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Biological Control of Potato Fusarium Dry Rot Using *Trichoderma asperellum* and *Bacillus subtilis*: Mechanisms, Applications and Future Perspectives

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Abstract

In the context of food security, the potato (*Solanum tuberosum L.,)* is one of the most important staple crops for human consumption, being the third most important one after food grains and oilseeds. Although potato is an agronomic and nutritional important crop, potato production and post-harvest preservation are significantly challenged by biotic factors and among them, Fusarium dry rot is considered as a highly destructive post-harvest disease. Dry rot is caused by a complex of Fusarium soil and tuber borne fungi which cause significant economic losses during storage, transit and seed multiplication, sometimes reducing up to 60% of the total harvest in long-term storage. Synthetic chemical fungicides have been traditionally used by management. This high-intensity chemical approach is now being called into doubt however, because of the ability of pathogen strains to rapidly become fungicide resistant, environmental toxicity, chemical residue in food and the global regulatory ban on the use of conventional synthetic fungicides. Biological control with microbial antagonists is an environmentally safe, very successful approach to synthetic chemistry. Of the various types of biological control agents (BCAs), the filamentous fungus, *Trichoderma asperellum* and the endospore-forming bacterium, *Bacillus subtilis* have proven to be particularly promising. They have a variety of multi-targeted mechanisms of action such as direct mycoparasitism, competition for nutrients and space, inhibition by a wide range of volatile organic compounds and non-ribosomal antimicrobial metabolites produced. Importantly, these BCAs also trigger systemic resistance (ISR) responses in the potato host, which activate the plant's innate defence mechanisms to resist the next attack. This review gives an overview of the biological control of potato dry rot caused by Fusarium species, including the taxonomy and epidemiology of the pathogens; details the molecular and biochemical mechanism of action of *T. asperellum* and *B. subtilis*; and investigates the synergistic effects of their co-cultivation and consortium formulations. Lastly, we discuss physiological, formulation and environmental factors that affect the efficiency of biocontrol; we list the existing challenges for commercialization and registration of biopesticides and forecast a future scenario where synthetic biotechnology, nanotechnology, CRISPR-based strain engineering and AI-based screening platforms will form the cornerstone of robust, climate-friendly biopesticide systems.

Keywords: *Potato, Fusarium Dry Rot, T. asperellum and B. subtilis, Biological Control, Induce Resistance, Postharvest Disease.*

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I. INTRODUCTION

The potato (*Solanum tuberosum L.*) is a key crop for dietary energy and of high-quality proteins as well as for essential vitamins and minerals to over a billion people globally (Birch et al., 2012). With the growing global population and the increasing pressures on agricultural production from climate change, achieving potato production with optimal yield and maintaining post-harvest quality is essential for the global food system (Devaux et al., 2020). Fusarium dry rot is a complex of Fusarium species and is one of the most severe potato post-harvest diseases affecting potato tubers (Tiwari et al., 2020). The disease reduces seed tuber quality, poor sprout emergence, weak field stands and is responsible for extensive parenchymal decay in storage warehouses (Wale, Platt, & Cattlin, 2008).

The typical solution to dry rot for the agricultural industry has been synthetic chemical fungicides and the use of these products has been commonplace for decades (Mari, Di Francesco, & Bertolini, 2014). But repeated application of these chemicals has led to the emergence of resistant strains of Fusarium, with a resulting decrease in treatment effectiveness (Moya-Elizondo & Jacobsen, 2016). Furthermore, pesticide residues on food crops pose an immediate threat to human beings and chemical leaching can have a negative impact on soil and water ecology (Pathak et al., 2022). In addition to global regulatory restrictions regarding the residue level and ban of chemical active ingredients, these challenges have led to the search for sustainable products (Leskovac & Petrović, 2023). These challenges, along with regulatory restrictions around the world regarding residue levels and bans on chemical active ingredients, have spurred the hunt for sustainable products using bio-based ingredients (Pinela, Añibarro-Ortega, & Barros, 2024).

There is a promising avenue of biological control through the use of microbial antagonists. *Trichoderma asperellum* is a filamentous fungus and *Bacillus subtilis* is a bacterium that are highly colonizing the plant rhizosphere and on the plant surface of the tubers and are good candidates for biocontrol (Kredics et al., 2024). These biological fungicides have a multi-targeted mode of action: they involve direct physical mycoparasitism (Liu, Zhang, & Wang, 2026), competitive exclusion and release of complex lipopeptides (Beheshti, Demková, & Bobuľská, 2026), lytic enzymes and volatile compounds (Fu et al., 2025) and plus triggering of the host plant's internal immune system (Fu et al., 2025). A comparative analysis of the mechanisms of both *T. asperellum* and *B. subtilis* is conducted in this review, followed by an analysis of their molecular and systemic interactions with the potato host, evaluation of the potential for synergism using combined and co-cultured applications and the identification of potential biotechnological interventions to ensure that these fungi can become an effective part of future integrated pest management strategies.

II. BIOLOGY AND EPIDEMIOLOGY OF POTATO FUSARIUM DRY ROT

- *Ecology and Pathogenicity*

Potato Fusarium dry rots are caused by a group of phylogenetically different species of Fusarium (Stefańczyk et al., 2016). The prevalence, distribution and virulence of these species can be very different from place to place according to the geographical region, local climate and storage conditions (Talhinhas, Loureiro, & Oliveira, 2018). *Fusarium sambucinum*: This species is known to be one of the most aggressive and widespread cause of potato dry rot in temperate regions (Tiwari et al., 2020). Highly virulent, it quickly invades mechanical injuries made during harvest and handling, causing rapid development of necrotic cavities (Cerruti, 2010). Pathogenic strains of *Fusarium oxysporum* are primarily or secondary dry rot pathogens and cause extensive dry rot in potato tubers under warm storage conditions and in the field (Christian, 2023). *Fusarium solani*: A soil-borne pathogen which causes dry rot in stored potato and can cause very severe root rot in potato crops (Sharma et al., 2024). Long-term persistence in agricultural soils. *Fusarium coeruleum* (sometimes referred to as *F. solani var coeruleum*): This pathogen is very common in cooler potato-production regions of Europe and North America and results in a specific blue-gray dry rot in storage (H. Xue, Q. Liu, & Z. Yang, 2023). *Fusarium avenaceum*: Indigenous and widespread in northern areas, may cause mild to moderate dry rot and has the capability to produce harmful mycotoxins under low temperatures during storage (Munkvold, 2016).

- *Disease Symptoms*

Dry rot symptoms are first observed as small, dark, surface circular pockets, usually at the tuber wound. The necrotic lesions increase in size and in the advanced stages of infection they go deeper into the ground and the underlying starch rich tissues decay dry, powdery or corky (Huali Xue, Qili Liu, & Zhimin Yang, 2023). From the outside, the wrinkled skin forms concentric circles over the shriveled areas. As decay progresses, internal cavities form in the tuber filled with thick, colored masses of the fungus mycelium and spores (Sharma & Chauhan, 2025). Their color vary from bright white to bright yellow to orange or salmon pink depending on the individual species of Fusarium (Zhang, O'donnell, & Sutton, 2015). Infected seed tubers tend to rot in the soil, resulting in seed piece decay, poor sprout emergence, slow vegetative growth and loss of total tuber production (Charkowski et al., 2020).

- *Disease Cycle*

The epidemiology of *Fusarium spp.* is well suited to survive in agricultural soils and storage areas. The pathogens are mostly viable in the soil or on the external surface of seed tubers as very persistent chlamydospores, microconidia and macroconidia (Abdel-Azeem et al., 2019). Most infections take place during harvesting, grading/transportation, where there is unavoidable mechanical injury, abrasion or bruising of tubers. Fusarium spores germinate rapidly and invade the exposed parenchyma after penetration by intact fungal structures

when the suberized periderm of tubers is broken by mechanical damage (Schmidt, 2006). Inside the tuber, the fungus grows in the intercellular spaces, using specific hydrolytic enzymes that digest cell walls. The ambient environmental factors greatly influence the rate of disease development in storage and increase rapidly at high relative humidity and temperatures above 15 ℃ to 20℃ (Clarkson et al., 2014).

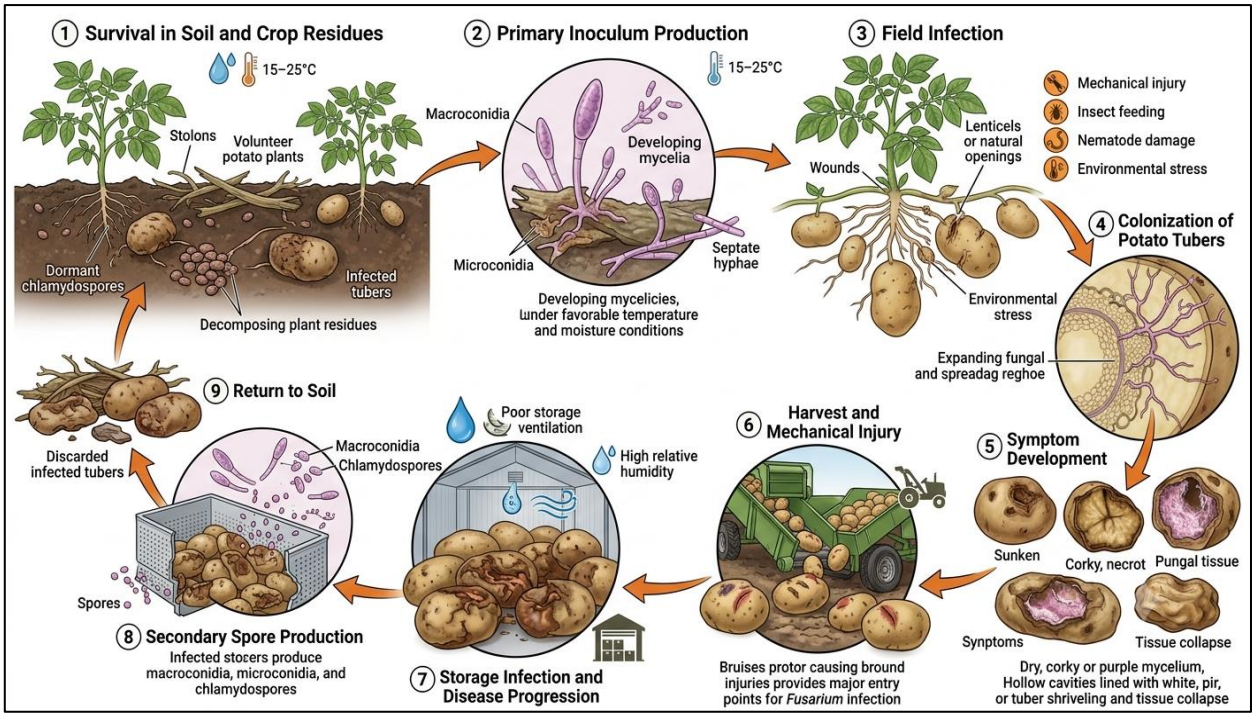

Fig 1 The Fusarium dry rot life cycle of potatoes is described in this infographic. Chlamydospores over winter in soil or debris and germinate in spring to form infectious spores. The spores enter developing tubers via wounds created by insects, machinery or stress. Silent colonization occurs until harvest, at which time the second (dry, corky) phase of rotting is evident, along with white, pink or purple mycelia in cavities. The disease is spread widely under humid conditions in poor storage, forming large secondary inoculum before the cycle is completed at the time of replanting or discarding the tubers.

III. CONVENTIONAL MANAGEMENT STRATEGIES

➢ *Cultural Practices*

Traditional, non-chemical control depends on high levels of sanitation and cultural practices (Katan, 2000). This includes a 3-4-year rotation of non-host crops to reduce the build-up of soil-borne spore banks (Singh, 2022), avoiding mechanical harvest where soil temperatures are below 10℃ (which causes bruising of tubers) and good ventilation in store to reduce wounding and suberization (Mikitzel, 2014).

➢ *Resistant Cultivars*

The tetraploid, highly heterozygous nature of commercial potato varieties and the multi-species nature of the Fusarium dry rot complex make breeding for resistance to Fusarium dry rot difficult (Chauhan et al., 2025). Many of the popular commercial cultivars are moderately to highly susceptible to harvest and post-harvest Fusarium infections, although some wild potato accessions contain useful quantitative trait loci (QTLs) for resistance (Gobin, 2024).

➢ *Chemical Fungicides*

Typical methods for controlling dry rot involve the use of synthetic fungicides applied as a spray to the tubers or as a pre-storage spray (Merlington, 2014). These are benzimidazoles (such as thiophanate-methyl) (Bai et al., 2024), quinone outside inhibitors (such as azoxystrobin) (Marin et al., 2022) and phenylpyrroles (such as fludioxonil) (Diskin et al., 2019). These compounds have a high fungicidal activity when tested under laboratory conditions.

Chemical control is seriously hampered by several biological and ecological barriers: Fungicide Resistance: Highly resistant populations of Fusarium become ubiquitous as a result of continuous single-site chemical pressure (Naqvi et al., 2025). For example, *F. sambucinum* is now widespread resistant to benzimidazoles, where the field efficacy of the traditional chemical treatments has been greatly diminished (Ocamb, Hamm, & Johnson, 2007). Chemical Residues: Dry Rot is a post-harvest disease and fungicides applied right before harvest can cause high levels of chemical residues on the tubers for direct human consumption, which is of great concern regarding food safety (Tiwari et al., 2020). Environmental Pollution: Water runoff from washing of tubers and chemical treatment plant releases synthetic compounds, which result in eco-toxicological effects on non-target aquatic organisms and affect beneficial soil microbial networks (Chakraborty, 2021). Globally, regulatory authorities are reducing the maximum residue limits (MRLs) and withdrawing registrations for many very effective and broad-spectrum fungicides, thus making it crucial to find sustainable alternatives (Lamichhane et al., 2016).

IV. BIOLOGICAL CONTROL AS A SUSTAINABLE ALTERNATIVE

➢ *Principles of Biological Control*

Biological control involves the use of a beneficial microorganism that is not pathogenic to control the population of pathogens and to achieve a reduction in disease below the economic damage levels (Bonaterra et al., 2022). Biocontrol agents (BCAs) most often have a multi-faceted mode of action, which makes the development of pathogen resistance difficult (Khan, Maymon, & Hirsch, 2017).

➢ *Advantages Over Fungicides*

BCAs have several unique benefits over synthetic chemical options: Environmental Safety, they are biodegradable, have no bioaccumulation in food webs or harmful residual on end-product product (Walia et al., 2021). Beneficial microbials become part of the natural soil microbial community, improving nutrient cycling and natural soil suppressiveness; this is microbial diversity conservation (Gupta et al., 2022). Long-Term Protection: Colonizing or spore forming BCAs can remain in the soil or on the surface of the tubers, providing protection throughout the crop cycle and into storage (He et al., 2026).

➢ *Commercial Biofungicides*

Global biofungicide market is growing at a rapid pace and more than 50% to 60% of the registered commercial biofungicides belong to species of Trichoderma and Bacillus (Meher et al., 2020). There are now a number of products registered for soil use, foliar use and post-harvest use that are based on *Trichoderma harzianum, Trichoderma asperellum, Bacillus subtilis* and *Bacillus amyloliquefaciens* (P. Narayanasamy, 2013). This has not been achieved to the same level of success as synthetic chemistry has been achieved under highly variable field conditions, however, optimization is needed.

Table 1 Representative Studies on Biological Control of Potato Fusarium Dry Rot

Microorganism	Fusarium Target	Experimental Condition	Disease Reduction (%)	Proposed Mode of Action	Reference
Trichoderma asperellum	*F. sambucinum*	Postharvest storage	60% – 90%	Hyphal coiling, mycoparasitism and secretion of hydrolytic chitinases.	(Loc et al., 2020) (Jangir, Pathak, & Sharma, 2017)
Trichoderma asperellum	*F. oxysporum*	Greenhouse pot trials	55% – 80%	Root colonization, nutrient competition and induction of host systemic resistance.	(Sehim et al., 2023) (Brizuela et al., 2023)
Bacillus subtilis	*F. sambucinum*	Postharvest storage	50% – 85%	Secretion of membrane-disrupting iturin and fengycin lipopeptides.	(Bie, 2024) (López-Arellanes et al., 2025)
Bacillus subtilis	*F. solani*	Field trials	45% – 75%	Biofilm establishment at tuber wounds and secretion of bacilysin.	(Rahman, 2016) (Santos-Lima et al., 2023)
Combined Consortium	Mixed *Fusarium* spp.	Field + storage	70% – 95%	Synergistic cell wall degradation and dual SAR/ISR defense priming.	(Yadav et al., 2024)

V. TRICHODERMA ASPERELLUM AS A BIOLOGICAL CONTROL AGENT

➢ *Taxonomy and Ecology*

Trichoderma asperellum is classified under the kingdom Fungi, phylum Ascomycota, class *Sordariomycetes*, order Hypocreales and family *Hypocreaceae* (Sokra, Meta, & Somaly, 2026). Historically it is included in the class Hyphomycetes, order Hyphomycetales, family *Moniliaceae* from under the asexual reproduction system (Ma WenYue et al., 2018). A ubiquitous soil borne, saprophytic fungus, with dark green conidia on extensively branched conidiophores (Sutthisa et al., 2024). *T. asperellum* is highly adaptive and rhizosphere-competent and is found in agricultural soils, organic matter and plant roots throughout the world (Pradhan, Bagagoni, & Makandar, 2023).

➢ *Colonization of Rhizosphere*

The colonization process of the rhizosphere by *T. asperellum* is a molecularly well-organized process. When conidia are applied to the soil or seed tubers, they germinate and form germ tubes which move towards plant root exudates by positive chemotaxis (Gao et al., 2025). Root surface adhesion is achieved through the secretion of specialised proteins in the cell wall, such as hydrophobins (TAShyd1) and expansin-like proteins, that help to physically hold the root to the outside epidermal cells (Gupta et al., 2020). The fungal hyphae infect the intercellular spaces of the root cortex and do not trigger a killing immune response from the host.

➢ *Mechanisms of Disease Suppression*

This course provides an overview of the mechanisms by which different diseases can be suppressed. Mycoparasitism: *T. asperellum* directly attacks and parasitizes and kills the Fusarium hyphae. Chemotropic growth of *T. asperellum* towards pathogen is the initial step in the process which is governed by the recognition of cell wall oligomers (Sharma & Sharma, 2020). Physical contact induces formation of a specialized structs sure with appressorium-like appearance that anchors the *Fusarium*

hyphae while *T. asperellum* coils around them. Secretes lytic enzymes which destroy the cell wall of the pathogen and thus permit direct penetration by the hyphae and ensuing collapse of the cell (Chethana et al., 2021).

Competition for Nutrients: *T. asperellum*, being a very aggressive species, rapidly consumes the simple sugars, amino acids and oxygen from the rhizosphere, wound sites, etc., depriving the pathogen of nutrients (Cao et al., 2025). It also produces high affinity ferric iron (Fe^{3+}) chelating siderophores including coprogen and ferricrocin that bind iron from the environment, thus inhibiting the germination of Fusarium spores (Al-Ani et al., 2021). Antibiotic Production: *T. asperellum* synthesizes a wide range of non-volatile antibiotics and secondary metabolites which are inhibitory direct against Fusarium vegetative growth and spore germination (Stracquadanio et al., 2020). Mycoparasitism: The fungus upregulates the production of hydrolytic enzymes of the cell wall (CWDEs), such as endochitinases (e.g., Chit42), β-1,3-glucanases and proteases (Haran, Schickler, & Chet, 1996). These enzymes break down the chitin and glucan polymers present in the structural backbone of Fusarium cell wall, causing leakage of cytoplasm and osmotic lysis of the pathogen (Panicker & Sayyed, 2022).

Volatile Organic Compounds (VOCs): Volatile metabolites like pyrones and terpenes inhibit the respiration of pathogens and the advancement of their mycelium in soil pores and in closed storage areas over a distance (Stotzky, Schenck, & Papavizas, 1976). Induced Systemic Resistance (ISR): Colonization of root surface by *T. asperellum* stimulates the plant's own defence system, resulting in systemic resistance that confers protection against subsequent attacks by pathogens (Martínez-Medina, Van Wees, & Pieterse, 2017).

- *Secondary Metabolites*

T. asperellum produces a number of compound classes that form the secondary metabolome which are very active: Peptaibols: Linear, membrane-active peptides with high amounts of the non-proteinogenic amino acid, α-aminoisobutyric acid (Finamore et al., 2025). Peptaibols are known to disrupt lipid bilayers by creating ion-channel pores in Fusarium cell membranes causing rapid leakage of the cytoplasm and killing the cells (Ghosh, 2022). Gliotoxin is an epipolythiodioxopiperazine which contains sulfur and inactivates essential thiol-containing enzymes in the pathogen, thereby disturbing the pathogen's cellular redox balance and triggering apoptosis (Traynor et al., 2019). Harzianic Acid: An effective inhibitor to Fusarium spore germination, it is a powerful tetramic acid derivative and an iron siderophore as well as an antibiotic (Patil, Patil, & Paikrao, 2016). 6-pentyl-α-pyrone (6-PP): A primary volatile lactone that has a coconut aroma. It is a direct inhibitor of fungal spore germination, inhibits expression of virulence genes of Fusarium and acts as a signaling molecule in the air in order to initiate plant defense pathways (Mendoza-Mendoza et al., 2024).

- *Experimental Studies Against Potato Dry Rot*

In vitro dual-culture confrontational assays show that *T. asperellum* isolates can suppress the vegetative radial growth of aggressive *F. sambucinum* (e.g. isolate PDR 6E) and *F. oxysporum* (e.g. isolate PDR 7.5.2) by 64.58% to 81.25% (Pooja et al., 2025). Wounded tubers of cultivar Desire were pre-treated with a conidial suspension of *T. asperellum* (1×107 conidia/mL) and then inoculated with *F. sambucinum* and stored for 5 to 6 weeks at 20°C to 24°C for storage trials (Shcherbakova et al., 2018). Dry rot lesion depth and volume were significantly reduced by pre-treatment with a conidial suspension of *T. asperellum* (1×107 conidia/mL) followed by inoculation with *F. sambucinum* after 5 to 6 weeks of storage (Gu et al., 2025).

- *Commercial Formulations*

Technologies involved in translating *T. asperellum* from laboratory to field are known as formulation technologies. High potency wettable powder (WP) and granules are prepared by traditional solid-state fermentation using agricultural by-products like wheat bran or barley straw (Mishra & Arora, 2016). Microencapsulation with biodegradable polymers has become one of the most important technologies to promote field survival. In particular, microcapsules made with 1% sodium alginate and 4% calcium chloride are found to have an efficiency of up to 95% and can protect conidia against thermal degradation and UV activity which would otherwise make them inactive (Qi et al., 2023). This will provide extended shelf-life and controlled and sustainable release of active conidia when applied to the crop rhizosphere or storage environment.

VI. BACILLUS SUBTILIS AS A BIOLOGICAL CONTROL AGENT

- *Biology and Ecology*

Bacillus subtilis is an aerobic-to-facultative, rod-shaped, flagellated, gram-positive bacterium that is typically present in soil and plant rhizosphere (Appelbaum, 2021). One physiological characteristic of *B. subtilis* is the ability to produce very resistant endospores when subjected to nutrient starvation (Hecker & Völker, 2001). The endospores of *B. subtilis* are very resistant to extreme temperatures, desiccation, UV radiation and chemical sanitizers, which makes it an excellent choice for bioformulation and long-term storage (Thakur & Singh, 2018).

- *Vegetative Propagation of the Spores*

B. subtilis has the ability to colonize plant roots and potato tubers and this colonization is mediated by chemotaxis (Blake, Christensen, & Kovács, 2021). The bacteria are able to sense and move towards root exudates that contain certain organic acids and sugars. Once at the surface, the bacterial cells adhere and develop into a multicellular matrix organized in a structure of exopolysaccharides and amyloid-like proteins (Linnet Naveena, 2024). This biofilm forms a physical barrier over the host tissue that prevents the pathogen from reaching it and also leads to the accumulation of the antimicrobial

metabolites produced by the bacterium at the site where the infection is likely to occur (Zhao, Sun, & Liu, 2023).

➢ *Mechanisms of Action*

Lipopeptides Antibiotics: A large portion of the bacterium's genome is dedicated to the non-ribosomal biosynthesis of cyclic lipopeptides that directly attack the cell membranes of the target fungi (Armenova et al., 2025). Biofilm Formation: Physical barrier, *Fusarium hyphae* can't find and reach host entry wounds; establishes spatial and nutrient dominance (Peremore, 2022). Siderophore Production: Secretion of catecholate siderophores, like bacillibactin, is thought to help limit the available Fe^{3+} in the environment and to inhibit the germination and elongation of the germ tube of Fusarium spores (Kumar et al., 2024). Competition: *B. subtilis* quickly consumes the simple sugars and amino acids excreted by damaged tissues of the tubers, thus depriving the initial growth of incoming pathogen spores of nutrients (Wang et al., 2018). Plant Growth Promotion: The bacterium produces phytohormones like indole-3-acetic acid (IAA), nitrogen fixation in the atmosphere and solubilization of insoluble inorganic phosphates, thereby improving root architecture and plant biomass (Timofeeva, Galyamova, & Sedykh, 2023). Induced Resistance: Secreted bacterial compounds are potent pathogen-associated molecular patterns (PAMPs) which either induce systemic acquired resistance (SAR) or induced systemic resistance (ISR) in the host plant (Kamle et al., 2020).

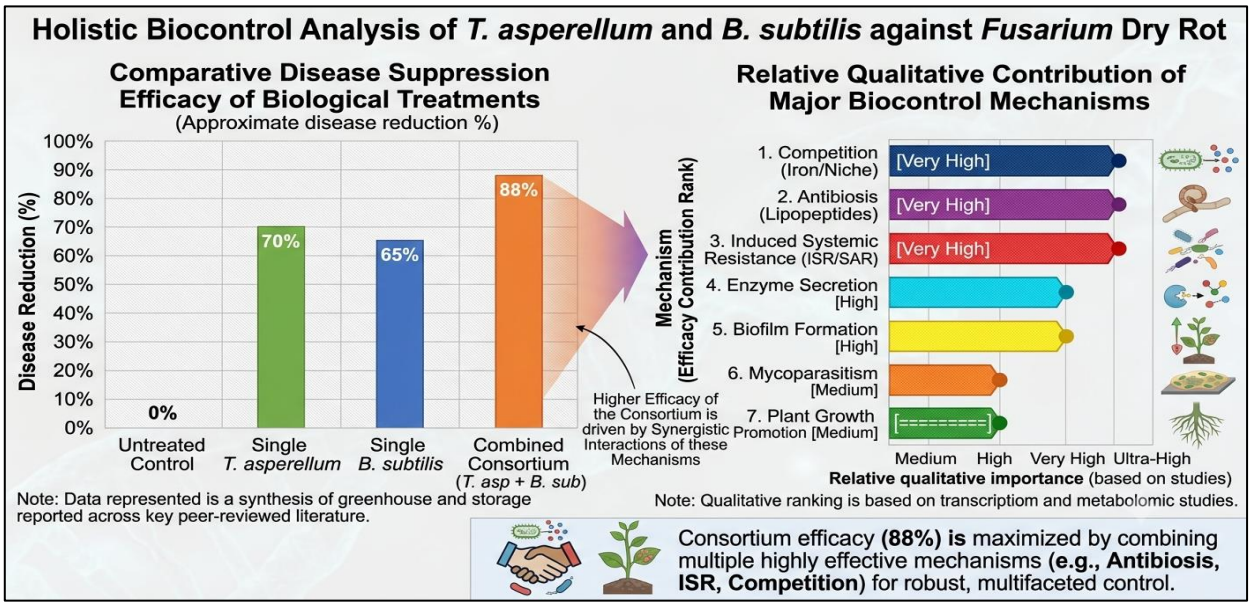

Fig 2 A complete study of biological control agents, *Trichoderma asperellum* and *Bacillus subtilis*, for Fusarium dry rot. Graphs of comparative efficacy showing approximate disease reduction percentages from single treatments as compared to the combined consortium (which is superior). (B) Relative qualitative contribution of the major biocontrol mechanisms of the consortium, based on molecular studies and showing the synergistic effects of several high impact biocontrol mechanisms for the maximum disease suppression (88%). Note: Efficacy data is syntheses of published averages and studies were used to determine the qualitative rankings.

➢ *Major Antimicrobial Metabolites*

Its cyclic lipopeptides (cLPs) and non-ribosomal peptides: Iturin: A group of heptapeptides with a chain of β-amino fatty acid are the main reasons for its therapeutic activity. Iturins act directly on membrane sterols (e.g. ergosterol in the walls of Fusarium) to form large pores which result in leakage of potassium ions and osmotic lysis of *Fusarium hyphae* (Wang et al., 2022). Fengycin: Decapeptides containing β-hydroxy fatty acid chain and an internal lactone ring. Fengycins specifically bind to fungal membrane lipids causing change in membrane permeability and structure. They are very good at inhibiting filamentous fungi even at low concentrations, with hyphal swelling and vacuolation (Y. Pan et al., 2026). Surfactin: Heptapeptides with a chain of β-hydroxy fatty acids. Surfactins are very strong biosurfactants, but low in direct fungicidal activity in comparison to iturin and fengycin. Surfactins lower surface tension, promote bacterial swarming, colonization and play a crucial role in the formation of biofilms and activation of host plant defense mechanisms (Kisil et al., 2023). Bacilysin: It is a simple dipeptide antibiotic, consisting of L-alanine and L-anticapsin. Bacilysin blocks the ability of bacteria to synthesize peptidoglycan and fungi to synthesize chitin/glucan, resulting in cell lysis (Mora Pons, 2013).

➢ *Recent Studies on Fusarium*

B. subtilis is effective against Fusarium pathogens, as indicated by recent studies. For example, *B. subtilis* strain V26 isolated from Tunisian soils contains all the complete set of the genes related to lipopeptides (ituC, fenA, fenB, fenD, srfAA, bae and bac) (Khedher, Mejdoub-Trabelsi, & Tounsi, 2021). V26 inhibited vegetative growth of *F. oxysporum*, *F. solani* and *F. sambucinum* by 54.7% to 85.3% in the dual assays (Samjik, 2024). In vivo, application of V26 as a preventative of dry rot on wounded tubers ranged from 42.8-63.8% in reducing dry rot development. Likewise, strain SF1 proved to be very efficient in vitro and in vivo against Fusarium wilt, mainly due to the ability to disrupt the membranes by surfactin (Liu et al., 2023).

➢ *Commercial Bioformulations*

The endospores of *B. subtilis* are extremely shelf-stable, allowing them to be formulated into commercial powders, suspension concentrates and water-dispersible granules (Droby et al., 2019). There are a number of popular products, including strain QST 713 which are extensively incorporated into vegetable production systems (Edgecomb & Manker, 2006). The high spore viability (more than 1×109 CFU/g) and the stability under warm storage conditions are suitable for the application of these formulations for postharvest treatments on potato tubers (Slininger et al., 2025).

VII. COMPARATIVE MECHANISMS OF TRICHODERMA ASPERELLUM AND BACILLUS SUBTILIS

An analysis of the comparative and complementary mechanisms of *T. asperellum* and *B. subtilis* shows that while *T. asperellum* utilizes direct physical mycoparasitism and active cell wall enzymatic degradation (Wu et al., 2017), *B. subtilis* relies primarily on biofilm barriers and lipopeptide-mediated membrane disruption (Saiyam et al., 2024).

Table 2 Comparative characteristics of *Trichoderma asperellum* and *Bacillus subtilis*

Characteristic	*Trichoderma asperellum*	*Bacillus subtilis*
Kingdom	Fungi	Bacteria
Rhizosphere Colonization	Excellent; forms symbiotic root-cortex associations.	Excellent; forms swarming multicellular biofilms.
Tuber Wound Colonization	High; mycelial network covers damaged surfaces.	High; rapid physical attachment and exopolymer deposition.
Mycoparasitism	Yes; active coiling and cellular penetration.	No.
Antibiotic Production	Moderate; synthesizes peptaibols and volatile pyrones.	Very High; non-ribosomally synthesizes lipopeptides.
Enzyme Secretion	High; produces diverse chitinases and glucanases.	Moderate; produces chitosanases and proteases.
Biofilm Formation	Low.	Excellent; forms thick, protective structural barriers.
Plant Growth Promotion	Moderate; increases root surface area.	High; fixes nitrogen and solubilizes soil phosphates.
ISR Induction	Strong; triggers JA/ET-dependent defense pathways.	Strong; activates both SA and JA/ET pathways.
Commercial Formulations	Numerous; dry spore powders and granules.	Numerous; highly stable endospore suspensions.
Environmental Adaptability	High; adapts well to diverse temperate climates.	Very High; resilient endospores survive extreme conditions.

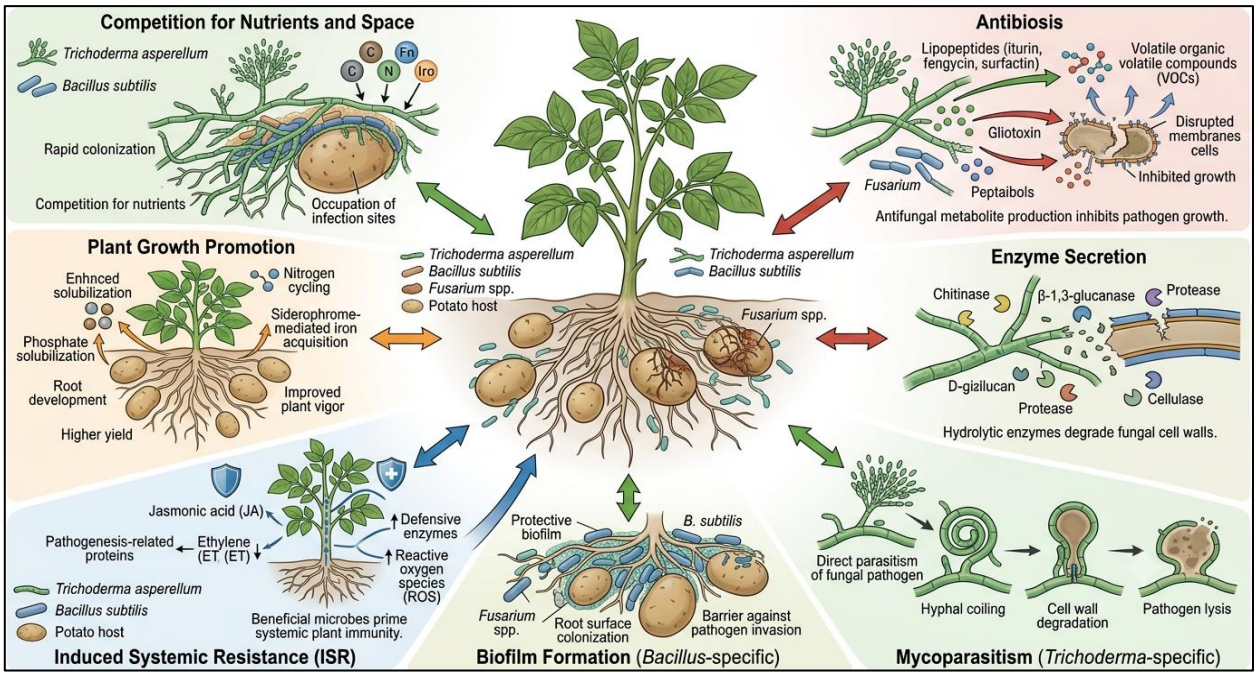

Fig 3 Modes of action of Trichoderma and Bacillus against Fusarium dry rot. Central panel shows diseased potatoes. Surrounding mechanisms (competition, antibiosis, enzyme secretion, mycoparasitism, biofilm formation, induced systemic resistance and plant growth promotion) illustrate the direct and indirect biocontrol activities of *T. asperellum* (green) and *B. subtilis* (blue) against Fusarium spp.

VIII. SYNERGISTIC USE OF TRICHODERMA ASPERELLUM AND BACILLUS SUBTILIS

➢ *Compatibility*

Ensuring ecological and physiological compatibility is one of the main difficulties in the formulation of multi-strain biocontrol agents. The fungus Trichoderma can in some cases show in vitro antagonism to the bacterium Bacillus, either via inhibition of Trichoderma germination by the lipopeptides of the bacterium or degradation of the bacterial enzymes by the proteases of the fungus (Fifani et al., 2022). Soil metagenomic analyses of 1680 samples worldwide, however, show a positive Pearson correlation coefficient ($r = 0.186$, $p = 1.33 \times 10\text{-}14$) between the abundance of Bacillus and Trichoderma (Xie et al., 2025). This suggests that these two genera are ecologically different in natural soil ecosystems and have evolved co-adaptive mechanisms that enable them to coexist in a stable manner.

➢ *Consortium Formulations*

Researchers will make use of these complementary strengths by creating co-cultured or consortium-based formulations. For instance, *B. subtilis* strain ZWZ-19 and *T. asperellum* strain PT-29 form a very compatible consortium when used in a 1:1 ratio (B1T1) (Hao et al., 2024). Metabolomics analyses of the co-culture fermentation broth, conducted by non-targeted liquid chromatography-mass spectrometry (LC-MS) detected 134 different metabolites related to amino acids, showing that co-cultivation has an impact on metabolic pathway and increases the production of important antimicrobial metabolites as compared to the monoculture (Hao et al., 2024).

➢ *Lower Cost of Seedling Production*

Consortium formulations offer greater disease protection in a variety of ways: Bacterial component is highly active in a range of soil conditions; fungal component gives long term activity and stability in a range of climates (Chaudhary et al., 2023). Bacillus lipopeptides which cause destabilization of fungal membranes and Trichoderma cell wall-degrading enzymes which remove chitin have a synergistic effect on cell wall degradation of Fusarium cell walls (Fogliano et al., 2002). The consortium activates two defense pathways in the host plant: the salicylic acid-dependent SAR pathway and the jasmonic acid/ethylene-dependent ISR pathway (Maksimov & Khairullin, 2016), which results in a strong multi-layered defense response (Báez-Astorga et al., 2025).

➢ *Field Evidence*

The results of the field tests have shown that the mixture of *T. asperellum* and *B. subtilis* is always more effective than the use of a single agent. A consortium, for example, proved to be effective in reducing dry rot and vascular wilt incidence by 70% to 95% when used as a pre-planting tuber dip and soil drenching (Thangavelu et al., 2020). This treatment also stimulated the growth of the crop, with potato production enhanced by as much as 21% and vitamin C content and total amino acid content of the tubers enhanced (Caradonia et al., 2022).

➢ *Challenges*

Although these advantages exist commercially, there are some limitations: Fermentation Complexity: It is difficult to design a fermentation medium which will support the growth of a fast-growing spore forming bacterium and a filamentous fungus, often separate fermentations are necessary and post-harvest blending is required (Sturme, van der Berg, & Kleter, 2025). Registration Barriers: The regulatory agencies may classify multi-organism consortia as new chemical products and each strain in the consortium must be individually tested for toxicological and environmental safety, thereby adding to the expense of registration (Acharya, Chakraborty, & Tringe, 2020). Special stabilisers and packaging are required to ensure the viable balance of both bacterial endospores and fungal conidia in a product over a typical two-year shelf-life, this is known as In-Storage Stability (Sindhu & Rensing).

IX. MOLECULAR BASIS OF DISEASE SUPPRESSION

➢ *Defense Signaling Pathways*

Phytohormones coordinate the defense response in potato immune system. Pathway 1: Salicylic Acid (SA) is the typical pathway involved in Systemic Acquired Resistance (SAR) (Métrauxs, 2001). When beneficial BCAs or pathogens interact with plants, free SA is produced, leading to the nuclear accumulation of a regulatory protein, NPR1 (Roychowdhury et al., 2024). This results in the transcription of pathogenesis-related (PR) genes, including StPR1b, StPR2 (β-1,3-glucanase) and StPR5 (thaumatin-like proteins), the enzymes that chemically attack the fungal structure (Van Loon & Van Strien, 1999). Jasmonic Acid (JA) and Ethylene (ET): These pathways are generally found to control the Induced Systemic Resistance (ISR) against the necrotrophic pathogens like Fusarium species (Yang et al., 2015). JA/ET priming results in accumulation of defense proteins including plant defensins (PDF1.2) and increases physical cell wall suberization to exclude fungal attack (Swaminathan, Lionetti, & Zabotina, 2022).

➢ *Defense Enzymes*

Application of *T. asperellum* or *B. subtilis* results in rapid induction of synthesis of core defense-related enzymes Phenylalanine Ammonia-Lyase (PAL): Gatekeeper enzyme of the phenylpropanoid pathway (Yadav et al., 2020). PAL stimulates the transformation of L-phenylalanine into trans-cinnamic acid, thus stimulating the biosynthesis of lignins, suberins and phytoalexins that strengthen cell walls at the site of pathogen attack (Saltveit, 2017). Polyphenol Oxidase (PPO): Converts mono- and di-hydric phenols to highly reactive quinones that are toxic to invading fungal pathogens and chemically bind to cell wall proteins to create physical barriers (Lam, 1971). Peroxidase (POD): Regulates the last stages of lignin polymerization and suberification. POD also

scavenges the production of ROS, which helps in reducing the oxidative stress in host tissue during infection (Zondo & Mafa, 2025). Chitinase and β-1,3-glucanase: Enzymes produced by the host, hydrolyse and break down the cell wall of *Fusarium hyphae* that invade the host, along with the BCA's own enzymes (P Narayanasamy, 2013).

➢ *Defense-Related Genes*

The Quantitative real-time PCR (qRT-PCR) analysis was used at the transcriptional level and demonstrated that the treatment with B. subtilus and *T. asperellum* led to a pronounced up-regulation of several immune related genes (Jain, Chatterjee, & Das, 2020). In 24-48 hrs after treatment, StNPR1 (the master regulator of SA signaling) and StPR1b are often up-regulated several folds followed by increased expression of jasmonate responsive lipoxygenase genes (StLOX) (Zenda, 2024).

➢ *Omics Approaches*

High throughput multi-omics have identified molecular mechanisms underpinning biocontrol efficacy: Transcriptomics: RNA sequencing of potato-BCA interactions shows differential expression of genes related to phenylpropanoid biosynthesis, calcium signaling cascades and pathways for cell wall reinforcement (Li et al., 2025). Proteomics: Proteomic analysis of Fusarium-infected treated tubers suggest an enrichment of heat-shock proteins, glutathione S-transferases and class III chitinases (Faramarzpour et al., 2025). Metabolomics: Non-targeted metabolomics reveals that secondary and primary metabolism of the host is reprogrammed by co-cultured BCAs (like B1T1 consortium) (H. Pan et al., 2026). This involves a considerable increase in phenolic compounds (chlorogenic acid, ferulic acid) and a re-distribution of free amino acid to boost host resistance and nutritional value of the crop.

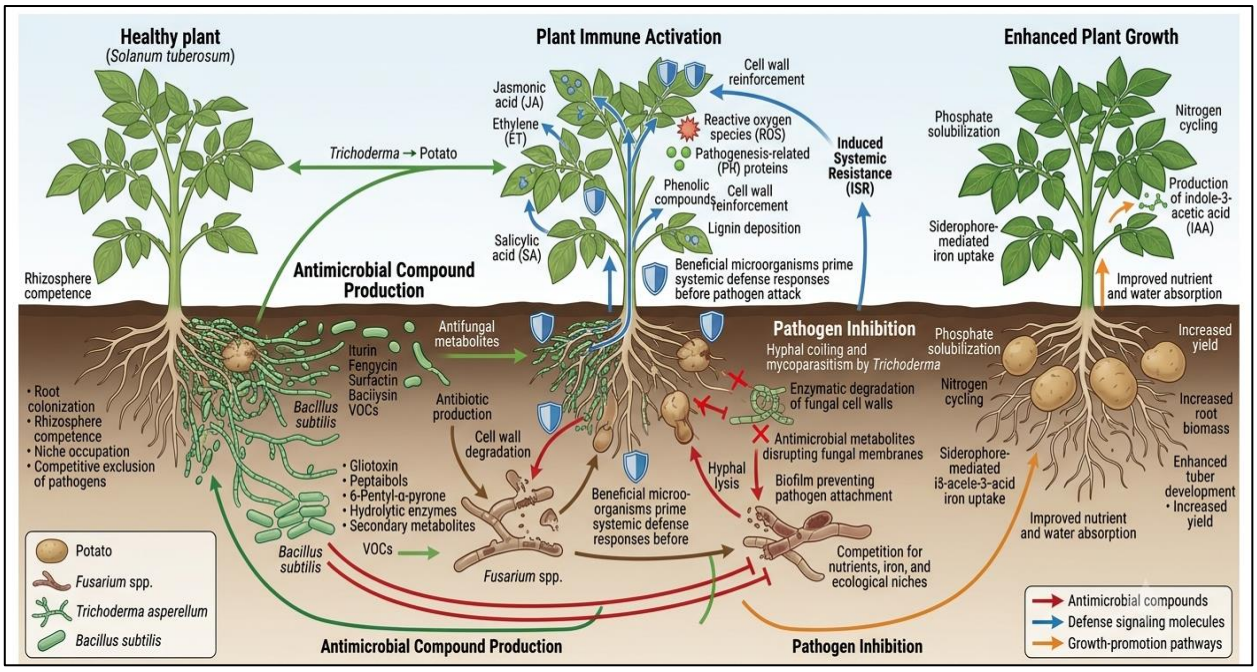

Fig 4 Schematic of integrated interactions between potato, the pathogen Fusarium and beneficial agents Trichoderma and Bacillus. Concurrently, the model shows root colonization and niche exclusion; production of antimicrobial compounds; activation of systemic plant immunity (ISR); direct pathogen inhibition via mycoparasitism; and enhanced plant growth through improved nutrient uptake and hormonal regulation. Defense signaling (blue), antimicrobial compounds (red), growth pathways (orange) are each distinguished by a different color.

X. FACTORS INFLUENCING BIOCONTROL EFFICIENCY

Environmental and biological factors have a strong impact on the field performance of *T. asperellum* and B. subtilis: Soil type and properties: (Soil organic matter content, pH and clay mineral composition directly affects the survival and motility of BCAs) (Mudgal et al., 2013). Bacterial survival of *T. asperellum* conidia is prolonged in soils with high organic carbon and in alkaline soils, trace minerals may be limiting bacteria survival. Temperature: *B. subtilis* endospores survive over a broad temperature range, but vegetative colonization and lipopeptide synthesis is best at temperatures between 25°C and 30°C. *T. asperellum* shows good growth of mycelium and conidial germination between 20°C and 25°C and the antagonistic activity reduces considerably below 15°C and above 35°C (Petrillo et al., 2020). Storage Conditions (Humidity and Temperature): Fusarium dry rot is a fast-growing disease under warm, moist storage conditions (20°C to 24°C), so the storage temperatures should be 4°C to 8°C with proper ventilation to prevent condensation, but the surface of the tubers should be kept free of BCA (Zehra et al., 2022). Biocontrol efficacy is host dependent (potato cultivar). Highly susceptible cultivars will need higher inoculant rates to elicit the same protection as response to induced systemic resistance (ISR) signals from *T. asperellum* and *B. subtilis*, while cultivars with high intrinsic suberization capacity will be more responsive to the induced signals (Wang et al., 2018). Inoculum Density: This is a critical number of "good" cells needed to cause suppressive dominance. Biofilm and pathogen suppression of *B. subtilis* requires a population of ≥ 1×108 CFU/mL. In the same way, in high disease pressure, *T. asperellum*

has a minimum threshold of 1× 106 conidia/mL for suppressing Fusarium colonization (Moreno Velandia, 2017). Appropriate Application Timing: Prevention is the key in biological control. 24 hours before wounding or pathogen application, BCAs are much more effective than curative treatments (Cook, Long, & Ganesh, 1999). This time delay enables the bacteria to germinate, form protective biofilms and start lipopeptide production before reaching the parenchymal tissue. Formulation Technology: In vegetative cells, a liquid formulation can have poor shelf-life and be very sensitive to osmotic stress (Teixidó, Usall, & Torres, 2022). On the other hand, advanced formulation methods, such as sodium alginate microencapsulation or lipid-based emulsions, render BCA more resistant to environmental stresses and facilitate their performance in the field (Lalarukh et al., 2025).

XI. CHALLENGES AND LIMITATIONS

Although they show great promise, there are several major limitations to their commercial use of *T. asperellum* and B. subtilis, Variable Field Performance: BCA's are living organisms, unlike synthetic chemical fungicides, which provide an extremely predictable knock-down effect. They are very sensitive to changing microclimates and soil moisture and are also affected by native microbial competition and disease suppression may vary from year to year (Mann, 2016).

Shelf-life constraint: Unformulated conidia and vegetative bacterial cells break down easily in ambient storage conditions. Bacillus endospores are very stable, whereas Trichoderma conidia need special packaging and control of temperature and humidity to guarantee high viability in long-term storage (Teixidó, Usall, & Torres, 2022). Environmental Stress Sensitivity: BCA colonization and vegetative growth may be suppressed under the intense UV exposure, soil salinity, extreme pH levels and drought stress, thereby reducing their protective capacity (Singh & Chauhan, 2017). Complicated registration procedures: The registration framework for biopesticides is often time-consuming, expensive and inadequate for living multi-strain consortia, which is a big hurdle for small-scale biotechnology companies (Puopolo, 2022). Slow Farmer Adoption: Many farmers are still not willing to switch from fast-acting chemical fungicides to biological control agents that often require more exact timing of application, special conditions and integrated control measures for similar effectiveness (Beckerman et al., 2023).

XII. FUTURE PERSPECTIVES

To overcome these constraints and increase the use of biological control, several innovative technological approaches are being looked into, Synthetic Microbial Consortia (SMC): Rather than random mixing of strains, the use of synthetic biology allows for the rational design of functional consortia that optimise niche partitioning, minimise metabolic overlap and maximise the biosynthetic pathways (Duncker, Holmes, & You, 2021). Nanotechnology Based Formulations: Active ingredients of BCAs may be encapsulated into biodegradable nanoparticles including chitosan, silica, or lipid-based, which can help protect the active ingredients from the effects of UV radiation, lower the dosages required for application and enable targeted and controlled release at the host-pathogen interface (Habiba et al., 2025). CRISPR-Assisted Strain Improvement: CRISPR/Cas9 genome editing can be used to improve desired biocontrol properties without the use of foreign DNA. This comprises the engineering of *B. subtilis* to over-express lipopeptide biosynthetic genes, or, the thermal and UV tolerance in *T. asperellum* (Kim et al., 2026). By rewiring microbial regulatory networks, triggered production of particular antifungal compounds could only occur in the immediate vicinity of pathogen exudates, thus limiting metabolic cost of biocontrol and maximizing the efficiency of protection (Sharma & Bora, 2025). Multi-Omics Studies: Continued developments in metagenomics, met transcriptomics and metaproteomics will further facilitate the understanding of the function of the soil-root-pathogen-BCA interactome at the system level under natural field conditions (Kumar et al., 2023). AI-Assisted Microbial Screening: By leveraging machine learning and artificial intelligence, researchers can quickly and efficiently scan through large genomic and metabolic databases, identifying high-performing highly compatible antagonist strains, significantly speeding up the conventional laboratory identification process (Antwi-Boasiako et al., 2026). Precision Agriculture: Using GPS guided, sensor driven sprayers, combined with real-time soil health monitoring, can help to use biologicals as effectively as possible by targeting areas of potential concern but minimizing use (Zhu et al., 2026). Biofungicides which are isolated and bred in extreme environments (hyper-arid or saline soils) can help develop bioformulations that are likely to be effective in the new climatic conditions as the result of the changes in temperature and moisture (Alsharif, Saad, & Hirt, 2020).

XIII. CONCLUSIONS

Fusarium dry rot is a serious disease of potato crops and in the post-harvest period, it is a significant cause of losses for seed tubers and is a major problem in potato production worldwide. Fungicide-resistant strains of the pathogens and more stringent restrictions on the levels of synthetic chemical residues in the environment are making control of this disease complex more difficult. As seen in this review, the beneficial fungus Trichoderma asperellum and the endospore-producing bacterium *Bacillus subtilis* provide a highly effective, environmentally friendly alternative. They inhibit Fusarium pathogens through various competitive and non-competitive mechanisms such as physical mycoparasitism, niche exclusion and lipopeptides that disrupt the membrane and trigger systemic resistance in the host plants.

Combining these two different agents into a single consortium or co-culture formulation takes advantage of their complementary efficacy. *B. subtilis* has the ability to colonize rapidly and form high-quality biofilms with immediate production of lipopeptides, whereas *T.*

asperellum shows targeted mycoparasitism and rhizosphere persistence. This combination of measures greatly improves overall disease control and it is highly improbable that any pathogen will develop resistance.

But in order to realize the full potential of these biocontrol agents, certain technical challenges need to be surmounted such as field performance, short shelf-life and high sensitivity to the environment. Moving forward, integration of new technologies like advanced delivery technologies based on nanotechnology, microbial consortia and strain optimization using CRISPR will be key. These innovative tools, together with accurate cultural practices and a sensor-based approach to application technologies, will enable agriculture to effectively move towards the highly resilient bio-based approach to potato disease management.

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