearum* can enhance the biosynthesis of virulence factors by utilizing host plant metabolites. For example, the L-glutamic acid of the host plant is a key active component that enhances the extracellular polysaccharide production, cellulase activity, swimming activity, and biofilm formation of *Ralstonia solanacearum*. L-glutamic acid also promotes the colonization of *R. solanacearum* in the roots and stems of tomato plants, accelerating the occurrence of diseases. RS01577, a hybrid sensor histidine kinase/response regulator is involved in the L-glutamate signal transduction of *R. solanacearum* [45]. Another key determinant of virulence is extracellular polymeric substances (EPS). EPS can cause blockage of xylem ducts, leading to plant symptoms, and can also bind to cell walls, protecting bacteria from the influence of plant defense [46]. Furthermore, A quorum sensing (QS) system RasI/R was

identified in *R. solanacearum*. This QS system generates and responds to QS signals, thereby regulating the survival and infection ability of *R. solanacearum* [47].

Interestingly, *R. solanacearum* can spontaneously convert (PC) from wild type to non-pathogenic. It reduces virulence by reducing extracellular polysaccharides, endoglucanase, pectin methylesterase activities, enhancing polygalacturonase activity and motility. Pre-inoculation of PC mutants in nightshade plants suppresses bacterial wilt. However, the control effect differs depending on the pre-inoculation method of the PC mutant [48].

On the other hand, research has found that some genes of *R. solanacearum* affect their invasion of the host. For example, the *pili, chpA, pilA,* and *fliC* genes of *R. solanacearum* play important roles in twitching motility, biofilm formation, natural transformation, and virulence [49]. However, the genes of *R. solanacearum* are dynamic during the infection process. Identifying the conditional specific expression of virulence and metabolic genes will provide a new dynamic perspective for the *R. solanacearum* infection process.

2.2.2. Soft rot/blackleg disease complex

The soft rotting causes systemic and vascular infections in potatoes. Symptoms of soft rot and blackleg are curled upper leaves, compact, small leaves, and green to yellow-green leaves, followed by blackleg symptoms on the lower stems. Affected plants have slimy, rotting, jet black or dark mushy stems when pulled (Fig. 2e (f)) [50]. Soft rot occurs when bacteria from contaminated seed potatoes spread upward in the stem [6]. Soft rot/blackleg complex caused by *Pectobacterium* and *Dickeya* species [6]. *P. carotovorum*, *P. brasiliense*, *P. parmentieri* and *P. odoriferum* are the primary pathogens causing soft rot in Chinese potatoes [51]. From a simple perspective of virulence level, the pathogenicity of *P. carotovorum* and *P. brasiliense* increased with increasing temperature. When *P. carotovorum* was co-inoculated with *P. brasiliense*, its pathogenicity was more severe, especially when the former showed an advantage in initial bacterial numbers [51].

Pectinobacteria mainly rely on the secretion of extracellular cell wall degrading enzymes, such as proteases, pectinases, and cellulases to exert their virulence effects. These enzymes can damage plant cell walls, leading to soaking or decay of tuber tissue [52]. For example, the cell wall degrading enzyme activity of *P. carotovorum* was higher than that of *P. brasiliense*, which brought more severe disease symptoms to potato tubers [51]. Meanwhile, the virulence of pathogens is often associated with the Type III secretion system (T3SS). And *D. dianthicola* strains with a T3SS may have an advantage over *P. parmentieri* that lacks the T3SS [52].

The virulence factors of *Pectinobacterium* and *Dickeya* also include the formation of biofilms, the production of siderophores, exopolysaccharide and the presence of lipopolysaccharides (LPSs). For example, exopolysaccharide purified from *Pectinobacterium actinidiae* (PCAP-1a) was found to induce rapid cell death in dicotyledonous plants, serving as a polysaccharide inducer to induce plant immunity. A series of PAMP triggered immunity (PTI) reactions are triggered, including the production of reactive oxygen species, phosphorylation of MAPK, and gene transcription reprogramming [53]. Furthermore, extracellular polysaccharides (Pba EPS) produced by *Pectinobacterium aerosepticum* can maintain the integrity of its own embolic structure. Pba-EPS can also scavenge reactive oxygen species and inhibit host plant PAMP induced responses [54]. In addition, the outer sugar portion of LPSs, namely O-polysaccharides (OPSs), is crucial for their virulence. OPSs help pathogens develop resistance to antimicrobial compounds, which may enhance their ability to infect plants [52].

On the other hand, a single gene will enable *Pectinobacterium* to overcome the host's chemical defense system. For example, The *tolC* gene reduces the sensitivity of *Pectinobacterium* to plant chemicals such as berberine, rhein, and genistein. And the deletion of *saxA* gene in *Pectinobacterium* can greatly reduce its virulence [55].

2.2.3. Common scab

Potato common scab is a disease affecting potatoes worldwide [12]. The symptoms of common potato scabs are mainly raised and/or depressed scabs on the surface of the tuber (Fig. 2g) [13–15]. Common potato scabs are mainly caused by *Streptomyces scabies*, *S. acidiscabiei* and *S. turgidiscabiei* [15]. The main virulence factors of *Streptomyces* include phytotoxins (thaxtomin A, concanamycins, coronafucosoyl phytoxins), secret protein (Nec1, TomA, Scabin), and phytohormones (cytokinins, IAA). Among them, thaxtomin A is the main pathogenic factor [56].

Thaxtomin A is a nitrodi peptide that inhibits cellulose synthesis, leading to defects in plant cell walls [13,57]. Understanding the biosynthesis of thaxtomin A is the primary condition for discovering their pathogenic mechanism. Tryptophan is the biosynthetic precursor of thaxtomin A. The addition of tryptophan to the medium inhibits thaxtomin A biosynthesis. Meanwhile, the expression of thaxtomin A biosynthesis genes *nos* and *txtA* was strongly inhibited when tryptophan was contained. Addition of tryptophan relieves disease symptoms by inhibiting thaxtomin A production and increasing IAA biosynthesis [58]. Furthermore, it has been found that the biosynthesis of thaxtomin involves conserved non-ribosomal peptide synthetases encoded by the *txtA* and *txtB* genes. The *txtA* and *txtB* genes are located on mobile pathogenic islands (PAIs) in the genome of *Streptomyces*. Horizontal gene transfer of PAI is responsible for the emergence of new pathogenic *Streptomyces* species [14,59]. On the other hand, exploring the regulatory mechanisms of thaxtomin A is also crucial. β-glucosidase targets both cello-oligosaccharide elicitors emanating from the hosts of *Streptomyces scabies*, and the scopolin phytoalexin generated by the host defense mechanisms, thereby occupying a key position to fine-tune the production of the main virulence determinant thaxtomin A [60]. However, more details on regulating thaxtomin A need to be further explored. Interestingly, some *Streptomyces* do not produce thaxtomin A, while produce other phytotoxins. For example, *Streptomyces* sp. 11-1-2 produces nigericin and geldanamycin. And adding *N*-acetylglucosamine to the culture medium can inhibit the biosynthesis of these two metabolites. Nigericin and geldanamycin have phytotoxic effects on radish seedlings and potato tuber tissues. And the combined application of the two compounds had a greater phytotoxic effect on potato tuber tissue than the single application [61].

Secret protein is another virulence factor of *Streptomyces*. For example, *S. scabiei* facilitates the penetration of pathogenic bacteria into host plant tissues by secreting an esterase that degrades suberin, a lipid biopolymer of potato peel [62]. In addition, *nec1* gene

encodes a 16 kDa secreted protein that exhibits necrotic activity in excised potato tissue. In plant bioassay using *Arabidopsis*, tobacco, and radish as hosts, the deletion of the *nec1* gene significantly reduced its virulence, and the mutant's ability to actively colonize radish roots was compromised [56]. However, the specific targets and functions of Nec1 are still unclear. Some speculate that Nec1 plays a role in the early stages of infection and may be involved in inhibiting plant defense responses.

3. Conservation strategies for potato plants—biocontrol

Biocontrol is a green measure for controlling potato pathogen diseases. More and more biocontrol strains have been discovered through high-throughput sequencing and isolation culture (Table 2). However, there are some questions. (1) Activity and stability in biocontrol. (2) What are the mechanisms of biocontrol? (3) What should be paid attention to in practical application?

3.1. Multiple strategies for biocontrol

3.1.1. Biocontrol strategies for single microbial

3.1.1.1. Beneficial fungi as biocontrol agents. Due to the potential biological activity of fungi, they have always received widespread attention. More and more fungi have been discovered by researchers and are attempting to understand their activity mechanisms. *Phomopsis liquidambaris* is a root symbiotic endophytic fungus that has beneficial effects on plants. Research has found that *Phomopsis liquidambaris* reduced the incidence rate of rice spikelet rot and fumonisin accumulation by 21.5 % and 9.3 %, respectively. *Phomopsis liquidambaris* reshaped the microbial community of rice by altering the metabolites hordenine and L-aspartic acid in spikelets, supporting the growth of the functional core microorganism *Pseudomonas*, inhibiting the growth of pathogens and the production of mycotoxins [73]. In addition, the use of yeast has always been one of the promising alternative methods for managing post harvest fungal diseases. Research has shown that antagonistic yeast *Wickerhamyces anomalus* can control *Alternaria tenuissima*. The control effect is achieved by inducing the expression of defense related genes such as polyphenol oxidase, peroxidase, β-1,3-glucanase, and increasing the levels of flavonoids and lignin in potato tubers [74]. Furthermore, *Trichoderma*, which exists in almost all types of soil, has the potential to resist pathogenic microorganisms and exists under a wide range of temperature conditions [2]. The volatile organic compounds released by *Trichoderma strains* T41 and T45 can inhibit the mycelial growth of *Phytophthora infestans* [20]. Meanwhile, *Aspergillus* is widely distributed in nature and has been reported to have biocontrol capabilities. For example, ergosterol, β-sitosterol, 5-pentadecylresorcinol, 5-hydroxymethyl-2-furancarboxylic acid, and succinimide were isolated from *Aspergillus niger* spore powder. Among them, 5-hydroxymethyl-2-furancarboxylic acid showed the most effective antibacterial activity against *Agrobacterium tumefaciens* T-37, *Erwinia carotovora* EC-1, and *Ralstonia solanacearum* RS-2 [72].

3.1.1.2. Beneficial bacteria as biocontrol agents. Due to the various advantages of bacteria, the current biocontrol is mainly focused on bacteria. Here we have summarized some bacteria with good biocontrol effects. *Bacillus* is a potential and sustainable strain that can persistently resist multiple pathogens [75]. The volatile organic compounds produced by *Bacillus velezensis* C16LPs exhibited considerable antagonistic activity against *A. solani*, with reduced colony diameter and significant inhibition of conidial germination [21]. Furthermore, lipopeptide biosurfactants (LPs) are the main class of antibiotics produced by *Bacillus* and have lytic, growth-inhibitory activity against a variety of fungi. There are three families of LPs, namely surfactins, iturins and fengycins. Fengycins are active against *Fusarium graminearum*, *Botrytis cinerea*, *Podosphaera fusca*. Iturins are active against *Colletotrichum deemiatium*, *Penicillium roqueforti*, *Aspergillus flavus*, *Rhizoctonia solani*. In addition, *Bacillus subtilis* spores contain 5%–15 % dipicolinic acid (DPA) (w/w). DPA is a novel broad-spectrum antifungal metabolite whose mode of action is based on chitin synthesis inhibition [66].

Pseudomonas spp. is a soil borne gram negative bacterium that produces antibiotics to achieve biocontrol of plant diseases. Research has found that *Pseudomonas fluorescens* VUPf5 can control *Gaeumannomys graminis* in wheat [76]. The most common antibiotics produced by *Pseudomonas* include pyrrolidone, 2,4-diacetyl-phenylenetriazole, and phenazine [77,78]. And the sulfur-containing volatile organic compounds released by *Pseudomonas* can inhibit the mycelial growth of *Phytophthora infestans* [20].

Table 2
Types of beneficial microorganisms that control pathogen diseases.

Beneficial microorganisms	Disease name	Pathogens	References
Serendipita herbaman, *Funneliformis mosseae*, *Bacillus amyloliquefaciens*, *B. velezensis*, *B. subtilis*, *B. mojavensis*, *Trichoderma harzianum*	Fusarium wilt/ dry rot	*Fusarium oxysporum*, *Fusarium equiseti*, *Fusarium solani*	[8,31,63,64]
Lactobacillus paracasei	Soft rot	*Pectobacterium carotovorum*	[65]
Bacillus subtilis	Fungal plant diseases	*Ceratocystis fimbriata*	[66]
Paenibacillus polymyxa, *Lactobacillus plantarum*	Tomato gray mold	*Botrytis cinerea*	[67,68]
Bacillus subtilis h-13, *B. subtilis*-I 5-12/23, *Streptomyces*, *Pseudomonas*, *Saccharothrix*, *Nocardiopsis*	Late blight	*Phytophthora infestans*	[22,69]
Bacillus velezensis SEB1, *Bacillus subtilis* BS-01, *B. siamensis strain* LZ88	Early blight	*Alternaria alternata*	[7,70,71]
Bacillus subtilis NCD-2	Verticillium wilt	*Verticillium* spp.	[5]
Aspergillus niger xj	Brown rot	*Ralstonia solanacearum*	[72]

Pantoea agglomerans ZJU23 was isolated from *Fusarium graminearum* perithecia and displayed the highest antagonistic activity towards mycelial growth of *Fusarium graminearum*. Herbicolin A, the key antifungal compound secreted by *Pantoea agglomerans* ZJU23, acts antifungal by directly binding and destroying lipid rafts containing ergosterol [79].

Stenotrophomonas maltophilia had significant disease inhibition effect after being applied to rice seed treatment and leaf spray treatment, and the disease was reduced to 55.6 % and 47.9 % [80]. The biocontrol effect of *Stenotrophomonas maltohilia* can be attributed to the direct mechanism of alkaline serine proteolytic enzyme production, and indirectly by inducing acquired resistance in the host system [81].

Fungichromin produced by *Streptomyces padanus* PMS-702 inhibited the release of zoospores by *Phytophthora infestans*. *Streptomyces* sp. FXP04, obtained from the rhizosphere soil of potato plants, can significantly inhibit the in vitro growth of *P. interans*, and reduce the incidence of disease and the disease index of potato late blight. In addition, the existence of piericidin A was determined from *Streptomyces* sp. FXP04. It can inhibit the growth of the mycelium of inflammatory bacteria [20].

Lactobacillus strains are capable of producing a variety of antimicrobial compounds, such as organic acids (including lactic and phenylacetic acid), diacetyl, hydrogen peroxide, and bacteriocins, which create a relatively harsh environment for any pathogen [82].

Serratia spp. is a gram negative bacterium typically associated with the roots of plants and is considered a beneficial rhizosphere bacterium with antifungal activity. For example, *Serratia marcescens* has been reported to have biocontrol effects on nematodes and fungi under greenhouse conditions, as well as promoting rhizosphere growth [83,84].

In addition, Dipyridyl formic acid extracted from *Paenibacillus aminolyticus* KMCLE06 as an effective antibacterial compound has significant inhibitory activity against both gram negative and gram positive bacteria [85]. And *Acinetobacter calcoaceticus* produces several antifungal agents and growth promoters under in vitro conditions, which increase the germination rate of seeds and the growth parameters of seedlings [86]. *Arthrobacter* spp. is known to inhibit plant pathogens. *Arthrobacter* spp. isolated from disease inhibiting marine compost can inhibit the growth of *Botrytis cinerea*, *Alternaria alternata*, *Fusarium sambucinum*, *Verticillium dahliae*, and *Pythium sulcatum*. The secondary metabolites produced by *Arthrobacter* spp. play a crucial role in their antibacterial properties [87–89].

3.1.2. Biocontrol strategies for synthetic microbial communities

However, most of the potential biocontrol agents mentioned above are only effective in laboratory or in vitro experiments, and due to differences in climate and soil, the stability and activity of biocontrol cannot be guaranteed in vivo experiments. These biocontrol agents are easily eliminated by local microorganisms and become ineffective [90]. Therefore, we need to take measures to improve the stability and activity of biocontrol agents.

The progress of next-generation sequencing methods indicates that soil inhibiting diseases is formed by the synergistic effect of microbial complexes, rather than by individual microbial strains [22]. Currently, attempts have been made to introduce synthetic communities (SynCom) that include multiple microbial strains into sterile or non inhibitory soils [91]. The key to synthesizing a community is to optimize its ability to inhibit pathogens using core microorganisms, which have an inhibitory effect that exceeds that of single strains and randomly formed microbial communities [92]. Studies have found that the optimized synthetic community exhibits a unique cooperative pattern, including key strains that have inhibitory effects on pathogenic microorganisms through the synthesis of antagonistic substances, while other members enhance their function by promoting the growth of key strains and plant growth [93].

However, due to the complexity of synthetic communities, forming communities and identifying their interactions is particularly challenging. Many studies have investigated the interactions between microbial community members in vitro, but due to differences in spatial and nutritional environments, these observations are difficult to translate into host related backgrounds [94,95]. In addition, many studies on the interaction between microorganisms are analyzed through collinear networks. An inherent drawback of all collinear network methods is that they infer ecological correlations based on abundance correlations, and therefore cannot prove direct interactions [73,94].

3.1.3. Biocontrol strategies combined with microcapsule technology

The goal of microcapsules is to generate a microenvironment to improve the survival rate of biocontrol agents during processing and storage, and to control the release of bioactive components at appropriate locations and times [96–98]. Chitosan reduces plant diseases by disrupting the plasma membrane of pathogens, interacting with pathogen DNA and RNA, metal chelating ability, deposition on pathogen surfaces, and inducing plant defense responses [99]. Chitosan can be used for encapsulation of biocontrol agents, and its encapsulation has good degradability and storage activity [100,101]. Furthermore, greenhouse experiments have shown that compared to free *Streptomyces fulvissimus*, encapsulated *Streptomyces fulvissimus* significantly reduces cucumber diseases and has a greater potential impact on increasing plant growth traits [102]. And after encapsulating *Pseudomonas* with alginate-whey protein microcapsules, potato showed 70 % reduction in the incidence of *Rhizotonia* disease [103]. Furthermore, greenhouse experiments have shown that alginate-whey protein concentrate (Alg-WPC) can enhance the ability of *Pseudomonas fluorescens* VUPF506 to survive [104].

However, microcapsule technology still has many limitations in encapsulating biocontrol agents. (1) Carbohydrate biopolymers are prone to microbial degradation, thereby reducing the long shelf life of biocontrol agents. (2) It is necessary to further understand the effects of different extraction sources, different contents and structures, and non-standard extraction and purification methods on their physicochemical properties [105–107]. (3) The efficiency of purifying polymers from natural raw materials is low and expensive. (4) It is necessary to explore substances that can endow capsules with additional functions, rather than just maintaining stability [100]. (5) Further exploration is needed on the interaction between capsule matrix and the physicochemical properties of soil or leaf rings, as well as the information on their interaction with agricultural ecosystems.

3.2. The defense mechanisms of biocontrol

On the basis of adopting appropriate biocontrol strategies, it is also necessary to understand the defense mechanisms of biocontrol. Biocontrol agents exert protective effects on host plants through various pathways. (Fig. 3). Firstly, biocontrol agents can compete with pathogens for limited nutrition and space (Fig. 3b). Among them, iron competition is an important biocontrol mechanism. For example, by creating iron-chelating ligands or siderophores, *Metschnikowia* yeast can successfully resist the development of various bacteria, yeast, and filamentous fungi [108,109]. In addition, under iron stress conditions, the siderophore chelates of *Pseudomonas aeruginosa* FP6 chelates iron in the soil, thereby negatively affecting the growth of several fungal pathogens [110].

On the other hand, biocontrol agents enhance their effectiveness by interacting with pathogens. Biocontrol agents can not only inhibit the growth of fungal hyphae and spore germination of pathogens, but also affect DNA processing enzymes and repair mechanisms by binding to pathogen DNA (Fig. 3a and c) [111,112]. For example, *Bacillus* strains and their volatiles can inhibit quorum sensing of competitive pathogens and down-regulate gene expression related to mycelial growth, penetration, sporulation and virulence of pathogens [113]. Additionally, *Bacillus* and *Pseudomonas* produce chitinases, glucanases and proteases involved in inhibiting many fungal diseases. Their production is mainly induced by fungal pathogen biomass and the presence of their cell walls [113]. Furthermore, antimicrobial peptides gather on the pathogen membrane in a carpet-like manner through electrostatic interaction. Under high concentrations of peptide, the cell membrane is destroyed, and micelles are formed [111]. It can also change the permeability of the pathogen membrane through pore formation [112]. In addition, antimicrobial peptides interact with carbohydrates in pathogen's cell wall and make the plasma membrane permeate, then ROS (reactive oxygen species) is accumulated [114]. In addition to these direct interactions, recent studies have found that microbial signaling molecules do not directly damage the growth and basic metabolism of pathogens, but rather interfere with their virulence. For example, anthranilic acid can interfere with the sigma factor (RpoS) of *Burkholderia plantarii*, leading to disease resistance in rice [115].

From the perspective of host plants, biocontrol strains can achieve anti-pathogen effects by activating the defense enzyme and PR (pathogenesis-related proteins) genes of host plants (Fig. 3d). For example, surfactin induces the defense response of potato plants by increasing the expression of defense-related enzyme activities (peroxidase, phenylalanine ammonia-lyase, catalase) [116]. Furthermore, *Pichia membranefaciens* has a significant biocontrol effect on peach Rhizopus rot. Transcriptome analysis showed that *Pichia membranefaciens* regulated transcription factors (TFs) by activating MAPK (mitogen-activated protein kinase) cascade signaling and signal transduction pathways of ethylene, jasmonic acid and salicylic acid in peach. Then, these TFs further mediate the expression of downstream defense-related genes, including the PR gene and glutathione *S*-transferase gene [117]. In addition, the anti-pathogen effect can be achieved by maintaining the ROS balance of host plants. For example, the application of *C. Rosea* resulted in the upregulation of several genes involved in the peroxisome, PPP (pentose phosphate pathway) and ASA (ascorbate) GSH (glutathione) cycle pathways. After activating peroxisome related proteins and proteins related to the ASA-GSH cycle pathway, remove ROS accumulated due to disease infection and maintain ROS balance to enhance plant resistance to *B. cinerea* [118]. And *Trichoderma harzianum* T-A66 strain increased antioxidant enzyme activity, phenolic compounds content by inducing rapid H_2O_2 burst and callose deposition, finally inducing resistance to *Fusarium oxysporum* in plant seedlings [119]. Additionally, potatoes may face specific

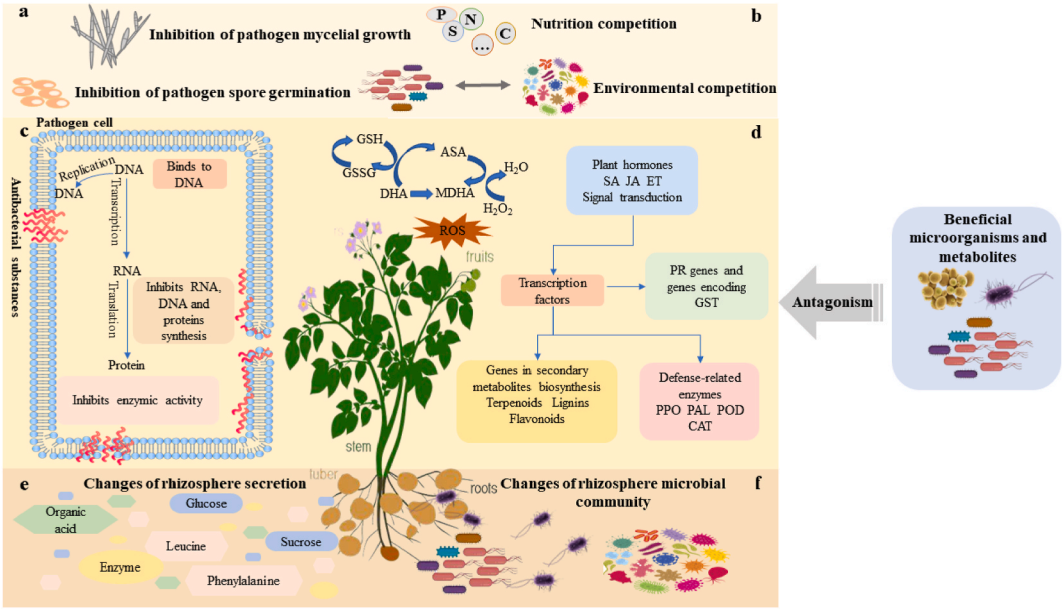

Fig. 3. Various modes of action of beneficial microorganisms against pathogens (SA, salicylic acid; JA, jasmonic acid; ET, ethylene; ASA, ascorbate; GSH, glutathione; GSSG, glutathione, oxidized; DHA, dehydroascorbate; MDHA, monodehydroascorbate; GST, *S*-transferase; PPO, polyphenol oxidase; PAL, phenylalanine ammonia lyase; POD, peroxidase; CAT, catalase; ROS, reactive oxygen species).

dilemmas when both pathogens and biocontrol agents are present. This dilemma refers to whether to allocate its resources to primary metabolism (e.g., sugar production) for basic survival or to allocate resources to secondary metabolism (e.g., phenolic production) for resistance effects [63].

Furthermore, biocontrol strains can change the rhizosphere microbial community, rhizosphere secretions and increase the abundance of beneficial microorganisms in the soil (Fig. 3e and f). For example, *Brevibacillus laterosporus* BL12 inhibits disease by reducing pathogen abundance and modulating soil bacterial communities. BL12 can colonize the tuber layer soil, and rhizosphere soil and become a critical bacterial species in the tuber layer soil bacterial community network. Beneficial bacteria such as *Pseudomonas* and *Microbacterium* were significantly positively correlated with BL12 and significantly negatively correlated with disease index [14]. Finally, the effect of the above biocontrol strains and their metabolites on inhibiting pathogens does not exist alone but often acts simultaneously.

3.3. Key points of biocontrol in practice

When applying biocontrol agents in practice, we need to pay attention to many issues. For example, we need to pay attention to when and how to add them. The timing of the addition of the biocontrol agent plays a crucial role in disease prevention. In many studies, more excellent protection was achieved only when the biocontrol strain was added a few weeks before the pathogen [63]. Furthermore, a few biocontrol agents (*B. cereus*, *P. lilacinum*, and *C. globosum*), reported human pathogens. For this reason, when using biocontrol agents, it is necessary to evaluate their toxicity, morbidity, and their safety [120].

On the other hand, yield is often a critical limitation in applying beneficial microbial metabolites to control pathogens. Microbial production of beneficial metabolites is constrained by many factors, such as nutrients, the growth rate of absorption, feedback inhibition, inducers, regulators, tRNA, and sigma factors etc. [121]. Physical and chemical factors can promote the production of beneficial metabolites by microorganisms. Specifically, beneficial metabolite production was facilitated by changing the culture medium composition and culture conditions, co-culture with different strains, and the addition of enzyme inhibitors and biosynthetic precursors. For example, the co-culture of *Streptomyces* sp. PTY08712 and *Staphylococcus aureus* resulted in increased production of granitic, granatomycin D and dihydro granitic B [121]. What's more, the optimization of co-culture conditions of *A. sydowii* and *Bacillus subtilis* induced the production of a variety of new antibacterial compounds, and the inhibition rate of *Staphylococcus aureus* was increased by 29.2 % [122]. In addition, recombinant DNA technology helps to induce new metabolites by developing plasmid vectors, protoplast fusion and transformation methods. Furthermore, the production of beneficial metabolites will be improved by domain knockdown or by the use of mutational synthesis methods.

Furthermore, most microorganisms that produce beneficial metabolites are not culturable [123]. Bioinformatics tools help predict pathways by identifying the biochemical steps catalyzed by the different enzymes encoded in biosynthetic gene clusters [123]. Genome mining strategies, whether the development of new technologies based on the CRISPR-cas9 system or the discovery of new actors for transcriptional regulation of the microbial secondary metabolome, will improve the efficiency, simplicity, and rapidity of genome-based approaches. However, future genome mining strategies require a deeper understanding of the mechanisms underlying the regulation of microbial beneficial metabolite synthesis and improved detection performance of existing bioinformatics tools for gene clusters [124].

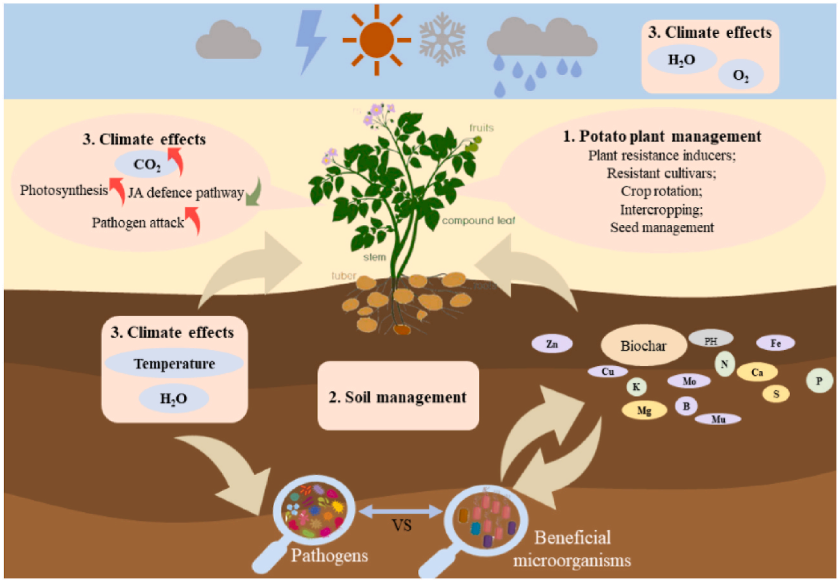

Fig. 4. The critical driving forces affecting potato pathogen infection in the biocontrol process.

4. The complexity of biocontrol—related driving forces

We must consider the key factors affecting potato pathogen infection in the biocontrol process. In this section, we will describe three fundamental driving forces: potato plant management, soil management and climate effects. Furthermore, the interaction results of these multiple driving forces are also emphasized (Fig. 4).

4.1. Potato plant management

There are still many untapped potentials in the research of potato crops. For example, potatoes lack disease-resistant phenotypes and available seeds [6]. Recent studies have shown that the endophytic bacteria *Sphingomonas melonis* in rice seeds endow rice with a disease resistant phenotype, so it is also possible to obtain disease resistant potato seeds by searching for key endophytic microorganisms in potatoes [115]. This insight gives us a new idea to study the disease-resistant potato.

On the other hand, changing the planting date to avoid conditions conducive to developing the late epidemic disease can alleviate the occurrence of disease [6]. Furthermore, multiple applications of nitrogen fertilizer will also reduce the incidence of early blight when seedlings emerge [125]. Selecting suitable crop rotation and rotation duration is a critical factor for future research work. For example, crop rotation, leisure rice potato, mung bean rice potato showed that the number of *Streptococcus scabies* in the soil decreased, leading to a decrease in the severity of scabies. The mung bean and hemp crop rotation also enhanced rhizosphere soil microflora, especially *Pseudomonas fluorescens* and *Trichoderma* [15].

4.2. Soil management

Soil has two factors that affect plant health. The first factor is the physical and biochemical properties of the soil, such as pH, organic matter, carbon and nitrogen. The second factor is biological and microbial composition [126]. They can affect the attachment, growth, interaction between microorganisms, antibiotic resistance and survival rate of microorganisms [127].

4.2.1. Soil nutrition

Soil nutrition is closely related to crop diseases. For example, the contents of organic carbon, total nitrogen, available potassium and phosphorus in the diseased soil were significantly higher than those in the healthy soil. And the contents of available phosphorus and organic carbon were negatively correlated with the incidence and severity of crop diseases. However, when the soil organic carbon content is higher than 1.3 %, it is positively correlated with disease incidence. When the C/N ratio is higher than 30, it is positively correlated with the disease severity [126].

Furthermore, soil amendments are various materials added to the soil. It can reduce water loss, inhibit weed growth, increase soil organic matter, inhibit soil-borne diseases, promote plant growth and enhance plant disease resistance to improve soil health [128]. As a key critical soil amendment, biochar contains a variety of organic acids and phenolic compounds. The physical and chemical properties of biochar depend on the raw materials used for pyrolysis [129]. Biochar may promote synergistic drug resistance by inducing ROS production in cells [127]. Biochar activates the plant defense mechanism against pathogens, which can change the function of plants. The response of tomato to *A. solani* invasion depends on the type of biochar, and the higher the amount of biochar applied, the better the effect of early blight prevention. In addition, different biochar types also differ due to their ability to induce defense gene expression or signaling pathways [129].

Recently, it was found that biocontrol microorganisms and soil amendments should be considered in controlling soil-borne diseases. After they are properly combined, they can stimulate plant defense response by mobilizing specific plant enzymes, nutrients and enhance the role of soil in inhibiting pathogens [130].

4.2.2. Soil microorganisms

Soil microbial communities include many pathogens and beneficial microorganisms. Soil microorganisms can regulate soil quality and fertility and change soil health [128]. Rhizosphere microbial communities play an essential in improving plant health [131]. Several mechanisms of joint or separate action have been proposed to explain the biological protection of arbuscular mycorrhizal fungi (AMF) against soil-borne pathogens in crops: enhancement of plant nutrition, damage compensation, changes in root anatomical structure and life span, competition between AMF and soil borne pests for colonization sites in roots and host photosynthetic products, activation of plant defense, and changes in rhizosphere microbial population [132]. In addition, soil microbial communities play a crucial role in fixing carbon in the atmosphere and soil [133].

4.3. Climate factors

Climate factors include CO_2 concentration, temperature and water availability. Climate change may affect the diversity and geographical distribution of pathogens, the severity of mycotoxins released, and may lead to the evolution of recessive and potential pathogens [132]. Plant resistance pathways, including PAMP triggered immunity (PTI), effect-triggered immunity (ETI), RNA interference and defense hormone network, are affected by climate factors [134].

The concentration of CO_2 is rising all over the world, which has a profound impact on crop biological diseases. For example, the increase in CO_2 level not only increases the sensitivity of wheat varieties but also increases the virulence of fungal isolates, leading to more severe diseases. With the increase of CO_2 concentration, the photosynthesis of plants will be enhanced. Meanwhile, the jasmonic

acid (JA) defense pathway will be weakened, eventually leading to the enhanced attack of pathogens on crops [132]. In contrast, in the interaction between some oomycetes and plants, 550 ppm CO_2 reduced the severity of the disease by more than 50 % [134].

There is an optimal temperature range for the interaction between plants and pathogens. Warming temperatures will lead to the possible prevalence of new pathogenic strains adapted to high temperatures [134]. In addition, high temperature causes some plant pathogen strains to have higher aggressiveness and resistance, then increases the risk of pathogens transferring from agricultural ecosystems to natural flora [132]. When studying the interaction between *Phytophthora infestans* and potatoes, 5 °C will also make plants more vulnerable than the constant daily temperature [134]. The temperature change will also lead to enhanced PTI signal. For example, in *Arabidopsis*, harsh temperature treatment induced higher PTI-related MAPK (mitogen-activated protein kinase) phosphorylation and PTI marker gene expression [134]. Furthermore, the effect of temperature on ETI depends on the temperature duration. Short-term high temperature adaptation may only remove part of the ETI signal pathway [134].

Water availability includes air water availability and soil water availability. Soil humidity is more critical to parasitic soil pathogens than air humidity. Lower soil moisture can reduce the infection rate of *Ralstonia solanacearum* in tomato plants. However, in the interaction between potato and *Streptomyces* spp., the pathogen of bacterial scab, lower soil moisture is conducive to developing the disease [134]. In addition, the continuous high soil water level is more conducive to disease development than the fluctuating state [9]. For many fungal pathogens, the duration of leaf surface moisture is critical to developing the disease. As the air can hold more water vapor at higher temperatures, the possibility of pathogen infection increases at higher temperatures. One study showed that higher relative air humidity would increase the expression of genes required for JA biosynthesis and signal transduction [134]. Humidity and water availability affect the effectiveness of PTI. High humidity also interferes with ETI-related HR. For example, when the air humidity is higher than 95 %, the reaction of tomato CfR protein to the effectors of *C. fulvum* Avr4 and Avr9 will be significantly reduced [134]. Furthermore, some effects of high humidity on pathogens do not directly translate into the reduction of crop yield but the reduction of the marketability of products [134].

4.4. Effect of driving forces interactions on biocontrol

It is challenging to study the overall impact of changes in various environmental conditions on disease infection. In *Arabidopsis thaliana*, the combined infection of high temperature, drought and turnip mosaic virus (TuMV) causes plant growth to be more severe than any single factor [134]. Furthermore, the content of nitrogen, phosphorus, potassium, carbon and other essential elements in the soil and pH value will change when temperature, rainfall and atmospheric composition change [132]. In addition, calmodulin binding transcriptional activator transcription factor plays a role in connecting temperature, drought and SA-regulated plant responses [134]. However, how the combined effects of various environmental conditions affect disease outcomes is still one of the most prominent and challenging issues in the future study of plant pathogen interactions.

5. The challenges and research directions of biocontrol

There is still potential for development regarding the biocontrol of potatoes. The research currently focuses on mature pathological systems and static environmental conditions. Future study urgently needs to use dynamic environmental conditions [134]. For example, combining the treatment of biocontrol strains with various driving forces in the system may have a synergistic effect on reducing pathogenic diseases [9]. It is also crucial to explore strategies for recruiting beneficial microorganisms in potato plants under various driving forces, which will further explore the detailed mechanisms of biocontrol. Meanwhile, it has practical significance to explore the mechanisms of interaction and co evolution between potato plants and microbial communities. Recent research has revealed the protection and variation of pathogen gene regulation on environmental changes by developing a web-based TCS regulatory system for *Pseudomonas syringae*. And seven TCS regulating type III secretion system, motor or extracellular polysaccharides production were also identified [135]. In addition, regional disease resistance differences of the same cultivar can be studied to unlock more biocontrol methods.

On the other hand, we need to focus on the isolation of microbial resources during potato plats growth [14]. Strains from the same species may have different biocontrol effects [3]. And the resistant strains of pathogenic fungus perithecia have potential development value. For biocontrol agents, further explore the detailed destruction mechanism of biocontrol on and within the cell membrane of the pathogen. As Sunde Xu has discovered that *Pantoea agglomerans* inhibits fungal pathogenesis by targeting lipid rafts [79].

We should also focus on potato diseases caused by viruses. *Potato virus Y* is the most widely infected [136,137]. Inoculation with *Potato virus Y* resulted in a dynamic increase in glutathione content in both resistant and susceptible potatoes, both *StGSTF1* and *StGSTF2* genes of potato glutathione s-transferase could be induced stably [138,139]. Furthermore, *Tomato leaf* curl *New Delhi virus* (ToLCNDV-potato; genus *Begomovirus*, family *Geminiviridae*) is a newly emerging pathogen that significantly reduces the size and quantity of potato tubers per plant. Infections caused by the viruses can affect plant carbon assimilation and metabolism [140]. In addition, the joint infection of two or three viruses usually leads to greater yield loss. The virus has a high mutation rate and genetic recombination rate, leading to rapid collapse of resistance and escape from breeding strategies [143]. Similarly, when the virus is co-infected with bacteria and fungi, it will cause serious losses to potato production. Therefore, in the future, it is necessary to identify the pathogenesis and control measures of the interaction between viruses, bacteria, and fungi.

In the future, we can focus on the following issues for research. How do pathogens induce tissue necrosis in potato plants? Can pathogens perceive host factors to activate potato specific virulence? What is the deep mechanism of interaction between potato plants and biocontrol agents? [144]. To combine modern biotechnology with traditional experimental tools to jointly address these challenges.

6. Conclusions

The biotic stress crisis faced by potato plants requires green and healthy measures. Biocontrol brings us hope to solve pathogenic diseases. As complementary strategies, synthetic communities (SynCom) and microcapsule technologies will further enhance the stability and activity of biocontrol. In practical applications, attention should be paid to the time and safety of biocontrol, and ultimately, it should be applied in the field at the lowest cost. In addition, find out the driving forces that affect potatoes' biocontrol, and try to use the driving forces to maximize the effect of biocontrol measures.

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Data availability statement

No data was used for the research described in the article.

CRediT authorship contribution statement

Huiqin Shi: Writing – original draft. **Wei Li:** Writing – review & editing. **Yun Zhou:** Writing – review & editing. **Jian Wang:** Writing – original draft. **Shuo Shen:** Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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