Available Online at EScience Press
Plant Protection
ISSN: 2617-1287 (Online), 2617-1279 (Print)
http://esciencepress.net/journals/PP

ROLE OF RHIZOBACTERIA ON PLANTS GROWTH AND BIOLOGICAL CONTROL OF PLANT DISEASES: A REVIEW

Muhammad Umer[1], Mustansar Mubeen[2], Yasir Iftikhar[2], Munsif Ali Shad[3], Hafiz Muhammad Usman[1], Muhammad Aamir Sohail[4], Muhammad Nauman Atiq[5], Aqleem Abbas[1], Muhammad Ateeq[6]

[1] State Key Laboratory of Agricultural Microbiology and Provincial Key Laboratory of Plant Pathology of Hubei Province, College of Plant Science and Technology, Huazhong Agricultural University, Wuhan 430070, Hubei, P. R. China.
[2] Department of Plant Pathology, College of Agriculture, University of Sargodha, Sargodha, 40100, Pakistan.
[3] National Key Laboratory of Crop Genetic Improvement, College of Life Science and Technology, Huazhong Agricultural University, Wuhan 430070, Hubei, P. R. China..
[4] National Key Laboratory of Plant Molecular Genetics, Center for Excellence in Molecular Plant Sciences, Institute of Plant Physiology and Ecology, Chinese Academy of Sciences, Shanghai, P. R. China.
[5] Hubei Insect Resources Utilization and Sustainable Pest Management Key Laboratory, College of Plant Science and Technology, Huazhong Agricultural University, Wuhan 430070, Hubei, P. R. China.
[6] Key Laboratory of Horticultural Plant Biology, Ministry of Education/College of Horticulture and Forestry Sciences, Huazhong Agricultural University, Wuhan 430070, P. R. China.

ARTICLE INFO

Article history
Received: 17th March, 2021
Revised: 18th April, 2021
Accepted: 18th April, 2021

Keywords
Rhizobacteria
Biocontrol agents
Systemic Resistance
Antifungal
Plant Growth Promoters

ABSTRACT

Rhizobacteria are plant root colonizers mainly found in soil naturally and impact plant growth and nourishment. When inoculated with rhizobacterial strains at an early growing stage, improve vigor and biomass production influence by the directly influenced shoot and root growth. Plants such as forest trees, crops, and horticultural crops inoculated with rhizobacteria may induce multiple effects on plant growth as on the enhancement of seedling germination. Plant stands health, vigor, height, root size, shoot, root biomass, early bloom, chlorophyll content, and enhanced nodulation in legumes. The beneficial influence of rhizobacteria on the nutrient uptake, yield, and growth of plants is diversifying mechanism. To fix nitrogen in legumes, they increase other nutrient supply, e.g., iron, copper, sulphur, and phosphorus, induce production of plant hormones, increase the activity of beneficial microbes, and act as antagonist disease-causing fungi, bacteria and check on the population of insect pests. New era new needs, so rhizobacteria gained importance for sustainable agriculture without altering the environment. Billions of dollars are being invested in the biocontrol research and increasing the number of biocontrol agents being commercialized for various plant crops. In this review, we have discussed multiple bacteria which act as biocontrol agents and their mechanisms.

Corresponding Author: Mustansar Mubeen
Email: mustansar01@yahoo.com

INTRODUCTION

Microbes used as a control agent are promising alternatives for replacing chemicals or reducing their use. About one hundred microbial products have been

marketed for biocontrol, but a product's success is variable. This is due to the varying field and biocontrol agent's varying conditions strongly influenced by the biotic and abiotic conditions. In greenhouse or control conditions, biocontrol activity is more successful than in the open field (Paulitz and Bélanger, 2001). In plant diseases, the term biocontrol or biological control, is widely used without alarming the environment. The organisms that suppress the growth of pathogens are referred to as biological control agents. Biocontrol is the suppression of pathogenic microorganisms by one or more other beneficial organisms or natural enemies. Since then, many studies have focused on biocontrol potential, which increases the knowledge of the interaction between pathogen, host, and antagonist (Pal and Gardener, 2006). It is an effective and environmentally sound means for suppressing pests or pathogens through antagonists (Elsevier, 2008). The term biocontrol uses early in 1893 by Dr. Carl Freiherr, when he published their research on biocontrol of insects of a forest, and in 1914, it was used to control fungal diseases of plants (Maloy and Lang, 2003). It is an interdisciplinary science now by combining microbiology, phytopathology, entomology, weed science, and virology to control and reduce insects, microorganisms, pathogens, and plants that damage domestic plants or crops. In this method microorganisms such as bacteria, fungi, viruses, or insects were used to control pathogenic organisms (Eilenberg et al., 2001). Aphids or scales population can be controlled by introducing wasps, aphids and weeds controlled by beetles, fungi such as *Trichoderma* spp. and *Gliocladium* spp. Controlled soil-borne fungal pathogens and bacteria such as *Pseudomonas* and *Bacillus* species caused soil-borne and foliar diseases (Jacobsen et al., 2004). Microbial biocontrol products are a great concern of society as a reference to biosafety. Many human, animals, and plant pathogens can be biocontrol agents to control plant diseases (Chiarini et al., 2006). These agents useto increase their population in the environment and may show their undesirable presence in food or forage. The fungal pathogen can cause soil-borne diseases, most commonly controlled by chemical fungicides (Roberts, 1994). The use of chemicals worldwide increases twelve times since the 1950 (Van Drieschez and Bellows, 1996). Fungicides are toxic and carcinogenic. They can persist in the environment for a long time and cannot be easily biodegradable. However, serious problems rose due to their residual effect on natural resources and non-targeted species (Campbell, 1989). Most reported biocontrol programs focus on root pathogens within the rhizosphere (Payne and Lynch, 1988). Although many biocontrol agents have been tested *in vitro*, a few have been commercialized. It cannot produce consistent results so, variable results are generated (Milner et al., 1996). Environment parameters influence disease progression. Few biocontrol studies extended their focus to understand nature and efficacy over time under different environmental factors. Biocontrol is not effective as chemical control often controls disease (Wilson et al., 1994). It helps explain the variation found in biocontrol agents effectiveness under field conditions if an understanding of the interaction between the pathogen, environment, host, and antagonist population. Biological control includes predation or parasitism, parasitism by fungal (myco-parasitism) or antimicrobial compounds production (Vinale et al., 2008).

Mechanisms of biocontrol

The studies of suppressive soil introduce the phenomenon of biocontrol by microbes about 70 years ago (Baker and Snyder, 1965). Suppressive soil plants do not suffer from pathogens, although plant pathogenic microorganisms are present in the soil. The ability of suppressive soils to suppress pathogens is due to antagonist activity, elimination by pasteurization, and gamma rays irradiations that allow the development of diseases (Cook and Rovira, 1976) Suppressiveness can be introduced into conducive-soils by adding at least 0.1% of suppressive soils; latter soil can suppress pathogens (Shipton et al., 1973). Biocontrol microbes can inhibit pathogens by producing antifungal metabolites, according to Baker and Snyder (1965). Biocontrol mechanisms include indirect and direct interactions (Figure 1).

Indirect interactions

Indirect interactions are phenomena in which antagonists do not act directly on the targeted pathogen, such as cross-protection, hypovirulence, and growth stimulation. It is a stimulating resistance mechanism or changing the surrounding area's ecology so that pathogens inhibit from germinating and infecting the plant (Fravel, 1988).

Hypo-virulence or cross-protection

Cross-protection is a phenomenon when an established virus inhibits another disease-causing virus entry

(Dodds, 1999). The disease-causing virus usually fails to establish in a host. Since this mode of action occurs only with viruses.

Induce systemic resistance

Systemic acquired resistance is the development of resistance throughout the whole plant. Plants are challenged by abiotic and biotic elicitors (agents inducing resistance), including non-pathogenic microbes. These defense mechanisms cause resistance and limit or even prevent subsequent infections by pathogens. Resistance development is spread from areas distant to the original inoculation site and can be very unspecific in its target pathogen. The systemic protection of plants by antagonist induces when applied to a plant known as induced systemic resistance (ISR) (Ramamoorthy et al., 2002).

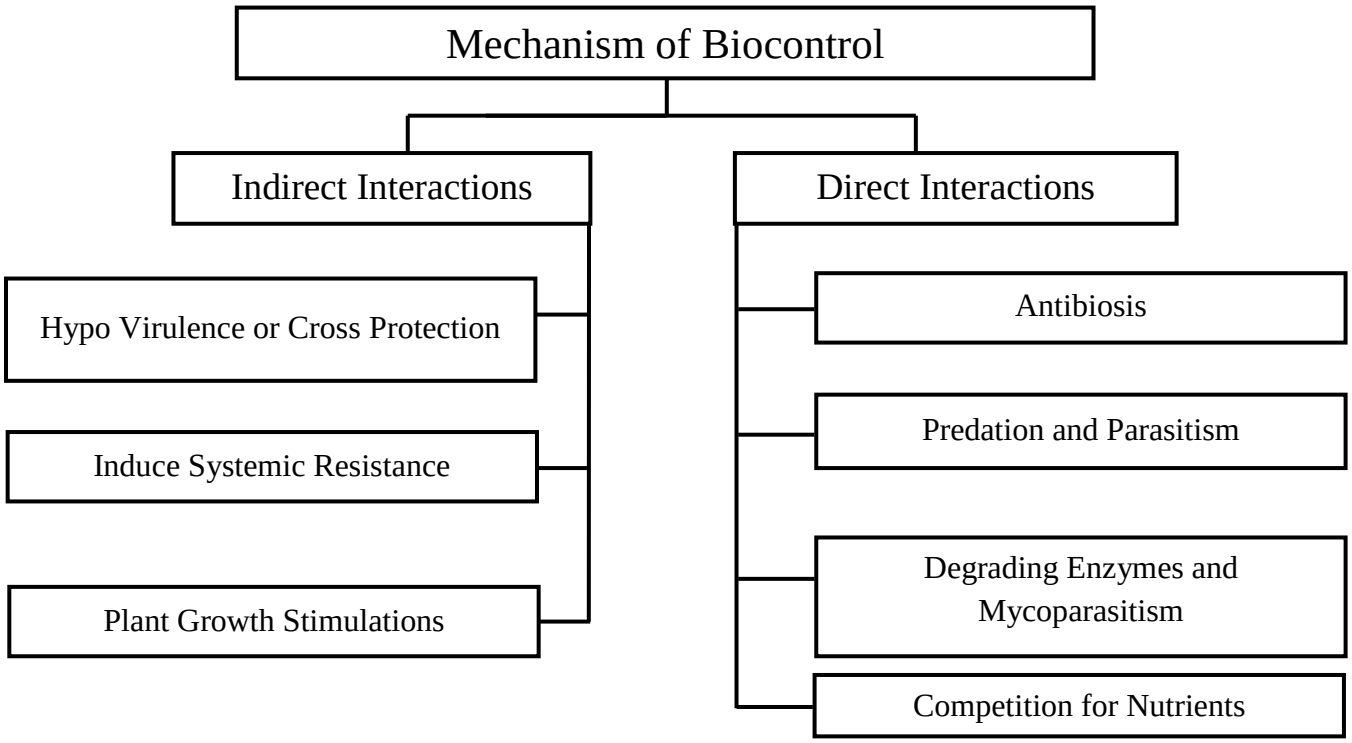

Figure 1. Mechanism of biocontrol activity.

Types of Elicitors: organic molecules, chemicals, and antagonists. Organic elicitors can involve in induced resistance include ethylene, chitin, salicylic acid, and chitosan oligosaccharides (Droby et al., 1996). Antagonistic organisms cause resistance, usually by producing a wide range of organic molecules. These molecules include pathogenesis-related proteins and jasmonates (Kogel et al., 1995). Elicitation can also induce physical means such as wounding, heat treatment, gamma radiation, and UV-light (Mari and Guizzardi, 1998) elicitors (Table 1). *Bacillus spp*. mediated elicitation of ISR in plants has been reported, such as *B.* cereus, *B. subtilis, B. amyloliquifaciens*, *B. mycoides* and *B. pumilisa* significant reduction in diseases. *Bacillus pumilis* strains have been reported in ISR by inducing phenolic compounds' accumulation when pea roots are attacked by *F. oxysporum* (Kloepper et al., 2004). The phenolic compounds enhance the mechanical strength of the plant cell wall and inhibit fungal growth because they are toxic to fungi. The results show *Bacillus* spp. efficacy as a biocontrol agent than to *Pseudomonas* spp. in the soil rhizosphere (Ramamoorthy et al., 2002). Chemicals induce resistance in plant tissue, including benzo (1,2,3) thiadiazole-7-carbothioic acid S-methyl ester, 2,6-dichloroisonicotinic, and F-3-aminobutyric acid. In plants, induction signaling molecules are produced by treating with elicitors and act as prime for activation of resistance in the rest of the host-host act upon signaling molecules by triggering their gene expression. Defense systems include lignification of cell walls by adding chemical cross-linkages in wall peptides, making it difficult for the pathogen to establish infection by lysis; suberification of

tissues, suberin infiltrate cell wall, making them corklike, and production of phytoalexins, chitinase, and beta-1,3-glucanases. When a pathogen attacks, a hypersensitive reaction in plants is elicited, and necrosis occurs. A series of test of electors against *Fusarium oxysporum* as a causal agent of tomato root and crown rot. Root cells of tomato show modifications after treated with elicitors. Different elicitors show different types of alterations in root cells. They suggested that there may be different pathways followed by elicitation. Induced resistance is an important resistance found in vegetative tissues of the plant and harvested fruits (Benhamou et al., 2001). Some reports enlighten that certain biocontrol agents may be able to cause interaction with host tissues, particularly during wounding and enhancing wound healing (Droby and Chalutz, 1994). The *Candida saitoana* also stimulated papillae and other protuberances in the tissue underlying the wounded area (El-Ghaouth, 1997).

These protuberances might contain phenolic-like substances and restrict the spread of the invading pathogens. Different combinations of induced resistance and other modes of action may be involved in biocontrol in many cases. A strain of *Pseudomonas fluorescens* CHAo, used to suppress *Thielaviopsis basicola* causal agent of black root rot disease of tobacco. *P. fluorescens* produce antibiotics and siderophores for stopping black root rot of tobacco. However, it was found that hydrogen cyanide production is also important. ISR after induction, protecting plants from a wide spectrum of pathogens; it also protects plants systematically following the application of an inducing agent. Except for ISR, other mechanisms of biocontrol are not systemic generally. A normal healthy plant has its defense genes (inducible genes) (Weller, 1988). Plant defense mechanisms were activated when appropriate signals induce endogenous defense mechanisms. The plants own defense mechanisms will be activated. The use of *Bacillus* spp. for the induction of ISR in plants is now becoming a novel plant protection strategy (Zhang et al., 2002).

Table 1. Rhizobacteria induce systemic resistance in host plants by producing antifungal compounds.

Biocontrol Agent	Plant species	Compounds or products	Reference
Pseudomonas fluorescens CHA0	Tobacco	Siderophore	Maurhofer et al. (1994)
Bacillus subtilis AF1	Groundnut	Lipoxygenase	Sailaja et al. (1998)
Pseudomonas fluorescens WCS417	Tomato	Lipopolysaccharide	Duijff et al. (1997)
Bacillus spp.	Grapes	Phytoalexin Induction	Paul et al. (1998)
Serratia marcescens 90-166	Cucumber	Siderophore	Press et al. (2001)
Bacillus mycoides Bac J	Sugar beet	Peroxidase, chitinase and β-1,3-glucanase	Bargabus et al. (2002)
*Bacillus pumilus*203-6	Sugar beet	Peroxidase, chitinase and β-1,3-glucanase	Bargabus et al. (2002)
Pseudomonas fluorescens BTP1	Beans	Z,3-hexenal	Ongena et al. (2004)
Bacillus subtilis GB03	*Arabidopsis*	2,3-butanediol	Ryu et al. (2004)

Plant growth stimulations

Plant growth stimulated by various types of bacteria has been known for decades and can also be introduced into the soil, on seed or roots to improve plant growth and health. Genus *Rhizobium* is growth-promoting organisms, the most widely known group (Raaijmakers et al., 2002). The changes in plant rhizosphere microbial community when treating soybeans with *Bacillus cereus* strain UW85. *B. cereus* UW85 becomes the dominant organism in the community and causes reduction in root disease (Gilbert et al., 1994). These results become the base of Gilbert's camouflage hypothesis. According to this hypothesis, the microbe community changes the root ecology to resemble that of the soil, disguising the root. The pathogen will not detect it or make it less attractive to pathogens and protect it from the disease. One mechanism in which antibiotics are produced by antagonist work. It may not act directly on the pathogen but indirectly influencing the microbial community to adapt (Milner et al., 1996). There are two basic approaches available in postharvest biocontrol: promoting and managing natural antagonists that

already exist on the surface or artificial introduction of target antagonists. It has been suggested that certain hosts may control the microbial populations on their surfaces by expressing their genes (Wilson and Wisniewski, 1989). The manipulation of the microbial community by a host is more suppressive to diseases. Modification in the host genetics ensures that a condition suppressive microbial population will be sustained. Some microbial antagonists may play a role in stimulating the growth of the host. Soybeans treated with *B. cereus* UW85 increased root nodulation and contributed to plant health (Milner et al., 1996). The antagonists act more indirectly by promoting plant health or altering microbial populations and keeping plants healthy useful in the future.

Direct interactions

Commonly direct interactions between the antagonist and pathogen are found. To date, studies on direct interactions have been more extensive compared to indirect interactions. Direct interactions include antibiosis, parasitism, nutrients competition, and space and volatile substances. The production of enzymes, volatile, and toxic substances by the antagonist can be seen as antibiosis (Fravel, 1988).

Antibiosis

The inhibition of one organism due to metabolite production of another organism (Baker and Cook, 1974). Antibiotics are organic compounds with low molecular weight produced by antagonists that are dangerous to other microbes' growth (Fravel, 1988). The antibiosis produces toxic metabolites like lytic enzymes, antibiotics, and volatile substances. However, antibiosis is the production of simple substances not commonly considered as antibiotics but could result from an alcohol or change in the environment's pH (Milner et al., 1996). Less attention has been given to non-volatile antibiotics have great consideration that antibiosis is mediated through volatile substances. Ammonia, alkyl pyrones, ethanol, isobutanol, isoamyl alcohol, and isobutyric acid are produced by volatile substances (Fravel, 1988). In, *in vitro* analysis molecules can directly inhibit fungi. *Bacillus subtilis* produces volatile substances to inhibit the growth of *Rhizoctonia solani* and *Pythium ultimum*. Hydrogen cyanide (HCN) is reported as a secondary antifungal metabolite produced by antagonist. Other antifungal metabolites' production belonged to a class of cyclic lipopeptide as visconsinamide and tensin (Bloemberg and Lugtenberg, 2001). Rhizosphere bacteria produce some secondary metabolites, which are small chain organic molecules for inhibiting other microorganisms. These compounds provide an advantage in colonization in the rhizosphere by the elimination of competitive organisms. Metabolites of antagonists are involved in antibiosis. Antibiosis is the first revealed biocontrol mechanism, and it is an efficient one, according to some scientists. Four approaches determine the role of antibiosis in antagonism (Milner et al., 1996); Firstly, mutants unable to produce antibiotic for tested activity. If they cannot have antibiotics, they cannot control pathogens showing antibiosis involvement (Leifert et al., 1995). Secondly, if it is effective to control disease in the field, purified and tested antibiotics are involved in antagonism. However, antibiotics can adsorb onto host tissue or soil particles for controlling pathogens. Thirdly, use a pathogen which is insensitive to an antibiotic. If antagonist inhibits pathogen growth, then antibiosis is not involved. Fourthly, a gene coding for antibiotic cloned in an expression vector and evaluated for antifungal activity. Phenazine-1-carboxylic acid is an antibiotic produced by *Pseudomonas fluorescens* strain 2-79 against *Gaeumannomyces graminis* var. *tritici* causal agent of take-all of wheat. Antibiotics produced by antagonists suppress the primary infection of a pathogen. It can also be isolated by the rhizosphere of healthy roots. Mutants cannot produce phenazine-1-carboxylic acid to suppress pathogens (Bull et al., 1991). Different approaches are present to exploit antibiosis. It self-produced, partially purified, and can be used as a biocontrol agent. The antagonist can produce numerous antibiotics (Tsuge et al., 1996). *Pseudomonades* are known to produce various inhibitory compounds for suppressing pathogen (O'sullivan and O'Gara, 1992). *P. fluorescens* strain CHAo produces hydrogen cyanide, antibodies such as 2,4-diacetylphloroglucinol, pyoluterorin and pyoverdine. Pyrrolnitrium suppressed *Rhizoctonia solani* and pyoluteorin suppressed *P. ultimum* on cotton seedling. Visconsin-amide produced by *Pseudomonas fluorescens* reduces the growth of *Pythium* spp. and *Rhizoctonia solani*. These induce encystment of *Pythium* zoospores and affect the mycelium of *R. solani* and *P. ultimum*, causing reduction of growth, intracellular activity, hypal swelling, and increased branching (De Souza et al., 2003). The*Pseudomonas fluorescens* strains antagonized *R. solani* and *P. ultimum,* investigation of sugar beet in the early seed germination and root develop increased by cyclic lipopeptide antibiotics *in vitro* (Nielsen and Sørensen, 1997). *T. basieola* causal agent of Tobacco

root rotis suppressed by hydrogen cyanide production 2,4-diacetylphloroglucinol also suppresses *G. graminis* causal agent of take-all of wheat. *B. subtilis* cell-free filtrates protect fruit from *Monilinia fruticola*. Several iturin peptides and active material were isolated and identified, having small toxicity and lacking allergenic properties are active against few bacteria but a wide variety of fungi (Gueldner et al., 1988). Direct effects of a few antibiotics have been determined by-products of the metabolic activity of *B. cereus* UW85 are antagonistic to oomycete and accumulate in culture supernatants. Some induce their antagonistic activity through the sequestering of calcium and the production of ammonium. Thus, pH of the medium increases, and lysis of oomycete zoospores occur. But increase in ammonium to calcium ratio does not count for the ability of *B. cereus* UW85 for suppressing disease. Zwittermicin A is a linear aminopolyol with a broad host range. It induces reversible inhibition of germ tube elongation of *Phytophthora medicaginis*. Antibiotic B is an aminoglycoside with a narrower targeted range than zwittermicin A, both of them are used to suppress bacteria and fungi. *B. cereus* UW85 also produces additional metabolites for antifungal activity rather than zwittermicin A and antibiotic B (Milner et al., 1996).

The genus *Bacillus* member*s* showed the production of antibiotics, and one of the most important species is *Bacillus subtilus* (Földes et al., 2000). One of the widely distributed bacterial species in the agricultural system is *Bacillus subtilus* and its strain GBO3, mostly commercially distributed. It is effectively colonized to roots and produced antifungal compounds used to form fungicide (McSpadden and Fravel, 2002). Recombinant DNA technology makes it easy to manipulate and exploited antibiotics to enhance disease suppression. The pathogen can also induce resistance against antibiotics by a single mutation or loss in antagonist efficacy. Natamycin is an antibiotic that is widely used in food preservation to which little resistance has been found. Some public concern remains about using antibiotics produced by antagonists against postharvest diseases (Table 2). The introduction of antibiotics in food supplies may have adverse effects on human resistance to antibiotics (Spadaro and Gullino, 2004).

Table 2. Antibiotics produced by antifungal rhizobacteria.

Biocontrol Agent	Antibiotic	Disease	Pathogen	Reference
Agrobacterium tumefaciens	Agrocin 84	Crown gall	*Agrobacterium radiobacter*	Kerr (1980)
Pseudomonas fluorescens	2, 4-diacetylphloroglucinol	Damping off	*Pythium spp.*	Shanahan et al. (1992)
Bacillus cereus UW85	Zwittermicin A	Damping off	*Phytophthora medicaginis*	Smith et al. (1993)
Bacillus licheniformis	Bacitracin A to F	Damping off	*Phytophthora infestant*	Podlesek et al. (2000)
Bacillus subtilis AU195	Bacillomycin D	Aflatoxin contamination	*Aspergillus flavus*	Moyne et al. (2001)
Pantoeaagglomerans C9-1	Herbicolin	Fire blight	*Erwinia amylovora*	Sandra et al. (2001)
Bacillus Isolates	Isocoumrin and Coumarin	Bacterial blight	*Xanthomonas campestris*	Pinchuk et al. (2002)
Bacillus amyloliquefaciens FZB42	Bacillomycin, fengycin	*Fusarium* Wilt	*Fusarium oxysporum*	Koumoutsi et al. (2004)
Bacillus subtilis QST713	Iturin A	Damping off Paulitz	*Botrytis cinerea* and *Rhizoctoniasolani*	Kloepper et al. (2004)
Bacillus subtilis BBG100	Mycosubtilin	Damping off	*Pythium aphanidermatum*	Leclère et al. (2005)

Predation and parasitism

The antagonist can directly attack plant pathogenic organisms by producing lytic enzymes such as chitinases, proteases, beta (1,3)-glucanases, and lipases for the cell wall degradation. Destruction and consumption of the pathogens cell wall by antagonists. They are using *Trichoderma* spp. The best-known example of microorganisms is parasitism and predation (Bolwerk et al., 2005).

Degrading enzymes and mycoparasitism

Parasitism for soil-borne and foliar fungal diseases by the antagonist is well known. It covers various interactions, such as morphological disturbance, overgrowth of one organism on another (especially in fungi), penetration, and direct parasitism by producing haustoria or lysis of cells (Wilson and Wisniewski, 1989). When parasite kills its host first and then takes off nutrient from its necrotrophic interaction occurs (Skidmore, 1976). Antagonist produces several enzymes for biocontrol activity, such as glucose oxidase, lipase, protease, laminarinase, beta-glucosidases, mannanases, xylanase, cellulases, chitinase and chitosanase (Picard et al., 2000). The involvement of enzymes in biocontrol distorts the distinction between parasitism and antibiosis. The antagonist producing cell wall degrading enzymes that simultaneously parasite the pathogen aid inhibits it through antibiosis (Table 3) (Fravel, 1988). *Bacillus* spp. X-b, produces different enzymes (chitinase, laminarinase, lipase, protease, and chitosanase). In postharvest diseases, little is known about antagonists direct parasitism to pathogens (Wilson et al., 1994). *Pichia guilliermondi* is a yeast that parasitized *Botrytis cinerea* hyphae. The antagonist can produce hydrolases that degrade the fungal cell wall (Droby et al., 1996). The postulated that yeast might have the ability to degrade fungal tissues. Fungal hyphae were after coming in contact with yeast showing alterations ranging from cell wall swelling to cytoplasm degradation (El-Ghaouth, 1997). The yeast can also be able to produce fungal cell wall degrading enzymes such as chitinase and beta-1,3 glucanase.

Table 3. Enzymes involved in biocontrol against fungi produced by antifungal rhizobacteria.

Biocontrol Agent	Enzymes	Pathogen	Reference
Bacillus cereus UW85	1,3-Glucanase	*Penicillium expansum*	Gilbert et al. (1994)
Bacillus polymyxa	Chitinase	*Rhizoctonia solani* and *Pythium ultimum*	Frändberg and Schnürer (1994)
Pseudomonas spp.	Chitinase	*Penicillium roqueforti*	Frändberg and Schnürer (1994)
Bacillus subtlis Af1	β-1,3-Glucanase	*Aspergillus niger*	Podile and Prakash (1996)
Bacillus pumlius	Glucanolytic and Proteolytic	*Aphanomyces cochleoides*	Nielsen and Sørensen (1997)
Corynebacterium spp.	Exo-β-1,3-Glucanase	*Penicillium roqueforti*	Jijakli and Lepoivre (1998)

Competition for nutrients

Vitamins, sugars, and organic acids exuded from roots and present in the rhizosphere are the most important nutrients for the microbes. The antagonist's ability to utilize nutrients and occupies sites on roots before pathogen's arrival is based on competition for nutrients. This mechanism is firstly observed in *Fusarium* wilt of carnation by nonpathogenic *F. oxysporum* strain 618-12 decreased disease incidence by 80% (Postma and Luttikholt, 1996). Non-pathogenic *F. oxysporum* strain Fo47 at the concentration of 10-100% higher than the pathogenic *F. oxysporum*, suppress disease (Bolwerk et al., 2005). The higher ratio of Fo47 made it superior at rhizosphere than pathogen does, making this strain capable of disease suppression. Efficient root colonization is an essential character of an antagonist. However, this mode of action is for fungus-fungus interaction. One of the strains *F. oxysporum* Fo47, is available in several countries (Paulitz and Bélanger, 2001). The microbial population's ability to compete for nutrients within the rhizosphere is an important character for effective biocontrol of soil-borne pathogens (de Weert et al., 2002).

Exudate consumption

The carbon content, fixed by photosynthesis in plants,

secretes 5-21% of all into the rhizosphere (Marschner, 2011). It depends on the substrate in which the plant is growing, and it is altered by microbes (Walker et al., 2004). The root exudates of cucumber, tomato and sweet pepper are similar in composition found in a recent study on root exudation of plants growing on stone wool. Major organic acids are citric, succinic, and malic acids, whereas major sugar includes fructose and glucose in developing ages of plant, organic acids, and sugars exudation increases. Carbon utilizable is higher by organic acids so. Their amounts were considerably higher than sugars (Kamilova et al., 2006). Good root colonizer efficiently consumes root exudates for their nourishment. Mutants of *Pseudomonas fluorescens* strain WCS365 impaired in organic acid utilization cannot effectively colonize the plant root (Lugtenberg et al., 2001).

Role of motility and chemotaxis

The flagella-less mutants can occupy on root part, which is proximity to the seed, but they cannot colonize the root tip efficiently. The soil type influence on motility, root colonization, the plant and bacterial strain used, flagella are most important for bacteria to move from along growing root to root tip (Lugtenberg et al., 2001). Plant roots do not produce exudates equally along their surface, but some intracellular junctions are supposed to be the major locations from exudates released. The root tip is another hot spot of exudation of a growing root. That is why intracellular junctions are penetration sites for pathogen into root tissue, and colonization of these sites by the antagonist is a key event in biocontrol (Bolwerk et al., 2005). Chemotaxis is the phenomenon for bacteria to enable track the exudation sites. The *P. fluorescens* strain WCS365 gives a positive chemotactic response towards root exudates, dicarboxylic and tricarboxylic acids are major components and several amino acids but not towards exudates sugars. The sugar utilization deficient mutant strains retain their root colonizing ability at the level of wild-type strains. The result shows that root exudates composition (i) sugars are not crucial as a carbon source for *P. fluorescens* strain WCS365 and (ii) chemotaxis drives this excellent colonizer towards several major root exudate compounds (Walsh et al., 1995).

Factors affecting biocontrol activity

The antagonist, which controls or suppresses pathogen in a laboratory, always does not effective in the field. The host passes from series of evolution or mutation day by day and changes its physical, biological, chemical properties. Pathogenic characteristics also determine the antagonist's efficacy. The antagonist may fluctuate while changing in environmental conditions, population, and microbial colonizer presence in the biological system (Milner et al., 1996). These factors affect the efficacy of the biocontrol agent (Figure 2).

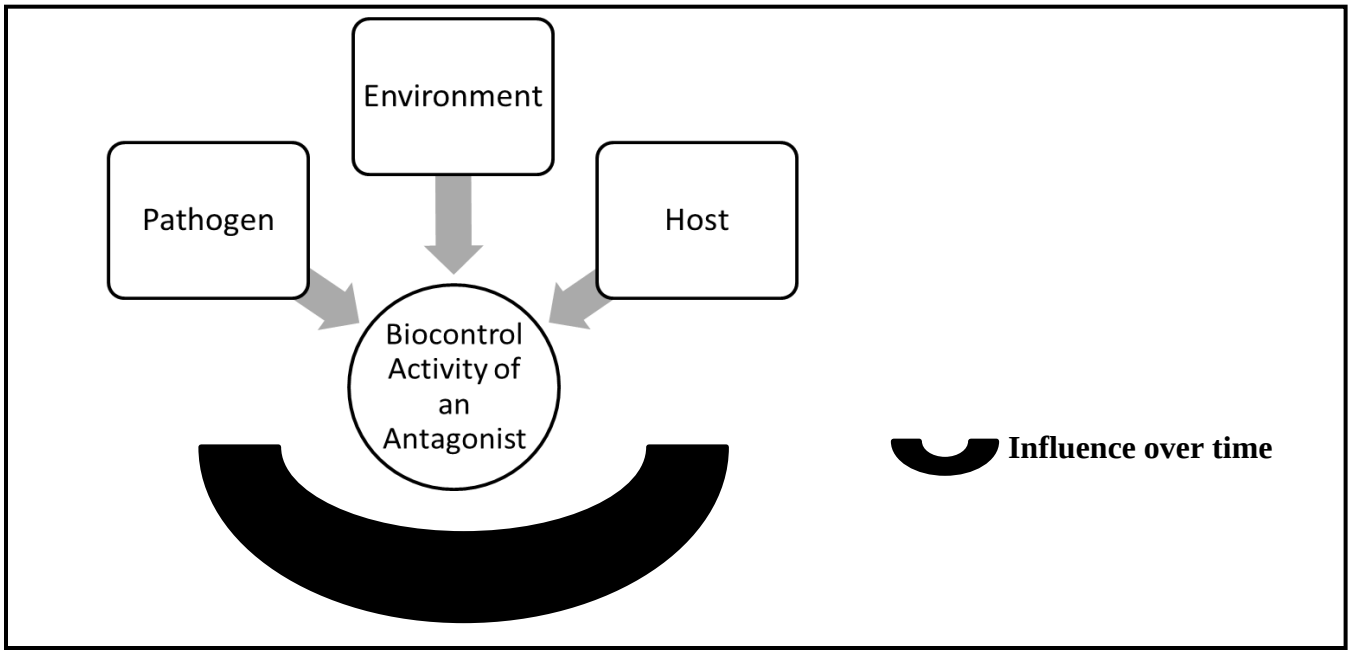

Figure 2. Influence of host, antagonist, and pathogen on biocontrol activity and their interaction with one another over time within an environment

Plant affecting biocontrol activity

Plant itself has a dual role in biocontrol activity. It suppresses pathogen activity through innate resistance through its own resistance mechanisms reduces the pathogen's activities (Droby et al., 1996). It also provides a site of action of pathogen and antagonist where the interaction of both occurs. The host excretion of exudates, ion and water uptake, gaseous exchange, and their surface temperature affect pathogen and antagonist interaction (Bellows, 1999). An environmental factor affects microbes' nature, influencing plant growth and development and microorganism-microorganism relations (Spurr, 1994). The micro-ecosystem is very complex, and its interactions are affected by physical and chemical variables on the plant surface (Morris et al., 1985). In the preharvest scenario, disease control is a strategy to keep plants as healthy and pathogenic inoculum low as possible (Ippolito and Nigro, 2000). The decay of fresh produce is due to fungal infection or physiological processes (senescence). The senescence-accelerated factors and microbial growth promotes postharvest decay. The mechanical and physiological injuries and undesirable storage conditions increase erosion. The rate of senescence slows, and microbial growth inhibits by any treatment. In postharvest disease control, it is a key factor mechanism (Roberts, 1994). The aerial portion of plants is a hostile environment for colonizing microbes (Campbell, 1989). The growth of microbes becomes restricted due to environmental factors. Nutrient levels, microclimate variability, such as temperature, moisture and irradiation (Van Drieschez and Bellows, 1996). As well as colonization, growth and effectiveness also affected of an antagonist (Romantschuk et al., 1996). Plant canopy, size, shape, and surface topography of leaves and fruits influenced the macro environment. Leaf age and position influenced the microbial colonizing population in the phyllosphere. Microbes' exposure increases on senescent and necrotic leaves when environmental extremes exist rather than living young leaves (Pfender, 1996). Ecological factors can easily control storage conditions (Pusey, 1994). Species of plants, cultivars, and at different growth stages, physical characteristics of plant surfaces vary. Plants' physical structure includes an epidermal, guard, and special functional cells (trichomes, or leaf hairs), ranging considerably in size, shape, and density (Spurr, 1994). Cuticle covered leaf surface and made up with long-chain hydrocarbons, alkyl esters, free primary alcohols, and fatty acids may contain wax, embedded into and upon on. Composition, distribution, thickness, and resistance to abrasion of resin are variable. Wax regeneration can do young leaves, but with the passage of age, this ability declines resulting in the retention of water films and leaching of nutrients. Plant surface chemical composition varies greatly. Carbohydrates, amino acids, organic acids, sugar alcohols, mineral trace elements, vitamins, hormones, and antimicrobial compounds such as phenols and terpenoids originated endogenously or exogenously in phylloplane (Derridji, 1996). Nutrients are important because they directly provide growth substrates for microbes and indirectly induce secondary metabolites such as antibiotics. The sources of nutrients soil particles, dust, ions, and solutes in rainwater, aphid honeydew, pollen, dead microbes, and bird and insect excrements are exogenous. Wounding, leaching action of rain, dew, fog, and active exudation through guttation by hydathodes or even cuticles endogenous nutrients removed (Schönherr and Baur, 1996). Host leaf position, plant surface, age, temperature, fertility, pH, leaching medium, leaf injury, exudates concentrations quantitatively and qualitatively varied. Nutrients affect the utilization of other nutrients, but some may be toxic to microbes. Necrotic tissue and senescent distinction are difficult between the plant surface and interior (Pfender, 1996). Bacteria, yeast, and fungi are biological compositions on the plant surface. Interacting community on the plant surface is not constant because microbes succeed one another over time. Microbial population density and host are affected under the influence of biotic and abiotic factors. Surface inhabitants are epiphytes (growing on the plant surface and utilizing available nutrients) and endophytes (parasitizing the internal plant tissues and using nutrients from the plant to grow). On phylloplane, bacteria are usually the first colonists, yeasts, and then filamentous fungi. The inoculum sources are soil, seed, air, and buds, as well as overwintering shoots. Air current carry spores may probably be the primary source of filamentous fungi. The inoculum, environment, and host phenology direct the phylloplane's sequential microbial colonization (Blakeman, 1985). The degree of insect infestation, existing weather conditions, and cropping practices alter this pattern. Colonization may be influenced by births, immigration, emigration, growth rate, or leaf and tree canopy (Lindow, 1996). Microbes’

colonization sites on leaves are along veins and in grooves above on the epidermal wall. That is because of localized concentrations of nutrients, trapping and deposition of the colonists, and protection from erosion or water film retention. Plant genes, when expressed; affect the microbial community on its surface and the area surrounding it. In certain cases, the rhizosphere microbial communities found on disease-resistant cultivars have similarities to the microbial communities in the surrounding soil than those of susceptible cultivars. This may play to protect the host from a pathogen (Gilbert et al., 1994).

Pathogen affecting biocontrol activity

Pathogen behavior is one of the most important considerations in selecting biocontrol agents; each pathogen has different behavior interactions with the host due to the genetic variability and diversity of ecological fitness. Fungi that successfully colonized on plant surface locate nutrients and convert them into a viable reproductive or migratory form without yielding to competition with neighbors, unfavorable conditions, or adverse host responses (Rayner, 1996). Pathogen behavior is different from the antagonist since pathogenicity and susceptibility to antagonist action. The pathogens are biotrophic, specialized necrotrophic, and unspecialized necrotrophic (Blakeman, 1985). A weak link of the pathogen life cycle should be identified for the successful biocontrol as an opportunity window. The antagonist should enter and fit in the opportunity window, disrupting the disease cycle. Unspecialized necrotrophic pathogens are *Bacillus cinerea, Alternaria, Cladosporium, Cochliobolus,* and *Septona* species. They grow saprophytically before the information of infection structure on the plant surface. Nutrients from the spore itself, nutrients leaked from the plant surface, and other nutrient sources like pollen and aphid honeydew act to sustain this group of pathogens. The window of opportunity applicable in this circumstance is to obstruct the uptake of nutrients required for growth. The saprophytic phase will be controlled when the antagonist competes for nutrients and preventing its establishment. When antagonistic organisms are present in high enough numbers in the area surrounding the pathogen spores, loss of endogenous nutrients from the spore may reduce or prevent germination. The production of enzymes or antibiotics by the antagonist may also be effective against these pathogens. In the saprophytic phase, the specialized necrotrophic pathogens absent or very limited before penetration on the plant surface and required less exogenous nutrients. *Colletotrichum* species belonging to this group are causing anthracnose. Appressoria developed directly from the spore or either no or a very short germ tube. Excess of nutrients encourages the pathogen to grow saprophytically and suppress their pathogenic behavior. Mechanism of survival and the available amount of nutrients, spores produced and persist on the host; pathogen infection cycle can begin with spore germination. When a pathogen already infected the host, more competitive species will be an effective measure (Bellows, 1999).

Antagonist affecting biocontrol activity

The antagonist will be more effective when an optimal relationship prevailed. The pathogen infects the host when wounding occurs, or microbial ecology changed on plant surface (Janisiewicz and Korsten, 2002). The antagonist application is important when timely applied. The microbe can control or suppress pathogen if used before the establishment of a pathogen. Two yeast and two *Pseudomonas* species against *Monillia fructicola* is a causal agent of brown rot of stone fruits. When an antagonist is applied before pathogen establishment, it protects from disease (Smilanick et al., 1993). Nevertheless, after the establishment of a pathogen, it cannot control the pathogen. It produces antibiotics, and enzymes can be self-regulated (growth phase, nutrient status). Environmental factors can also trigger it. Spore-forming bacteria such as *Bacillus* species, when sporulation is initiated or stationary, appear antibiotics are produced (Lin et al., 1999). An antibiotic phenazine produced by *Pseudomonas aureofaciens* is regulated by cell density (Pierson and Weller, 1994). The effect of temperature and nutrients on the growth of *B. cereus* UW85 and its accumulation of antibiotic zwittermicin A (Milner et al., 1995).

Conclusion and future aspects

Microbes used as a control agent are promising alternatives for replacing chemicals or reducing their use. About one hundred microbial products have been marketed for biocontrol, but the product success is variable. This is due to the varying field, and the biotic and abiotic conditions strongly influence the biocontrol agent varying condition. In greenhouse or control conditions, biocontrol activity is more successful than in the open and colonization, growth, and effectiveness are also affected by antagonist plant canopy, size, shape, and surface topography of leaves and fruits influenced the macro environment. Leaf age and position influenced the

microbial colonizing population in phyllosphere microbe exposure increases on senescent and necrotic leaves when environmental extremes exist rather than living young leaves (environmental factors can easily control storage conditions species of plants, cultivars, and at different growth stages, physical characteristics of plant surfaces vary. Plant physical structure includes an epidermal, guard, and special functional cells (trichomes, or leaf hairs), ranging considerably in size, shape, and density cuticle covered leaf surface and made up with long-chain hydrocarbons, alkyl esters, free primary alcohols, and fatty acids also may contain wax embedded. Composition, distribution, thickness, and resistance to abrasion of resin are variable. Wax regeneration can do young leaves, but with the passage of age, this ability declines to retain water films and leaching of nutrients. Plant surface chemical composition varies greatly. Carbohydrates, amino acids, organic acids, sugar alcohols, mineral trace elements, vitamins, hormones, and antimicrobial compounds such as phenols and terpenoids originated endogenously or exogenously in phylloplane. Nutrients are important because they directly provide growth substrates for microbes and indirectly induce secondary metabolites such as antibiotics. The sources of nutrients soil particles, dust, ions, and solutes in rainwater, aphid honey dew, pollen, dead microbes, as well as bird and insect excrements are exogenous. Wounding, leaching action of rain, dew, fog, and active exudation through guttation by hydathodes or even cuticles endogenous nutrients removed the antagonist will be more effective when an optimal relationship prevailed. The pathogen infects the host when wounding, or microbial ecology changes on plant surface the antagonist application is important when timely applied. The microbe can control or suppress the pathogen if used before the establishment of the pathogen.

COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that the review complies with ethical standards of the journal.

COMPETING FINANCIAL INTERESTS

The authors declare no competing financial interests.

CONFLICT OF INTEREST

The authors declare no conflict of interests and give their consent for publishing the material.

RESEARCH INVOLVING HUMAN PARTICIPANTS AND/OR ANIMALS

The authors declare that the manuscript does not contain research involving human participants and/or animals.

AUTHORS' CONTRIBUTION

All the authors equally contributed in gathering literature and manuscript write up and formatting.

REFERENCE

Baker, K.F., Cook, R.J., 1974. Biological control of plant pathogens. Freeman and Company., San Francisco.

Baker, K.F., Snyder, W.C., 1965. Ecology of soil-borne plant pathogens, Biological Control ed, University of California, Berkeley, USA.

Bargabus, R.L., Zidack, N.K., Sherwood, J.E., Jacobsen, B.J., 2002. Characterisation of systemic resistance in sugar beet elicited by a non-pathogenic, phyllosphere-colonizing *Bacillus mycoides*, biological control agent. Physiological and Molecular Plant Pathology 61, 289-298.

Bellows, T.S., 1999. Foliar, flower and fruits pathogens, in: Bellows, T.S., Fisher, T.W. (Eds.), Handbook of Biological Control: Principles and Applications of Biological Control. Academics press, San Diego, USA, pp. 841-852.

Benhamou, N., Bélanger, R.R., Rey, P., Tirilly, Y., 2001. Oligandrin, the elicitin-like protein produced by the mycoparasite *Pythium oligandrum*, induces systemic resistance to Fusarium crown and root rot in tomato plants. Plant Physiology and Biochemistry 39, 681-696.

Blakeman, J.P., 1985. Ecological succession of leaf surface microorganisms in relation to biological control, in: Windels, C.E., Lindow, S.E. (Eds.), Biological Control on the Phyllosphere. The American Phytopathological Society, St. Paul, Minnesota, USA, pp. 6-30.

Bloemberg, G.V., Lugtenberg, B.J.J., 2001. Molecular basis of plant growth promotion and biocontrol by rhizobacteria. Current Opinion in Plant Biology 4, 343-350.

Bolwerk, A., Lagopodi, A.L., Lugtenberg, B.J.J., Bloemberg, G.V., 2005. Visualization of interactions between a pathogenic and a beneficial Fusarium strain during biocontrol of tomato foot and root rot. Molecular Plant-Microbe Interactions 18, 710-721.

Bull, C.T., Weller, D.M., Thomashow, L.S., 1991. Relationship between root colonization and suppression of *Gaeumannomyces graminis* var. *tritici* by *Pseudomonas fluorescens* strain 2-79. Phytopathology 81, 954-959.

Campbell, R.E., 1989. Biological control of microbial plant pathogens. Cambridge University Press, , Cambridge, UK.

Chiarini, L., Bevivino, A., Dalmastri, C., Tabacchioni, S., Visca, P., 2006. *Burkholderia cepacia* complex species: health hazards and biotechnological

potential. Trends in Microbiology 14, 277-286.
Cook, R.J., Rovira, A.D., 1976. The role of bacteria in the biological control of *Gaeumannomyces graminis* by suppressive soils. Soil Biology and Biochemistry 8, 269-273.
De Souza, J.T., Weller, D.M., Raaijmakers, J.M., 2003. Frequency, diversity and activity of 2, 4-diacetylphloroglucinol-producing *Pseudomonas* spp. in Dutch take-all decline soils. Phytopathology 93, 54-63.
de Weert, S., Vermeiren, H., Mulders, I.H.M., Kuiper, I., Hendrickx, N., Bloemberg, G.V., Vanderleyden, J., De Mot, R., Lugtenberg, B.J.J., 2002. Flagella-driven chemotaxis towards exudate components is an important trait for tomato root colonization by *Pseudomonas fluorescens*. Molecular Plant-Microbe Interactions 15, 1173-1180.
Derridji, S., 1996. Nutrients on the leaf surface, in: Morris, C.E., Nicot, P.C., Nguyen, C. (Eds.), Aerial Plant Surface Microbiology. Plenum Press, New York, USA, pp. 25-42.
Dodds, J.A., 1999. Cross protection and systemic acquired resistance for the control of plant diseases, in: Bellows, T.S., Fisher, T.W. (Eds.), Handbook of Biological Control: Principles and Applications of Biological Control. Academic press, San Diego, USA, pp. 549-556.
Droby, S., Chalutz, E., 1994. Mode of action of biocontrol agents of postharvest diseases, in: Wilson, C.L., Wisniewski, M.E. (Eds.), Biological Control of Postharvest Diseases Theory and Practice. CRC Press, Boca Raton, pp. 63-75.
Droby, S., Chalutz, E., Wisniewski, M.E., Wilson, C., L., 1996. Host response to introduction of antagonistic yeasts used for control of postharvest decay, in: Morris, C.E., P.C. Nicot, P.C., Nguyen, C. (Eds.), Aerial Plant Surface Microbiology. Plenum Press, New York, USA, pp. 73-89.
Duijff, B.J., Gianinazzi-Pearson, V., Lemanceau, P., 1997. Involvement of the outer membrane lipopolysaccharides in the endophytic colonization of tomato roots by biocontrol *Pseudomonas fluorescens* strain WCS417r. New Phytologist 135, 325-334.
Eilenberg, J., Hajek, A., Lomer, C., 2001. Suggestions for unifying the terminology in biological control. BioControl 46, 387-400.
El-Ghaouth, A., 1997. Biologically based alternatives to synthetic fungicides for the control of postharvest diseases. Journal of Industrial Microbiology and Biotechnology 19, 160-162.
Elsevier, 2008. Biological Control.
Földes, T., Banhegyi, I., Herpai, Z., Varga, L., Szigeti, J., 2000. Isolation of Bacillus strains from the rhizosphere of cereals and in vitro screening for antagonism against phytopathogenic, food-borne pathogenic and spoilage micro-organisms. Journal of Applied Microbiology 89, 840-846.
Frändberg, E., Schnürer, J., 1994. Chitinolytic properties of *Bacillus pabuli* K1. Journal of Applied Bacteriology 76, 361-367.
Fravel, D.R., 1988. Role of antibiosis in the biocontrol of plant diseases. Annual Review of Phytopathology 26, 75-91.
Gilbert, G.S., Handelsman, J., Parke, J.L., 1994. Root camouflage and disease control. Phytopathology 84, 222-225.
Gueldner, R.C., Reilly, C.C., Pusey, P.L., Costello, C.E., Arrendale, R.F., Cox, R.H., Himmelsbach, D.S., Crumley, F.G., Cutler, H.G., 1988. Isolation and identification of iturins as antifungal peptides in biological control of peach brown rot with *Bacillus subtilis*. Journal of Agricultural and Food Chemistry 36, 366-370.
Ippolito, A., Nigro, F., 2000. Impact of preharvest application of biological control agents on postharvest diseases of fresh fruits and vegetables. Crop Protection 19, 715-723.
Jacobsen, B.J., Zidack, N.K., Larson, B.J., 2004. The role of Bacillus-based biological control agents in integrated pest management systems: plant diseases. Phytopathology 94, 1272-1275.
Janisiewicz, W.J., Korsten, L., 2002. Biological control of postharvest diseases of fruits. Annual Review of Phytopathology 40, 411-441.
Jijakli, M.H., Lepoivre, P., 1998. Characterization of an exo-β-1, 3-glucanase produced by *Pichia anomala* strain K, antagonist of *Botrytis cinerea* on apples. Phytopathology 88, 335-343.
Kamilova, F., Kravchenko, L.V., Shaposhnikov, A.I., Azarova, T., Makarova, N., Lugtenberg, B., 2006. Organic acids, sugars, and L-tryptophane in exudates of vegetables growing on stonewool and their effects on activities of rhizosphere bacteria. Molecular Plant-Microbe Interactions 19, 250-256.
Kerr, A., 1980. Biological control of crown gall through production of agrocin 84. Plant Disease 64, 25-30.
Kloepper, J.W., Ryu, C., Zhang, S., 2004. Induced systemic resistance and promotion of plant growth by *Bacillus* spp. Phytopathology 94, 1259-1266.
Kogel, K., Ortel, B., Jarosch, B., Atzorn, R., Schiffer, R., Wasternack, C., 1995. Resistance in barley against the powdery mildew fungus (*Erysiphe graminis* f. sp. *hordei*) is not associated with enhanced levels of endogenous jasmonates. European Journal of Plant Pathology 101, 319-332.
Koumoutsi, A.l., Chen, X., Henne, A., Liesegang, H., Hitzeroth, G., Franke, P., Vater, J., Borriss, R., 2004. Structural and functional characterization of gene clusters directing nonribosomal synthesis of

bioactive cyclic lipopeptides in *Bacillus amyloliquefaciens* strain FZB42. Journal of Bacteriology 186, 1084-1096.

Leclère, V., Béchet, M., Adam, A., Guez, J., 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.

Leifert, C., Li, H., Chidburee, S., Hampson, S., Workman, S., Sigee, D., Epton, H.A.S., Harbour, A., 1995. Antibiotic production and biocontrol activity by *Bacillus subtilis* CL27 and *Bacillus pumilus* CL45. Journal of Applied Bacteriology 78, 97-108.

Lin, T., Chen, C., Chang, L., Tschen, J.S., Liu, S., 1999. Functional and tra*nscriptional analyses of a fengycin synthetase gene, fenC, from Bacillus subtilis*. Journal of Bacteriology 181, 5060-5067.

Lindow, S.E., 1996. Role of immigration and other processes in determining epiphytic bacterial populations, in: Morris, C.E., Nicot, P.C., Nguyen, C. (Eds.), Aerial Plant Surface Microbiology. Plenum press, New York, pp. 155-168.

Lugtenberg, B.J.J., Dekkers, L., Bloemberg, G.V., 2001. Molecular determinants of rhizosphere colonization by Pseudomonas. Annual Review of Phytopathology 39, 461-490.

Maloy, O.C., Lang, K.J., 2003. Carl Freiherr von Tubeuf: Pioneer in biological control of plant diseases. Annual Review of Phytopathology 41, 41-52.

Mari, M., Guizzardi, M., 1998. The postharvest phase: emerging technologies for the control of fungal diseases. Phytoparasitica 26, 59-66.

Marschner, H., 2011. Marschner's mineral nutrition of higher plants, Second ed. Academic Press, London.

Maurhofer, M., Hase, C., Meuwly, P., Metraux, J., Defago, G., 1994. Induction of systemic resistance of tobacco to tobacco necrosis virus by the root-colonizing *Pseudomonas fluorescens* strain CHA0: influence of the gacA gene and of pyoverdine production. Phytopathology 84, 139-146.

McSpadden, G.B., Fravel, D.R., 2002. Biological control of plant pathogens: research, commercialization, and application in the USA. Plant Health Progress 3, 17.

Milner, J.L., Raffel, S.J., Lethbridge, B.J., Handelsman, J., 1995. Culture conditions that influence accumulation of zwittermicin A by *Bacillus cereus* UW85. Applied Microbiology and Biotechnology 43, 685-691.

Milner, J.L., Silo-Suh, L., Lee, J.C., He, H., Clardy, J., Handelsman, J.O., 1996. Production of kanosamine by *Bacillus cereus* UW85. Applied and Environmental Microbiology 62, 3061-3065.

Morris, C.E., Rouse, D.I., Windels, C., Lindow, S.E., 1985. Role of nutrients in regulating epiphytic bacterial populations, in: Windels, C.E., Lindow, S.E. (Eds.), Biological Control on the Phylloplane. The American Phytopathological Society, St. Paul, Minnesota, USA pp. 63-82.

Moyne, A.L., Shelby, R., Cleveland, T.E., Tuzun, S., 2001. Bacillomycin D: an iturin with antifungal activity against *Aspergillus flavus*. Journal of Applied Microbiology 90, 622-629.

Nielsen, P., Sørensen, J., 1997. Multi-target and medium-independent fungal antagonism by hydrolytic enzymes in *Paenibacillus polymyxa* and *Bacillus pumilus* strains from barley rhizosphere. FEMS Microbiology Letters 22, 183-192.

O'sullivan, D.J., O'Gara, F., 1992. Traits of fluorescent *Pseudomonas* spp. involved in suppression of plant root pathogens. Microbiology and Molecular Biology Reviews 56, 662-676.

Ongena, M., Duby, F., Rossignol, F., Fauconnier, M.L., Dommes, J., Thonart, P., 2004. Stimulation of the lipoxygenase pathway is associated with systemic resistance induced in bean by a nonpathogenic *Pseudomonas* strain. Molecular Plant-Microbe Interactions 17, 1009-1018.

Pal, K.K., Gardener, B.M., 2006. Biological control of plant pathogens. The Plant Health Instructor 10, 1094.

Paul, B., Chereyathmanjiyil, A., Masih, I., Chapuis, L., Benoît, A., 1998. Biological control of *Botrytis cinerea* causing grey mould disease of grapevine and elicitation of stilbene phytoalexin (resveratrol) by a soil bacterium. FEMS Microbiology Letters 165, 65-70.

Paulitz, T.C., Bélanger, R.R., 2001. Biological control in greenhouse systems. Annual Review of Phytopathology 39, 103-133.

Payne, C.C., Lynch, J.M., 1988. Biological control, in: Lynch, J.M., Hobbie, J.E. (Eds.), Micro-organisms in Action: Concepts and Applications in Microbial Ecology. Blackwell Scientific Publications, Oxford, UK, pp. 261-287.

Pfender, W.F., 1996. Microbial interactions preventing fungal growth on senescent and necrotic aerial plant surfaces, in: Morris, C.E., Nicot, P., Nguyen, C. (Eds.), Aerial Plant Surface Microbiology. Plenum press, New York, USA, pp. 125-138.

Picard, K., Tirilly, Y., Benhamou, N., 2000. Cytological effects of cellulases in the parasitism of *Phytophthora parasitica* by *Pythium oligandrum*. Applied and Environmental Microbiology 66, 4305-4314.

Pierson, E.A., Weller, D.M., 1994. To suppress Take-all and improve the growth of wheat. Phytopathology 84, 940-947.

Pinchuk, I.V., Bressollier, P., Sorokulova, I.B., Verneuil, B.,

Urdaci, M.C., 2002. Amicoumacin antibiotic production and genetic diversity of *Bacillus subtilis* strains isolated from different habitats. Research in Microbiology 153, 269-276.

Podile, A.R., Prakash, A.P., 1996. Lysis and biological control of *Aspergillus niger* by *Bacillus subtilis* AF 1. Canadian Journal of Microbiology 42, 533-538.

Podlesek, Z., Comino, A., Herzog-Velikonja, B., Grabnar, M., 2000. The role of the bacitracin ABC transporter in bacitracin resistance and collateral detergent sensitivity. FEMS Microbiology Letters 188, 103-106.

Postma, J., Luttikholt, A.J.G., 1996. Colonization of carnation stems by a nonpathogenic isolate of *Fusarium oxysporum* and its effect on *Fusarium oxysporum* f. sp. *dianthi*. Canadian Journal of Botany 74, 1841-1851.

Press, C.M., Loper, J.E., Kloepper, J.W., 2001. Role of iron in rhizobacteria-mediated induced systemic resistance of cucumber. Phytopathology 91, 593-598.

Pusey, P.L., 1994. Enhancement of biocontrol agents for postharvest diseases and their integration with other control strategies, in: Wilson, C.L., Wisniewski, M.E. (Eds.), Biological Control of Postharvest Diseases-Theory and Practice. CRC Press, Boca Raton, pp. 77-88.

Raaijmakers, J.M., Vlami, M., De Souza, J.T., 2002. Antibiotic production by bacterial biocontrol agents. Antonie van Leeuwenhoek 81, 537-547.

Ramamoorthy, V., Raguchander, T., Samiyappan, R., 2002. Induction of defense-related proteins in tomato roots treated with *Pseudomonas fluorescens* Pf1 and *Fusarium oxysporum* f. sp. *lycopersici*. Plant and Soil 239, 55-68.

Rayner, A.D.M., 1996. Antagonism and Synergism in the Plant Surface Colonisation Strategies of Fungi, in: Morris, C.E., Nicot, P.C., Nguyen, C. (Eds.), Aerial Plant Surface Microbiology. Plenum Press, New York. USA, pp. 139-154.

Roberts, R.G., 1994. Integrating biological control into postharvest disease management strategies. HortScience 29, 758-762.

Romantschuk, M., Roine, E., Björklöf, K., Ojanen, T., Nurmiaho-Lassila, E.-L., Haahtela, K., 1996. Microbial attachment to plant aerial surfaces, in: Morris, C.E., Nicot, P.C., Nguyen, C. (Eds.), Aerial Plant Surface Microbiology. Plenum Press, New York, USA, pp. 43-57.

Ryu, C.-M., Farag, M.A., Hu, C.-H., Reddy, M.S., Kloepper, J.W., Paré, P.W., 2004. Bacterial volatiles induce systemic resistance in Arabidopsis. Plant Physiology 134, 1017-1026.

Sailaja, P.R., Podile, A.R., Reddanna, P., 1998. Biocontrol strain of *Bacillus subtilis* AF 1 rapidly induces lipoxygenase in groundnut (*Arachis hypogaea* L.) compared to crown rot pathogen *Aspergillus niger*. European Journal of Plant Pathology 104, 125-132.

Sandra, A.I., Wright, S.A.I., Zumoff, C.H., Schneider, L., Beer, S.V., 2001. *Pantoea agglomerans* strain EH318 produces two antibiotics that inhibit *Erwinia amylovora in vitro*. Applied and Environmental Microbiology 67, 284-292.

Schönherr, J., Baur, P., 1996. Cuticle permeability studies, in: Morris, C.E., Nicot, P.C., Nguyen, C. (Eds.), Aerial Plant Surface Microbiology. Plenum Press, New York, USA, pp. 1-23.

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.

Shipton, P., Cook, R., Sitton, J., 1973. Occurrence and transfer of a biological factor in soil that suppress take-all of wheat in eastern Washington. Phytopathology 63, 511-517.

Skidmore, A.M., 1976. Interactions in relation to biological control of plant pathogens, in: Dickinson, C.H., Preece, T.F. (Eds.), Microbiology of Aerial Plant Surfaces. Academic Press, London, pp. 507-528.

Smilanick, J.L., Denis-Arrue, R., Bosch, J.R., Gonzalez, A.R., Henson, D., Janisiewicz, W.J., 1993. Control of postharvest brown rot of nectarines and peaches by *Pseudomonas* species. Crop Protection 12, 513-520.

Smith, K.P., Havey, M.J., Handelsman, J., 1993. Suppression of cottony leak of cucumber with *Bacillus cereus* strain UW85. Plant Disease 77, 139-142.

Spadaro, D., Gullino, M.L., 2004. State of the art and future prospects of the biological control of postharvest fruit diseases. International Journal of Food Microbiology 91, 185-194.

Spurr, H.W., 1994. The microbial ecology of fruit and vegetable surfaces: its relationship to postharvest biocontrol, in: Wilson, C.L., Wisniewski, M.E. (Eds.), Biological Control of Postharvest Diseases-Theory and Practice. CRC Press, Boca Raton, pp. 11-23.

Tsuge, K., Ano, T., Shoda, M., 1996. Isolation of a gene essential for biosynthesis of the lipopeptide antibiotics plipastatin B1 and surfactin in *Bacillus subtilis* YB8. Archives of Microbiology 165, 243-251.

Van Drieschez, R.G., Bellows, T.S.J., 1996. Biological Control. Chapman and Hall, New York, USA.

Vinale, F., Sivasithamparam, K., Ghisalberti, E.L., Marra, R., Woo, S.L., Lorito, M., 2008. Trichoderma–plant–

pathogen interactions. Soil Biology and Biochemistry 40, 1-10.

Walker, T.S., Bais, H.P., Déziel, E., Schweizer, H.P., Rahme, L.G., Fall, R., Vivanco, J.M., 2004. *Pseudomonas aeruginosa*-plant root interactions. Pathogenicity, biofilm formation, and root exudation. Plant Physiology 134, 320-331.

Walsh, G.A., Murphy, R.A., Killeen, G.F., Headon, D.R., Power, R.F., 1995. Detection and quantification of supplemental fungal β-glucanase activity in animal feed. Journal of Animal Science 73, 1074-1076.

Weller, D.M., 1988. Biological control of soilborne plant pathogens in the rhizosphere with bacteria. Annual Review of Phytopathology 26, 379-407.

Wilson, C.L., El Ghaouth, A., Chalutz, E., Droby, S., Stevens, C., 1994. Potential of induced resistance to control postharvest diseases of fruits and vegetables. Plant Disease 78, 837-844.

Wilson, C.L., Wisniewski, M.E., 1989. Biological control of postharvest diseases of fruits and vegetables: an emerging technology. Annual Review of Phytopathology 27, 425-441.

Zhang, S., Reddy, M.S., Kloepper, J.W., 2002. Development of assays for assessing induced systemic resistance by plant growth-promoting rhizobacteria against blue mold of tobacco. Biological Control 23, 79-86.