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Antagonistic bioagent mechanisms of controlling potato soft rot

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Abstract: Bacterial antagonists are effective as an alternative to synthetic bactericides in the control of potato soft rot. The use of bioagents reduces the application of synthetic bactericides, which are harmful to humans and the environment. However, the mechanisms of some bioagents, such as some fungi and bacteria, are not yet understood. This paper reviews the current situation of potato soft rot, biological controls, antagonistic bioagents and their mechanisms, application strategies and future directions in today's agriculture. These mechanisms include mycoparasitism, competition, rhizosphere colonisation, synthesis and release of metabolites. Bioagents increased the defensive system of plants by increasing the antioxidants genes, such as superoxide dismutase, peroxidase (POD) and catalase (CAT), and eventually increased the plant growth and yield production.

Keywords: bacteria; biological control; phytopathogens; disease; induced systemic resistance

Potatoes (*Solanum tuberosum*, L.) are an economically essential staple crop grown on a huge scale all over the world, with successful large-scale production, consumption, and affordability, as well as easy open-market availability (FAOSTAT 2015). At present, the cultivation is affected by many diseases (Walker 2004), such as blackleg, scab, late blight, brown rot (Agrios 2006). Among them, soft rot continues to be a problem for the potato production industry in many growing regions of the world (Czajkowski et al. 2015; Pritchard et al. 2016). Potato soft rot is caused by several species of *Dickeya* and *Pectobacterium* (Agrios 2006). The integrated production of several exoenzymes, such as pectinases, cellulases, and proteases by *Pectobacterium* spp. degrades the plant cell walls and releases nutrients for bacterial growth (Degefu et al. 2013; Massart et al. 2015). The major exoenzymes involved in the disease development (Cladera-Olivera et al. 2006), pectinases, break down pectins in the middle lamella and plant cell walls, leading to tissue breakdown, cell damage, and cell leakage (Wiesel et al. 2014; Romanazzi et al. 2016; Syed Ab Rahman et al. 2018), and finally, then the host shows symptoms of soft rot.

Many approaches, including physical methods, have been used to control the soft rot of potatoes, but these methods are costly, time-consuming, and have not been able to eliminate the pathogen's passage (Hajhamed et al. 2007). Chemical approaches using synthetic bactericides have also been applied to suppress bacterial pathogens, but are not more useful due to their harmful effects on humans and the environment and the risk of selecting multidrug-resistant bacterial strains (Gracia-Garza et al. 2002; Jess et al. 2014).

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The use of bacterial agents is an essential alternative to synthetic bactericides (Santoyo et al. 2012). A successful bio-bactericide must produce factors harmful to the pathogens and bring beneficial bacteria to the right place at the right time and then colonise it. Therefore, endophytic bioagents have advantages over synthetic bactericides because they colonise host tissues internally without harming the hosts or causing disease symptoms (Reinhold-Hurek & Hurek 2011). In addition, biological controls are recognised as a safe and environmentally friendly method to reduce the soft rot of potatoes (Algeblawi & Adam 2013). Biological agents can invade the internal tissues of host plants without damaging the cell (Oshnoei et al. 2017). Bacteria such as *Pseudomonas fluorescence*, *Bacillus subtilis*, *Bacillus licheniformis*, *Bacillus thuringiensis* and *Pantoea agglomerans* are the most promising biocontrol agents against soft rot pathogens under different environmental conditions (Algeblawi & Adam 2013). These bioagents have shown the biological control of potato soft rot by producing several secondary antibacterial metabolites including siderophores, antibiotics, lytic enzymes, and surfactants (Abd-El-Khair & Karima 2007). Metabolites released by antagonistic bacteria and fungi affect the survival and virulence of pathogens by mycoparasitism, competition, antibiotics and rhizosphere colonisation to destroy or damage the pathogens on the host plants (Kai et al. 2007; Marimuthu et al. 2013). However, the use of antagonistic bacteria and fungi is contemporary as they can be applied directly to the seed at planting or mixed into the soil before or after planting (Zhao et al. 2013). Therefore, biological controls based on the use of antagonists are considered a promising alternative to defending against soft rot pathogens (Etminani & Harighi 2018).

Unlike synthetic bactericides, biological controls with bio-antagonists do not leave toxin residues that remain in the environment and do not create resistant insect strains (Kefi et al. 2015; Doolotkeldieva et al. 2016). They use natural enemies of pathogens to eliminate their population in the environment (Arwiyanto & Hartana 2001). This paper reviews the current situation of potato soft rot, the biological controls, antagonistic bioagents and their mechanisms, strategies for the application of antagonists and future directions in current agriculture to provide a basis for the broad control of soft rot.

Current situation of potato soft rot

Soft rot is one of the most serious potato diseases that occurs wherever potatoes are grown (Ma 2007). It is caused by different types of bacterial pathogens, such as *Clostridium, Dickeya* and *Pectobacterium* (Agrios 2006). Soft rot disease causes an estimated loss of between 15–30% of the total yield (Walker 2004). Pathogenic bacteria enter the potato tubers through wounds or open cuts, which usually occur during harvesting and grading, where bruises are created on the tubers.

In the field, symptoms of soft rot include weak plants with curled and drooping leaves that usually look like bacterial wilt disease or a water deficiency (Ngadze et al. 2010). Leaf yellowing occurs when the bacteria invade the tissues and block the vascular system, leading to leaf wilting. In storage, symptoms of soft rot begin as water-soaked areas on the small part of the tuber and later spread to other parts if not treated. The affected tubers become soft and slimy with a slight colour change often ending with an unpleasant odour as a result of secondary infections (Walker 2004).

In addition, bacterial soft rot has been reported to affect most cruciferous and other crops, such as cabbages, cauliflowers, carrots, turnips, radishes, rape, tomatoes, lettuces, onions, beetroots, spinach, mangoes, celery, sunflowers, chicory, coriander, arracacha, cucumbers, giant pumpkins (Takimoto 1931; Smith 1944; Chakravarti & Rangarajan 1966; Arsenijevic 1970; Wimalajeewa 1976; Guevara et al. 1980; Romeiro et al. 1988; Gallois et al. 1992; Schuerger & Batzer 1993; Phokim et al. 2006). Soft rot is responsible for about 30% of losses in potato tubers (Farrar et al. 2009). Moreover, Rahman et al. (2012) reported that *Pectobacterium* species causing potato soft rot in Bangladesh reduced the tuber reserves by about 37% each year under storage conditions.

Biological control of soft rot

The application of antagonistic microbes to a host plant that inhibits pathogen growth is referred to as a biological control (Charkowski 2015; Selim et al. 2017). The degree of disease suppression achieved with biocontrol agents can be comparable to that achieved with chemicals (Makhlouf & Abdeen 2014). The use of chemicals is widespread due to their relatively low cost, ease of application and efficacy availability and stability. In addition to these advantages, the use of chemi-

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cals has the following disadvantages: they are toxic to the target organisms and other beneficial organisms, only effective for a short period and harmful to the health of some plants and animals. Considering the negative effects of chemical bactericides on the environment and natural habitats, this article presents an alternative method of controlling potato soft rot caused by bacterial pathogens with direct implications for the protection of humans and the environment.

The biological control of plant diseases involves the use of one or more antagonistic microbes against pathogenic agents (Choudhary & Johri 2008). Mechanisms of bioagent antagonism include antibiosis, competition, mycoparasitism, or the production of cell wall degrading enzymes, the production of secondary metabolites and organic compounds (Bélanger et al. 2012; Calvo-Garrido et al. 2014; Spadaro & Droby 2016; Heimpel & Mills 2017) as shown in Figure 1. Ideally, the development of environmentally friendly control measures against soft rot-causing bacteria can reduce losses during storage and improve the potato yield quality (Pieterse et al. 2014).

Numerous studies have described encouraging results on the biological control of soft rot bacteria in potatoes with bacterial competitors or plant-growth-promoting rhizobacteria from the genera *Pseudomonas*, *Bacillus*, *Serratia*, *Lactobacillus*, *Lactococcus* and quorum-quenching bacteria from the genera *Delftia*, *Ochrobactrum*, and *Rhodococcus* showing up to a 50% reduction in the soft rot infestation (Basu 2009; Czajkowski et al. 2011; Diallo et al. 2011) (Table 1). The possibility of the biological control of soft rot with antagonistic bacteria or with plant-growth-promoting rhizobacteria, *P. fluorescent*, and endophytic bacteria in potatoes has been successfully demonstrated in *in vitro* studies (Krzyzanowska et al. 2012; Nissinen et al. 2012).

Another biological measure to control soft rot is the use of bacteriophages, which are viruses that infect and degrade bacterial cells (Buttimer et al. 2017). They are specific to their hosts without infecting other pathogens, self-replicating, constant in the

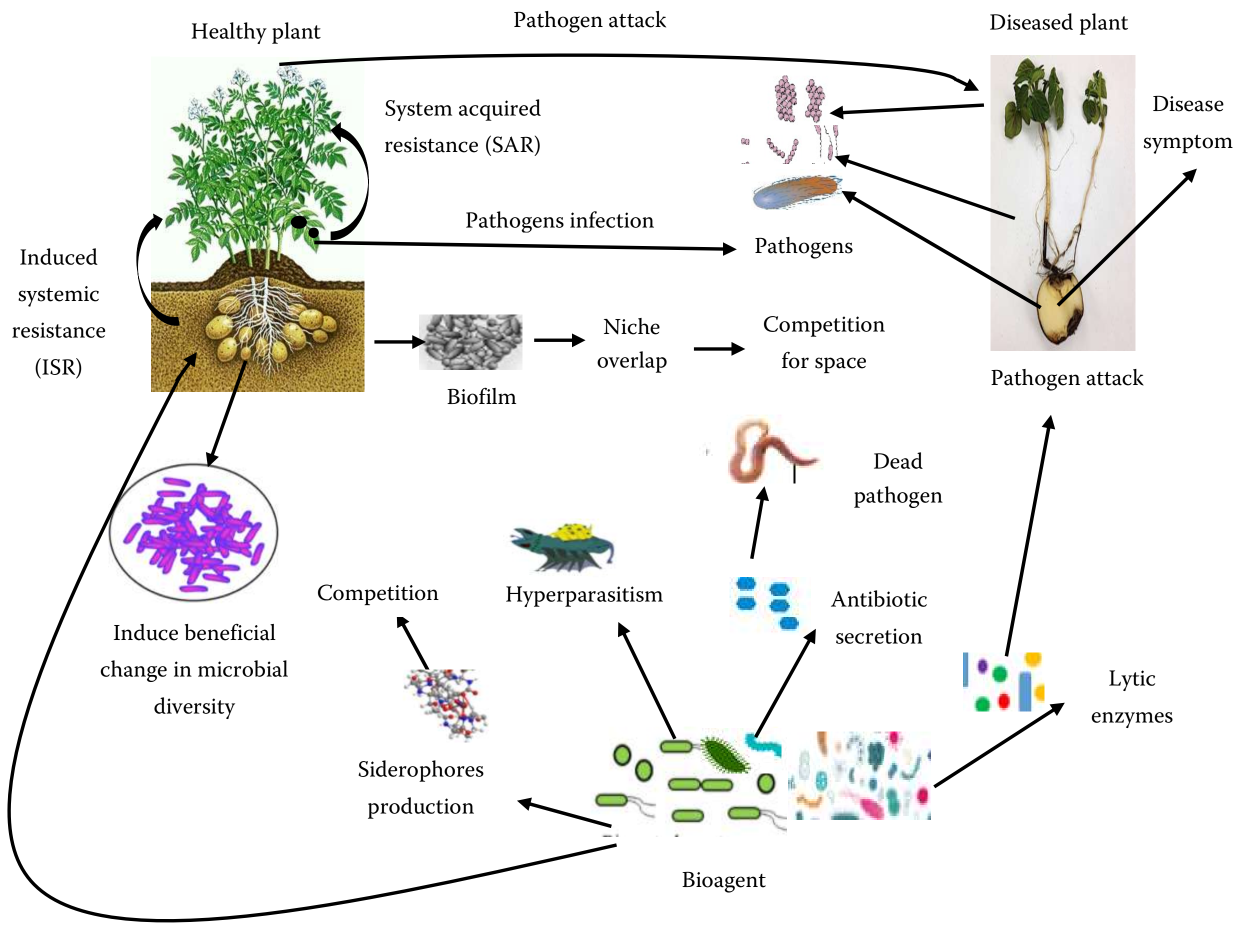

Figure 1. Mechanism of actions by bioagents for controlling potato soft rot

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Table 1. Bioagents used in controlling soft rot

Bioagent	Mechanism	Host plant	Reference
Bacillus thuringiensis	antibiosis, ISR	potato	Bravo et al. (2007)
Bacillus subtilis	antibiosis	potato	Chen et al. (2016)
Bacillus amyloliquefaciens	antibiosis, toxins	potato	Munir et al. (2018)
Pseudomonas fluorescens	antibiosis	potato	Haas and Defago (2005)
Pseudomonas aeruginosa	antibiosis, toxins	potato	Rahme et al. (1997)
Pseudomonas putida	mycoparasitism	potato	Ling et al. (2010)
Streptomyces lydicus	competition	potato	Yuan and Crawford (1995)
Pseudomonas brassicacearum 3Re2-7	antibiosis	potato	Nelkner et al. (2019)
Bacillus simplex BA2H3	antibiosis	potato	Khayi et al. (2015)
Trichoderma harzianum	competition	potato	Chen et al. (2016)

ISR = induced systemic resistance

environment, and safe to use, as they are not harmful to the health of humans and animals (Cladera-Olivera et al. 2006). Bacteriophages have been found to have the potential to control plant pathogenic bacteria such as *Pectobacterium carotovorum* (Jones, 1901) Waldee, 1945, and *Agrobacterium tumefaciens* (Smith & Townsend, 1907) (Jones et al. 2007). However, their applications are limited although they are stable and control pathogens rapidly (Kamysz et al. 2005). In summary, the biological control method is environmentally friendly, and harmless to crops and humans, and has a long-lasting effect.

Merits of antagonistic bacteria over chemical bactericides in pathogen control

Chemical bactericides, such as bismerthiazol, amicarthiazol, ethylicin, starner, micronite soreil, streptomycin sulfate, and thiadiazole copper, have been used in agriculture for many years to successfully control pathogens and, thus, increase crop production (Paoletti & Pimentel 2000). Despite their benefits, they also pose a serious threat to plant and animal life because they do not degrade or decompose and they pollute the environment (Gilden et al. 2010). Synthetic bactericides are also non-targeting because they affect a wide range of microorganisms including plant beneficial bacteria. Bio-bactericides are a promising alternative to chemical bactericides. Bio-bactericides have several advantages over conventional bactericides. Compared to synthetic bactericides, bio-bactericides are safe to use and have targeted activity against specific pathogens (Jankutė et al. 2020). They are also more readily degradable than conventional bactericides (Thakore 2006). Rhizobacteria can inhibit the growth of various phytopathogens in different ways; they compete for space and nutrients, produce bacteriocins, lytic enzymes, antibiotics, and siderophores (Jing et al. 2007). Similarly, antagonistic bacteria deprive the pathogen of iron by producing siderophores and ultimately exclude the pathogen from the slot (Beneduzi et al. 2012). Several bacterial genera have demonstrated their importance as antagonists against plant pathogens under greenhouse experiments, and these include *Bacillus*, *Azospirillum*, *Serratia*, *Pseudomonas*, *Pythium* and *Coniothyrium* (Heidarzadeh & Baghaee-Ravari 2015). Over time, the application of these microorganisms has proven successful in colonising the rhizosphere of plants and promoting their growth (Berg 2009; Tariq et al. 2010; Becker 2018).

Mechanism of antagonistic bacteria

Biological control agents control pathogens that cause damage to potato plants through different mechanisms (Bélanger et al. 2012). For example, they induce resistance to pathogenic infections without direct antagonistic interactions with the pathogen, while others act through nutrient competition or other mechanisms that modulate the pathogen growth conditions (Pieterse et al. 2014; Conrath et al. 2015).

Since the biological control is a pool of different interactions among microbes, researchers have paid much attention to characterising the particular mechanisms that occur in different experimental situations (Islam et al. 2005). Bacteria, as bioagents, negatively affect the growth of other pathogenic bacteria and other microbes. However, pathogens

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are antagonised by the presence and activities of other microbes with which they are confronted.

Siderophores are low molecular weight substances that chelate iron. In the microbial rhizosphere, iron is solubilised by the release of siderophores. However, iron siderophores are formed and diffuse to cell surfaces (Andrews et al. 2003). The production of siderophores as a bacterial mechanism has proximity to the formation of a complex with ferric ions which enhances the solubilisation of iron and allows its removal from natural complexes or minerals (Zhou et al. 2016). A low supply of iron (III) in the environment leads to the reduced growth of pathogens, which eventually leads to the eviction of pathogens from the niche (Hibbing et al. 2010). The iron siderophores complex has a significant effect on the uptake of iron by potato plants when other metals, such as cadmium and nickel, are present (Beneduzi et al. 2012). Iron plays an important role in the cellular growth and metabolism through the production of siderophores which is an important factor for the competitive fitness of bacteria around plant roots and competition with other microbes for iron in the rhizosphere (Haas & Defago 2005). Siderophores produced by *Pseudomonas* are conspicuous for their high affinity for iron ions. Pyoverdines are effective siderophores that can suppress the growth rate of bacteria that are not effective in iron reduction under *in vitro* conditions. *P. putida* produces pseudofactin siderophores that can prevent pathogens from the rhizosphere by reducing the soil's iron supply (Beneduzi et al. 2012). Several bacterial genera have been reported to produce siderophores, these include *Streptomyces* (Goudjal et al. 2016), *Azospirillum* (Banik et al. 2016), *Paenibacillus* (Liu 2017), *Pseudomonas* (Deori et al. 2018), and *Azotobacter* (Romero-Perdomo et al. 2017).

The use of antibiotics is considered the most efficient treatment and has an antagonistic effect to suppress phytopathogens (Figure 2). However, antibiotics play an important role in disease control as they can be used as biocontrol agents (Fernando et al. 2005). Antibiotics are low molecular weight organic compounds involved in the inhibition of growth and metabolic activities of various pathogens. Antibiotics produced by the plant growth-promoting rhizobacteria include kanosamine, 2,4-diacetylphloroglucinol, oligomycin A, butyrolactones, xanthobaccin phenazine-1-carboxylic acid, pyrrolnitrin, and viscosinamide (Viveros et al. 2010). They play an important role in controlling soft rot.

Bacteriocins are proteinaceous toxins secreted by bacteria living in a competitive microbial environment. They destroy neighbouring bacterial species by damaging bacteriocinogenic cells (Riley & Wertz 2002; Beneduzi et al. 2012). Bacteriocins have a limited killing spectrum compared to conventional antibiotics and have a damaging effect on the bacteria closely related to the bacteriocin-producing bacteria (Riley & Wertz 2002). Since bacteriocins are very effective in suppressing the growth of soft rot pathogens, there is a need to work on them to improve their antagonistic potentials.

Finally, polymeric compounds, such as cellulose, hemicellulose, chitin and protein, can be hydrolysed by the lytic enzymes produced by a variety of microbes. Microbes can directly inhibit the growth and activities of pathogens by secreting lytic enzymes. Hydrolytic enzymes, including glucanases, proteases, chitinases, and lipases, are involved in the lysis of pathogen cell walls (Neeraja et al. 2010). These enzymes either consume the pathogens or affect components of the cell wall of bacterial pathogens. This is one of the important mechanisms for the environmental-friendly control of bacterial pathogens (Kobayashi & El-Barrad 1996).

Mechanism of antagonistic fungi

The antagonism of pathogens can be direct or indirect. Direct antagonism results from physical contact between two microbes where the bioagent defeats the pathogen through space occupancy and nutrient competition (Harman et al. 2004). The indirect antagonism mechanism, on the other hand, involves the use of biocidal agents that do not target a pathogen, but rather enhance and stimulate plant defence mechanisms (Harman et al. 2004). However, the effectiveness of antagonists as biocontrol agents depends on the efficient colonisation of the plant root zone (des Essarts et al. 2016; Abdallah et al. 2018; Munir et al. 2018). The application of *Trichoderma harzianum* Rifai and *Bacillus subtilis* (Ehrenberg, 1835) Cohn, 1872 to potato tubers prior to planting prevented the development of soft rot disease (Chen et al. 2016).

Trichoderma suppresses the pathogen growth population in the rhizosphere through competition, thus reducing disease development. It produces antibiotics and toxins, such as trichothecene and a sesquiterpene, trichodermin, which have a direct effect

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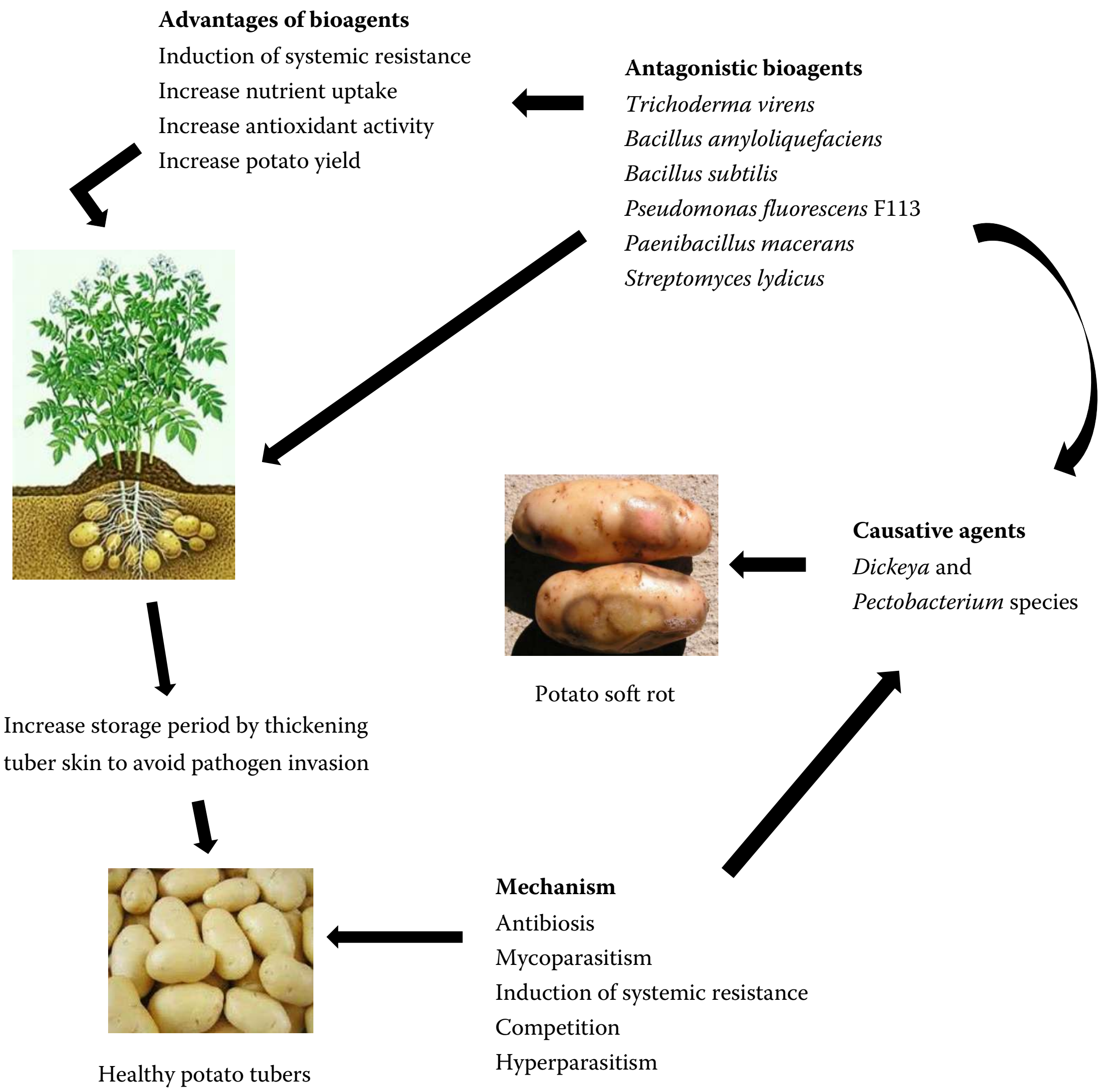

Figure 2. Impact of antagonistic microbes on potato plant

on other organisms. The mode of action of *T. harzianum* is described as mycoparasitism, secreting cell wall-degrading enzymes, such as glucanases and chitinases, but *T. harzianum* is also known to produce antifungal compounds, such as alkylpyrones, inhibitory furanones, and antibiotic peptides (Lugtenberg et al. 2017; Ghorbanpour et al. 2018). These antibiotics function by either killing or suppressing the bacterial growth (Table 2). Microbial genomic analyses have revealed a large number of cryptic antibiotic gene clusters encoding antibiotics (Raaijmakers & Mazzola 2012; Koch et al. 2018). Antimicrobial metabolites are often considered the most potent action mechanism of microbes against competitors, enabling antibiotic-producing microorganisms to compete in resource-limited environments (Raaijmakers & Mazzola 2012; Garge & Nerurkar 2017). Induced plant defence mechanisms, involving the reduction of reactive oxygen species, phytoalexins, phenolic compounds, or the elevation pathogenesis-related proteins or the formation of physical barriers, such as modifications of cell walls and cuticles, by the induced plant (Harman 2006; Wiesel et al. 2014).

Application strategies

Overall application. The successful application of biological control strategies requires more knowledge-intensive management (Heydari et al. 2004). Knowledge of the timing, method and correct bioagent use against a particular pathogen can be profitable in integrated pest management systems (Heydari et al. 2004). From previous work, the consideration of the timing and method of ap-

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Table 2. Antibiotic mechanism of bioagents in controlling potato soft rot pathogens

Bioagents	Antibiotic	Target pathogen	Disease	Reference
Bacillus amyloliquefaciens	bacillomycin, fengyci	*Pectobacterium atrosepticum*	soft rot	Koumoutsi et al. (2004)
Bacillus subtilis	xanthobaccin A	*E. carotovora* subsp. *carotovora*	soft rot	Islam et al. (2005)
Lysobacter sp. strain SB-K88	gliotoxin	*Rhizoctonia solani*	soft rot	Wilhite et al. (2001)
Trichoderma virens	mycosubtilin	*Pythium aphanidermatum*	soft rot	Leclere et al. (2005)
Bacillus subtilis BBG100	2,4-diacetylphloroglucinol	*Pythium* spp.	soft rot	Shanahan et al. (1992)
Pseudomonas fluorescens F113	agrocin 84	*Pectobacterium carotovorum*	soft rot	Azaiez et al. (2018)
Bacillus subtilis QST713	herbicolin	*Erwinia amylovora*	soft rot	Sandra et al. (2001)

plication of a biological control strategy can lead to success (Heydari et al. 2004). A direct application, such as coating the tubers and soaking them with the antagonistic bacteria and fungi in powder form or suspension treatments, to protect the tubers can be used (Heydari & Misaghi 2003; Heydari et al. 2004). It is considered necessary to apply bioagent products to the infected and unaffected areas of tubers to reduce the spread of soft rot pathogens. Also, a one point and time application is another strategy involving biological controls. In this strategy, bioagents are applied in the same location each cropping year, but at lower populations, which then breed and spread to other plant parts that are protected from bacterial pathogens. For example, using plant growth-promoting rhizobacteria and fluorescent *Pseudomonas* strains on potato tubers (Bloom et al. 2003; Kloepper et al. 2004). However, the one-time application at lower populations allows pathogens to multiply before antagonists arrive, which is detrimental to plant growth. As a result, it is critical to know the mode of application of the antagonists to prevent a pathogen invasion.

Pathogen populations are kept below threshold levels by a single application. Hypovirulent strains of the pathogen, on the other hand, may develop resistance in the inoculated host plant (Milgroom & Cortesi 2004). If the antagonists are only used once, they may fail to multiply and suppress pathogen populations below threshold levels as a result of environmental changes. As a result, it is recommended that a second application should be considered if the first application fails to keep pathogen populations below threshold levels.

Soil treatment. Bacteria and fungi soil treatments are one of the most widely used methods for successfully controlling several bacterial plant pathogens. Application of *Pseudomonas fluorescens* Migula, 1895 to the soil at the point of the mini tuber placement was effective in controlling soft rot in potatoes (De Capdeville et al. 2002; Janisiewicz & Peterson 2004).

P. fluorescence, *B. subtilis*, and *E. herbicola* showed activity against *E. carotovora* subsp. *carotovora* (Vanneste & Yu et al. 1996). *Streptomyces* is a well-known genus of the family Actinomycetaceae. They usually colonise the soil and often improve the soil's fertility. The application of these bacteria to the soil can colonise the root zone of plants and, thus, inhibit the growth of pathogens. These prokaryotes have properties that make them useful as biocontrol agents against bacterial plant pathogens (Kieser et al. 2000; Algeblawi & Adam 2013). Treating the soil with a plant growth-promoting rhizobacteria can improve the uptake of nutrients for plants and/or produce plant growth-promoting compounds. They also protect plant root surfaces from colonisation by pathogenic microbes through direct competitive action and the production of antimicrobial agents (Kloepper 1993).

Seed treatment. Potato seedlings are protected from pathogens by fungi spore suspension and bacteria pre-treatment. Although seed treatment will not control stem and foliar diseases that attack the plants, the root is the first contact of pathogen interaction in the soil, and the spore of either the fungi or the bacteria colonises the root at its initial emergence. It is an excellent alternative for reducing soft rot by directly applying bioagent materials to potato seeds/tubers before planting. Botanicals, such as garlic and Allamanda tablets, as well as the BAU-bio-fungicide, are promising bioagents used for the treatment of seeds. Both of these are reported to be an effective and environmentally friendly method of controlling soft rot (Janisiewicz & Peterson 2004). BAU-bio-fungicide is derived from *Trichoderma* grown on an organic

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substrate to protect against various pathogen-causing diseases such as potato soft rot.

Future directions

Biological control research related to pathogen control has had a lot of success under controlled conditions (*in vitro*), but it was not that successful under open field conditions. However, in order to predict the long-term effects of bioagents that have been released into the environment, new developmental directions must be added to the previous success and moved forward. Because bacteria pathogens are so diverse, and their pathogenicity varies depending on the host plants, it is necessary to look for new and different biocontrol agents with different mechanisms. As a result, the following areas require further investigation: the use of uncharacterised microbes as biological control agents, research into the roles of genes and gene products involved in pathogen suppression, and the efficacy of different strain combinations in comparison to individual agents.

Potato soft rot has been effectively controlled by biological control agents that act as bio-protectants. The development of new formulations is, without a doubt, the most difficult challenge in antagonistic biocontrol research. In China, progress has been made in recognising the new impact on the production process of quality biocontrol products and high-efficiency methods for identifying factors that affect the efficacy and shelf life of bioagents that have been developed (Liu 2017; Zang et al. 2020). Overall, tremendous progress has been made in recent decades, which bodes well for the future applications of biocontrol antagonistic fungi and bacteria.

CONCLUSION

Various bioagents, including fungi and bacteria, have been reported by different researchers for potato disease management. The efficacy of the bioagents varied between *in vitro* and open field conditions. This could be due to the non-synchronous environment between the *in vitro* conditions and the field. Some *Trichoderma* spp., *Pseudomonas* spp. and *Bacillus* spp. showed significant results in reducing potato disease incidence in both *in vitro* and open field conditions. These bioagents need to be used on a larger scale. In addition, new bioagents with a wider range of applications need to be explored. The defined mechanisms of the bioagents in controlling potato soft rot are the production of antibiotics, siderophores, cell wall degrading enzymes, volatile organic compounds, mycoparasitism, and competition for space and nutrients. It can be concluded that fungal biocontrol agents, such as *T. harzianum*, *Trichoderma viride* Pers. and *Trichoderma virens*, and bacterial biocontrol agents, such as *Bacillus subtilis, Bacillus pumilus, Bacillus megaterium,* and *P. fluorescens,* can control most pathogens of the potato soft rot disease. Combinations of chemicals, such as chitosan, and biological agents, such as *Pseudomonas*, *T. viride,* or *Bacillus,* have been proven to control *P. carotovorum* subsp. *carotovorum* during potato tuber storage (Abd-El-Khair & Karima 2007). However, to our knowledge, no combination of bacterial biocontrol agents has yet been reported upon to protect potatoes against soft rot diseases. We, therefore, suggest that the combination of multiple biocontrol agents strengthens the reproducibility of crop protection, but also potentially increases the range of the target pathogens.

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REFERENCES

Abd-El-Khair H., Karima H.E.H. (2007): Application of some bactericides and bio-agents for controlling the soft rot disease in potato. Research Journal of Agricultural and Biological Sciences, 3: 463–473.

Abdallah D.B., Frikha-Gargouri O., Tounsi S. (2018): Rizhospheric competence, plant growth promotion and biocontrol efficacy of *Bacillus amyloliquefaciens* subsp. *plantarum* strain 32a. Biological Control, 124: 61–67.

Agrios G. (2006): Bacterial Soft Rots. San Diego, Academic Press.

Algeblawi A., Adam F. (2013): Biological control of *Erwinia carotovora* subsp. *carotovora* by *Pseudomonas fluorescens*, *Bacillus subtilis*, and *Bacillu thuringiensis.* International Journal of Chemical, Environmental and Biological Sciences, 5: 70–79.

Andrews S.C., Robinson A.K., Quiñones F.R. (2003): Bacterial iron homeostasis. FEMS Microbiology Review, 27: 215–237.

Arsenijevic M. (1970): A bacterial soft rot of sunflower. Phytopathologica Academiae Scientiarum of Hungary, 5: 317–326.

Arwiyanto T., Hartana I. (2001): Field experiment of biological control of tobacco bacterial wilt (*Ralstonia solanacearum*). Mediagama, 3: 7–14.

Azaiez S., Slimene I.B., Karkouch I., Essid R., Jallouli S., Djebali N., Tabbene O. (2018): Biological control of the soft rot bacterium *Pectobacterium carotovorum* by *Bacillus amyloliquefaciens* strain Ar10 producing glycolipid-like compounds. Microbiological Research, 217: 23–33.

Banik A., Mukhopadhaya S.K., Dangar T.K. (2016): Characterization of N_2-fixing plant growth promoting endophytic and epiphytic bacterial community of Indian cultivated and wild rice (*Oryza* spp.) genotypes. Planta, 243: 799–812.

Basu A. (2009): Employing eco-friendly potato disease management allows organic tropical Indian production systems to prosper. Asian Journal of Food and Agro-Industry, 3: 80–87.

Becker M. (2018): Comparative genomics reveal a flagellar system, a type VI secretion system and plant growth-promoting gene clusters unique to the endophytic bacterium *Kosakonia radicincitans*. Frontiers in Microbiology, 9: 1997. doi: 10.3389/fmicb.2018.01997

Bélanger R.R., Labbé C., Lefebvre F., Teichmann B. (2012): Mode of action of biocontrol agents: All that glitters is not gold. Canadian Journal of Plant Pathology, 34: 469–478.

Beneduzi A., Ambrosini A., Passaglia L.M. (2012): Plant growth-promoting rhizobacteria (PGPR): Their potential as antagonists and biocontrol agents. Genetic and Molecule Biology, 35: 1044–1051.

Berg G. (2009): Plant-microbe interactions promoting plant growth and health: Perspectives for controlled use of microorganisms in agriculture. Applied Microbiology and Biotechnology, 84: 11–18.

Bloom B., Ehlers R., Haukeland-Salinas S., Hoddanen H., Jung K. (2003): Biological control agents: Safety and regulatory policy. Biological Control, 48: 477–484.

Bravo A., Gill S.S., Soberon M. (2007): Mode of action of *Bacillus thuringiensis* Cry and Cyt toxins and their potential for insect control. Toxicon, 49: 422–435.

Buttimer C., McAuliffe O., Ross R.P., Hill C., O'Mahony J., Coffey A. (2017): Bacteriophages and bacterial plant diseases. Frontier Microbiology, 4: 23. doi: 10.3389/fmicb.2017.00034

Calvo-Garrido C., Viñas I., Elmer P.A., Usall J., Teixidó N. (2014): Suppression of *Botrytis cinerea* on necrotic grapevine tissues by early-season applications of natural products and biological control agents. Pest Management Science, 70: 595–602.

Cladera-Olivera F., Caron G.R., Motta A.S., Souto A.A., Brandelli A. (2006): Bacteriocin-like substance inhibits potato soft rot caused by *Erwinia carotovora*. Canadian Journal of Microbiology, 52: 533–539.

Conrath U., Beckers G.J.M., Langenbach C.J.G., Jaskiewicz M.R. (2015): Priming for enhanced defense. Annual Reviews of Phytopathology, 53: 97–119.

Czajkowski R., Pérombelon M.C.M., van Veen J.A., van der Wolf J.M. (2011): Control of blackleg and tuber soft rot of potato caused by *Pectobacterium* and *Dickeya* species: A review. Plant Pathology, 60: 999–1013.

Czajkowski R., Pérombelon M.C.M., Jafra S., Lojkowska E., Potrykus M., van der Wolf J.M., Sledz W. (2015): Detection, identification and differentiation of *Pectobacterium* and *Dickeya* species causing potato blackleg and tuber soft rot: A review. Annals of Applied Biology, 166: 18–38.

De Capdeville G., Wilson C.L., Beer S.V., Aist J.R. (2002): Alternative disease control agents induce resistance to blue mold in harvested Red Delicious apple fruit. Phytopathology, 92: 900–908.

Degefu Y., Potrykus M., Golanowska M., Virtanen E., Lojkowska E. (2013): A new clade of *Dickeya* spp. plays a major role in potato blackleg outbreaks in North Finland. Annals of Applied Biology, 162: 231–241.

Deori M., Jayamohan N.S., Kumudini B.S. (2018): Production, characterization and iron binding affinity of hydroxamate siderophores from rhizosphere associated fluorescent *Pseudomonas*. Journal of Plant Protection Research, 58: 36–43.

des Essarts Y.R., Cigna J., Quetu-Laurent A., Caron A., Munier E., Beury-Cirou A., Helias V., Faure D. (2016): Biocontrol of the potato blackleg and soft rot diseases caused by *Dickeya dianthicola*. Applied Environmental and Microbiology, 82: 268–278.

Diallo S., Crépin A., Barbey C., Orange N., Burini J.F., Latour X. (2011): Mechanisms and recent advances in biological control are mediated through the potato rhizosphere. FEMS Microbiology Ecology, 75: 351–364.

Doolotkeldieva T., Bobusheva S., Suleymankisi A. (2016): Biological control of *Erwinia carotovora* ssp. *carotovora* by *Streptomyces* species. Advanced Microbiology, 6: 104–114.

Etminani F., Harighi B. (2018): Isolation and Identification of endophytic bacteria with plant growth-promoting activity and biocontrol potential from wild Pistachio trees. Plant Pathology Journal, 34: 208–217.

FAOSTAT (2015): Food and Agriculture Organisation of the United Nations. Rome, FAO. Available at https://www.fao.org/faostat/en/#home.

Farrar J.J., Nunez J.J., Davis R.M. (2009): Losses due to lenticel rot are an increasing concern for Karen county potato growers. California Agriculture, 63: 127–130.

Fernando W.D., Nakkeeran S., Zhang Y. (2005): Biosynthesis of antibiotics by PGPR and its relation in biocontrol

https://doi.org/10.17221/166/2020-PPS

of plant diseases. In: Siddiqui Z.A. (ed.): PGPR: Biocontrol and Biofertilization. Dodrecht, Springer: 67–109.

Gallois A., Samson R., Ageron E., Grimont P.A.D. (1992): *Erwinia carotovora* subsp. *odorifera* subsp. nov., associated with odorous soft rot of chicory (*Cichorium intybus* L.). International Journal of Systematic Bacteriology, 42: 582–588.

Garge S.S., Nerurkar A.S. (2017): Evaluation of quorum quenching *Bacillus* spp. for their biocontrol traits against *Pectobacterium carotovorum* subsp. *carotovorum* causing soft rot. Biocatalysis Agriculture and Biotechnology, 9: 48–57.

Ghorbanpour M., Omidvari M., Abbaszadeh-Dahaji P., Omidvar R., Kariman K. (2018): Mechanisms underlying the protective effects of beneficial fungi against plant diseases. Biological Control, 117: 147–157.

Gilden R.C., Huffling K., Sattler B. (2010): Pesticides and health risks. European Journal of Obstetrics, Gynecology and Reproductive Biology, 39: 103–110.

Goudjal Y., Zamoum M., Sabaou N., Mathieu F., Zitouni A. (2016): Potential of endophytic *Streptomyces* spp. for biocontrol of *Fusarium* root rot disease and growth promotion of tomato seedlings. Biocontrol Science and Technology, 26: 1691–1705.

Gracia-Garza J.A., Blom T.J., Brown W., Allen W. (2002): Pre- and post-plant applications of copper-based compounds to control *Erwinia* soft rot of calla lilies. Canadian Journal of Plant Pathology, 24: 274–280.

Guevara Y.M., Rondon A.G., Solorzano R. (1980): Bacterial infection of the mango (*Mangifera indica* L.) in Venezuela. I. Symptomology and identification. Agronomía Tropical, 30: 65–76.

Haas D., Defago G. (2005): Biological control of soil-borne pathogens by fluorescent pseudomonads. Nature Reviews Microbiology, 3: 307–331.

Hajhamed A., Sayed W.M.A.E., Yazied A.A.E., Ghaffar N.Y.A.E. (2007): Suppression of bacterial soft rot disease of potato. Egyptian Journal of Phytopathology, 35: 69–80.

Harman G.E. (2006): Overview of mechanisms and uses of *Trichoderma* spp. Phytopathology, 96: 190–194.

Harman G.E., Howell C.R., Vertibo A., Chet I., Lorito M. (2004): *Trichoderma* species – Opportunistic, avirulent plant symbionts. Nature Reviews Microbiology, 2: 43–56.

Heidarzadeh N., Baghaee-Ravari S. (2015): Application of *Bacillus pumilus* as a potential biocontrol agent of *Fusarium wilt* of tomato. Archives of Phytopathology and Plant Protection, 48: 841–849.

Heimpel G.E., Mills N. (2017): Biological Control: Ecology and Applications. Cambridge, Cambridge University Press.

Heydari A., Misaghi I.J. (2003): The role of rhizosphere bacteria in herbicide-mediated increase in *Rhizoctonia solani*-induced cotton seedling damping-off. Plant Soil, 257: 391–396.

Heydari A., Fattahi H., Zamanizadeh H.R., Zadeh N.H., Naraghi L. (2004): Investigation on the possibility of using bacterial antagonists for biological control of cotton seedling damping-off in a greenhouse. Applied Entomology and Phytopathology, 72: 51–68.

Hibbing M.E., Fuqua C., Parsek M.R., Peterson S.B. (2010): Bacterial competition: Surviving and thriving in the microbial jungle. Nature Reviews Microbiology, 8: 15–25.

Chakravarti B.P., Rangarajan M. (1966): Occurrence of *Erwinia aroideae* on two new hosts in India. Plant Disease Report, 50: 701–702.

Charkowski A. (2015): Biology and control of *Pectobacterium* in potato. American Journal of Potato Research, 92: 223–229.

Chen X., Zhang Y., Fu X., Li Y., Wang Q. (2016): Isolation and characterization of *Bacillus amyloliquefaciens* PG12 for the biological control of apple ring rot. Postharvest Biological Technology, 115: 113–121.

Choudhary D.K., Johri B.N. (2008): Interactions of *Bacillus* spp. and plants with special reference to induced systemic resistance (ISR). Microbiology Research, 164: 493–513.

Islam M.T., Hashidoko Y., Deora A., Ito T., Tahara S. (2005): Suppression of damping-off disease in host plants by the rhizoplane bacterium *Lysobacter* sp. strain SB-K88 is linked to plant colonization and antibiosis against soilborne Peronosporomycetes. Applied Environmental Microbiology, 71: 3786–3796.

Janisiewicz W.J., Peterson D.L. (2004): Susceptibility of the stem pull area of mechanically harvested apples to blue mold decay and its control with a biocontrol agent. Plant Diseases, 88: 662–664.

Jankutė A., Guobužaitė S., Jakubovskis R., Gribniak V., Urbonavičius J. (2020): Investigating viability of alkaliphilic *Bacillus* species in biological self-healingconcrete. In: FEMS Online Conference on Microbiology, Oct 28–31, 2020, Electronic abstract book.

Jess S., Kildea S., Moody A., Rennick G., Murchie A.K., Cooke L.R. (2014): European Union policy on pesticides: Implications for agriculture in Ireland. Pest and Management Science, 70: 1646–1654.

Jing Y.D., He Z.L., Yang X.E. (2007): Role of soil rhizobacteria in phytoremediation of heavy metal contaminated soils. Journal of Zhejiang University Science, 8: 192–207.

Jones J.B., Jackson L.E., Balogh B., Obradovic A., Iriarte F.B., Momol M.T. (2007): Bacteriophages for plant disease control. Annual Review of Phytopathology, 45: 245–262.

Kai M., Effmert U., Berg G., Piechulla B. (2007): Volatiles of bacterial antagonists inhibits mycelial growth of the plant pathogen *Rhizoctonia solani*. Archive Microbiology, 187: 351–360.

https://doi.org/10.17221/166/2020-PPS

Kamysz W., Krolicka A., Bogucka K., Ossowski T., Lukasiak J., Lojkowska E. (2005): Antibacterial activity of synthetic peptides against plant pathogenic *Pectobacterium* species. Journal of Phytopathology, 153: 313–317.

Kefi A., Ben Slimene I., Karkouch I., Rihouey C., Azaeiz S., Bejaoui M., Belaid R., Cosette P., Jouenne T., Limam F. (2015): Characterization of endophytic *Bacillus* strains from tomato plants (*Lycopersicon esculentum*) displaying antifungal activity against *Botrytis cinerea* Pers. World Journal of Microbiology and Biotechnology, 31: 1967–1976.

Khayi S., des Essarts Y.R., Mondy S., Moumni M., Hélias V., BeuryCirou A., Faure D. (2015): Draft genome sequences of the three *Pectobacterium*-antagonistic bacteria *Pseudomonas brassicacearum* PP1-210F and PA1G7 and *Bacillus simplex* BA2H3. Genome Announcements, 3: e01497-14. doi: 10.1128/genomeA.01497-14

Kieser T., Bibb M.J., Buttner M.J., Chater K.F., Hopwood D.A. (2000): Practical *Streptomyces* Genetics. Norwich, The John Innes Foundation.

Kloepper J.W. (1993): Plant growth-promoting rhizobacteria as biological control agents. In: Metting FB Jr (ed.): Soil Microbial Ecology. New York, Dekker: 255–274.

Kloepper J.W., Ryu C.M., Zhang S. (2004): Induce systemic resistance and promotion of plant growth by *Bacillus* spp. Phytopathology, 94: 1259–1266.

Kobayashi D., El-Barrad N.H. (1996): Selection of bacterial antagonists using enrichment cultures for the control of summer patch disease in Kentucky bluegrass. Current Microbiology, 32: 106–110.

Koch E., Becker J.O., Berg G., Hauschild R., Jehle J., Köhl J. (2018): Biocontrol of plant diseases is not an unsafe technology. Journal of Plant Diseases and Protection, 125: 121–125.

Koumoutsi A., Chen X.H., Henne A., Liesegang H., Gabriele H., Franke P., Vater J., Borris R. (2004): Structural and functional characterization of gene clusters directing nonribosomal synthesis of bioactive lipopeptides in *Bacillus amyloliquefaciens* strain FZB42. Journal of Bacteriology, 186: 1084–1096.

Krzyzanowska D.M., Potrykus M., Golanowska M., Polonis K., Gwizdek-Wisniewska A., Lojkowska E., Jafra S. (2012): Rhizosphere bacteria as potential biocontrol agents against soft rot caused by various *Pectobacterium* and *Dickeya* spp. strains. Journal of Plant Pathology, 94: 367–378.

Leclere V., Bechet M., Adam A., Guez J.S., Wathelet B., Ongena M., Thonart P., Gancel F., Chollet-Imbert M., Jacques P. (2005): Mycosubtilin overproduction by *Bacillus subtilis* BBG100 enhances the organism's antagonistic and biocontrol activities. Applied and Environmental Microbiology, 71: 4577–4584.

Ling N., Xue C., Huang Q.W., Yang X.M., Xu Y.C., Shen Q.R. (2010): Development of a mode of application of bioorganic fertilizer for improving the biocontrol efficacy to *Fusarium* wilt. BioControl, 55: 673–683.

Liu D. (2017): Promotion of iron nutrition and growth on peanut by *Paenibacillus illinoisensis* and *Bacillus* sp. strains in calcareous soil. Brazilian Journal of Microbiology, 48: 656–670.

Lugtenberg B., Rozen D.E., Kamilova F. (2017): Wars between microbes on roots and fruits. F1000Research, 6: 343. doi: 10.12688/f1000research.10696.1

Ma H. (2007): Progress on control of potato soft rot in China. Biotechnology Bulletin, 1: 42–44.

Makhlouf A.H., Abdeen R. (2014): Investigation on the effect of chemical and biological control of bacterial soft rot disease of potato in storage. Journal of Biology, Agriculture and Healthcare, 4: 31–44.

Marimuthu S., Ramamoorthy V., Samiyappan R., Subbian P. (2013): Intercropping system with combined application of *Azospirillum* and *Pseudomonas fluorescens* reduces root rot incidence caused by *Rhizoctonia bataticola* and increases seed cotton yield. Journal of Phytopathology, 161: 405–411.

Massart S., Martinez-Medina M., Jijakli M.H. (2015): Biological control in the microbiome era: Challenges and opportunities. Biological Control, 89: 98–108.

Milgroom M.G., Cortesi P. (2004): Biological control of chestnut blight with hypovirulence: A critical analysis. Annual Review of Phytopathology, 42: 311–338.

Munir S., Li Y., He P., Cui W. (2018): *Bacillus subtilis* L1-21 possible assessment of inhibitory mechanism against phytopathogens and colonization in different plant hosts. Pakistan Journal of Agriculture Science, 55: 996–1002.

Neeraja C., Anil K., Purushotham P., Suma K., Sarma P. (2010): Biotechnological approaches to develop bacterial chitinases as a bioagent against fungal diseases. Critical Reviews in Biotechnology, 30: 231–241.

Nelkner J., Torres Tejerizo G., Hassa J., Lin T.W., Witte J., Verwaaijen B., Schlüter A. (2019): Genetic potential of the biocontrol agent *Pseudomonas brassicacearum* (formerly *P. trivialis*) 3Re2-7 unraveled by genome sequencing and mining, comparative genomics and transcriptomics. Genes, 10: 601. doi: 10.3390/genes10080601

Ngadze E., Coutinho T.A., van der Waals J.E. (2010): First report of soft rot of potatoes caused by *Dickeya dadantii* in Zimbabwe. Plant Disease, 94: 1263. doi: 10.1094/PDIS-05-10-0361

Nissinen R.M., Männistö M.K., van Elsas J.D. (2012): Endophytic bacterial communities in three arctic plants from low arctic fell tundra are cold-adapted and host-plant specific. FEMS Microbiology Ecology, 82: 510–522.

https://doi.org/10.17221/166/2020-PPS

Oshnoei F.T., Harighi B., Abdollahzadeh J. (2017): Isolation and identification of endophytic bacteria with plant-growth-promoting and biocontrol potential from the oak tree. European Journal for Pathology, 47: 1–8.

Paoletti M.G., Pimentel D. (2000): Environmental risks of pesticides versus genetic engineering for agricultural pest control. Journal of Agricultural and Environmental Ethics, 12: 279–303.

Phokim C., Jitareerat P., Photchanachai S., Cheevadhanarak S. (2006): Detection and classification of soft rot *Erwinia* of vegetables in Thailand by DNA polymerase chain reaction. In: Proceedings of the 4th International Conference on Managing Quality in Chains – The Integrated View on Fruits and Vegetables Quality, Aug 7, 2006, Bangkok, Thailand: 917–925.

Pieterse C.M.J., Zamioudis C., Berendsen R.L., Weller D.M., Van Wees S.C.M., Bakker P.A.H.M. (2014): Induced systemic resistance by beneficial microbes. Annual Review of Phytopathology, 52: 347–375.

Pritchard L., Glover R.H., Humphris S., Elphinstone J.G., Toth I.K. (2016): Genomics and taxonomy in diagnostics for food security: Soft-rotting enterobacterial plant pathogens. Analytical Methods, 8: 12–24.

Raaijmakers J.M., Mazzola M. (2012): Diversity and natural functions of antibiotics produced by beneficial and plant pathogenic bacteria. Annual Reviews of Phytopathology, 50: 403–424.

Rahman M.M., Ali M.E., Khan A.A., Hashim U., Akanda A.M., Hakim M.A. (2012): Characterization and identification of soft rot bacterial pathogens in Bangladeshi potatoes. African Journal of Microbiology Research, 6: 1437–1445.

Rahme L.G., Tan M.W., Le L., Wong S.M., Tompkins R.G., Calderwood S.B., Ausubel F.M. (1997): Use of model plant hosts to identify *Pseudomonas aeruginosa* virulence factors. Proceedings of the National Academy of Sciences of the United States of America, 94: 13245–13250.

Reinhold-Hurek B., Hurek T. (2011): Living inside plants: Bacterial endophytes. Current Opinion in Plant Biology, 14: 435–443.

Riley M.A., Wertz J.E. (2002): Bacteriocins: Evolution, ecology, and application. Annual Reviews Microbiology, 56: 117–137.

Romanazzi G., Sanzani S.M., Bi Y., Tian S., Martínez P.G., Alkan N. (2016): Induced resistance to control postharvest decay of fruit and vegetables. Postharvest Biology and Technology, 122: 82–94.

Romeiro R.S., Sousa R.M., Muchovej J.J., Kimura O. (1988): Soft rot of Peruvian carrot due to *Erwinia carotovora* in Brazil. Plant Pathology, 37: 300–302.

Romero-Perdomo F., Abril J., Camelo M., Moreno-Galván A., Pastrana I., Rojas-Tapias D., Bonilla R. (2017): *Azotobacter chroococcum* as a potentially useful bacterial biofertilizer for cotton (*Gossypium hirsutum*): Effect in reducing N fertilization. Revista Argentina de Microbiología, 49: 377–383.

Sandra A.I., Wright C.H., Zumoff L.S., Steven V.B. (2001): *Pantoea agglomerans* strain EH318 produces two antibiotics that inhibit *Erwinia amylovora in vitro*. Applied and Environmental Microbiology, 67: 282–292.

Santoyo G., Orozco-Mosqueda M.D.C., Govindappa M. (2012): Mechanisms of biocontrol and plant growth-promoting activity in soil bacterial species of *Bacillus* and *Pseudomonas*: A review. Biocontrol Science and Technology, 22: 855–872.

Selim H.M.M., Gomaa N.M., Essa A.M.M. (2017): Application of endophytic bacteria for the biocontrol of *Rhizoctonia solani* (Cantharellales: Ceratobasidiaceae) damping-off disease in cotton seedlings. Biocontrol Science and Technology, 27: 81–95.

Shanahan P., O'Sullivan D.J., Simpson P., Glennon J.D., O'Gara F. (1992): Isolation of 2,4-diacetylphloroglucinol from a fluorescent pseudomonad and investigation of physiological parameters influencing its production. Applied and Environmental Microbiology, 58: 353–358.

Schuerger A.C., Batzer J.C. (1993): Identification and host range of an *Erwinia* pathogen causing stem rots on hydroponically grown plants. Plant Disease, 77: 472–477.

Smith M.A. (1944): Bacterial soft rot of spinach. Phytopathology, 34: 747–752.

Spadaro D., Droby S. (2016): Development of biocontrol products for postharvest diseases of fruit: The importance of elucidating the mechanisms of action of yeast antagonists. Trends Food Science and Technology, 47: 39–49.

Syed Ab Rahman S.F., Singh E., Pieterse C.M.J., Schenk P.M. (2018): Emerging microbial biocontrol strategies for plant pathogens. Plant Sciences, 267: 102–111.

Takimoto S. (1931): A soft rot of sugarbeet and its causal organisms. Annals of the Phytopathological Society of Japan, 2: 350–356.

Tariq M., Yasmin S., Hafeez F.Y. (2010): Biological control of potato black scurf by rhizosphere associated bacteria. Brazilian Journal of Microbiology, 41: 439–451.

Thakore Y. (2006): The bio-bactericide market for global agricultural use. Indian Biotechnology, 2: 194–208.

Vanneste J.L., Yu J. (1996): Biological control of fire blight using *Erwinia herbicola* Eh252 and *Pseudomonas fluorescens* A506 separately or in combination. Acta Horticulture, 411: 351–353.

Viveros O.M., Jorquera M.A., Crowley D.E., Gajardo G., Mora M.L. (2010): Mechanisms and practical considerations involved in plant growth promotion by rhizobacteria. Journal of Soil Science and Plant Nutrition, 10: 293–319.

https://doi.org/10.17221/166/2020-PPS

Walker J. (2004): Bacterial soft rot. In: Chupp C. (ed.): Manual of Vegetable Plant Diseases. New Delhi: Shristi Book Distributors.

Wiesel L., Newton A.C., Elliott I., Booty D., Gilroy E.M., Birch P.R.J. (2014): Molecular effects of resistance elicitors from the biological origin and their potential for crop protection. Frontier Plant Science, 5: 655. doi: 10.3389/fpls.2014. 00

Wilhite S.E., Lumsden R.D., Strancy D.C. (2001): Peptide synthetase gene in *Trichoderma virens*. Applied and Environmental Microbiology, 67: 5055–5062.

Wimalajeewa D.L.S. (1976): Studies on bacterial soft rot of celery in Vicotoria. Australian Journal of Experimental Agriculture and Animal Husbandry, 16: 915–920.

Yuan W.M., Crawford D.L. (1995): Characterization of *Streptomyces lydicus* WYEC108 as a potential biocontrol agent against fungal root and seed rots. Applied and Environmental Microbiology, 61: 3119–3128.

Zang L.S., Wang S., Zhang F., Desneux N. (2020): Biological control with *Trichogramma* in China: History, present status and perspectives. Annual Review of Entomology, 66: 463–484.

Zhao Y., Li P., Huang K., Wang Y., Hu H., Sun Y. (2013): Control of postharvest soft rot caused by *Erwinia carotovora* of vegetables by a strain of *Bacillus amyloliquefaciens* and its potential modes of action. World Journal of Microbiology and Biotechnology, 29: 411–420.

Zhou D., Huang X.F., Chaparro J.M., Badri D.V., Manter D.K. (2016): Root and bacterial secretions regulate the interaction between plants and PGPR leading to distinct plant growth promotion effects. Plant Soil, 401: 259–272.

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