Phytopathologia Mediterranea (2016) 55, 3, 301−322
DOI: 10.14601/Phytopathol_Mediterr-18079

REVIEW

Modes of action for biological control of *Botrytis cinerea* by antagonistic bacteria

Rana HAIDAR[1,2], Marc FERMAUD[1], Carlos CALVO-GARRIDO[1], Jean ROUDET[1] and Alain DESCHAMPS[1]

[1] SAVE, Bordeaux Science Agro, INRA, 33882, Villenave d'Ornon, France
[2] Tichreen University, Faculty of Science, Biology Department, PO Box 2231, Latakia, Syrian Arab Republic

Summary. The role of beneficial bacteria in biocontrol of plant diseases, particularly those caused by the necrotrophic fungus *Botrytis cinerea*, has been investigated by testing many bacteria under laboratory and field conditions. Bacteria may protect plants against *B. cinerea* by direct antagonistic interactions between biocontrol agents and this pathogen, as well as indirect effects through the induction of host resistance. This review focuses on various bacteria that act as biological control agents (BCAs) of *B. cinerea* and their associated mechanisms. The modes of action (MoAs) include: i) synthesis of anti-fungal metabolites, such as antibiotics, cell wall-degrading enzymes and volatile organic compounds (VOCs); ii) competition for nutrients and/or a niche; and iii) induction of host resistance. The challenge for development of BCAs is to reduce the variability of efficiency and to prove persistence under a large range of conditions. We discuss the advantages and drawbacks of MoA for future applications of bacteria in the field and in post-harvest storage, as well as combination of different MoAs as a strategy to achieve a more regular efficacy.

Key words: biocontrol, grey mold, antibiosis, competition, induced systemic resistance.

Introduction

Botrytis cinerea is a major necrotrophic fungal pathogen causing grey mold, a serious disease affecting a large number of economically important agricultural and horticultural crops. This pathogen leads to considerable yield and quality losses in field production and postharvest storage worldwide (Jarvis, 1977; Williamson *et al.*, 2007; Sharma *et al.*, 2009). In spite of the availability of various anti-*Botrytis* fungicides, their use in pre- and/or post-harvest conditions is not considered as sustainable because of their potential adverse effects on human and environmental health (Komárek *et al.*, 2010) and the appearance of resistant strains (Leroux, 2004; Walker *et al.*, 2013; Hahn, 2014; Romanazzi and Feliziani, 2014). Because of its high genetic variability, short life cycle, and prolific reproduction, *B. cinerea* is considered a high-risk pathogen for the development of fungicide resistance (Brent and Hollomon, 1998; Leroux *et al.*, 2002). This resistance has been detected in many countries and on numerous crops (Leroux, 2004; Zhao *et al.*, 2010; Walker *et al.*, 2013; Hahn, 2014). Development of complementary and alternative methods to chemical control, such as the use of non-pathogenic microorganisms (or their secretions) as biological control agents (BCAs), before and/or after harvest, is increasingly considered as a promising and attractive alternative.

In recent decades, there has been continued and rigorous research worldwide with a greater impetus to explore a wide range of bacteria possessing antagonistic properties against *B. cinerea* (Elmer and Reglinski, 2006; Compant *et al.*, 2013). However, in the majority of these studies, the efficacy of the BCAs was evaluated under controlled conditions, and the fact that most of them fail in the field is now widely

Corresponding author: R. Haidar
E-mail: haidarrana@gmail.com

www.fupress.com/pm
Firenze University Press
ISSN (print): 0031-9465
ISSN (online): 1593-2095

known. Despite the large number of scientific papers published on this topic, the number of efficient bacteria commercialized for use as microbial fungicides against *B. cinerea* in the pre- and/or postharvest stages remains limited (Nicot *et al.*, 2011; Romanazzi *et al.*, 2016) (Table 1).

Specific attention is given to the mechanisms by which beneficial bacteria antagoniz plant pathogen activity. It is important to know the precise mode(s) of action (MoAs) of a BCA to develop and implement an adapted control strategy in the field. Therefore, understanding the MoAs may help to improve the regularity of biocontrol efficiency by using the BCA in an active form and with the appropriate inoculum quantity. This knowledge should help to devise successful and reproducible biological control methods under pre- and/or post-harvest conditions. Furthermore, the MoA may be among the key parameters for product development, and may also be relevant for marketing purposes (Köhl *et al.*, 2011).

Interest in different MoAs exhibited by bacterial BCAs against *B. cinerea* has increased in the last decades. Early studies conducted by Blakeman and co-workers have reported the important role of the competition for nutriments by bacteria in the inhibition of the conidial germination of *B. cinerea* (Sztejnberg and Blakeman, 1973; Brodie and Blakeman, 1975). In a recent review about the biological control of grapevine pathogens (Compant *et al.*, 2103), the authors indicated only a few examples of beneficial bacterial strains for control of grey mold with their potential MoAs. Recently, several reviews have presented data on the use of plant growth promoting rhizobacteria (PGPR) as soil inoculants for the biocontrol of plant diseases. Some of these studies have taken account of the mechanisms of the biocontrol bacteria against a wide range of pathogens (Bloemberg and Lugtenberg, 2001; Labuschagne *et al.*, 2010; Karunaratne, 2011; Pan and Bhagat, 2011; Bhattacharyya and Jha, 2012; Glick, 2012; Gupta *et al.*, 2015). These reviews addressed the biological control of *B. cinerea* and also included other plant pathogens.

To our knowledge, there have been two reviews dealing with the mechanisms involved in the biological suppression of *B. cinerea* (Elad, 1996; Elad and Stewart, 2004). The authors discussed the involvement of different MoAs in the biological suppression of *B. cinerea*, not only by bacteria but also using other microorganisms. In the present, we have restricted the scope to the different MoAs of bacterial antagonists against *B. cinerea* because of the huge breadth of the subject matter dealing with this important plant pathogen. We give a special emphasis to the different mechanisms by which beneficial bacteria might inhibit *B. cinerea.* We report various examples of bacteria that exert direct and/or indirect effects on the pathogen in a wide range of crop pathosystems. The diversity and function of the inhibiting bacteria cited in the literature were examined, which is helpful for

Table 1. Commercially available biopesticides based on bacteria, for control of gray mold on different crops.

®Trade name	Bacterial strain	Company (and/or country)
Pantovital®	*Pantoea agglomerans*	IRTA (Spain)
Serenade Max®	*Bacillus subtilis*	Bayer, formerly BASF (Germany)
Bio-save®	*Pseudomonas syringae*	Jet harvest solutions (USA)
Amylo-X®	*Bacillus amyloliquefaciens*	Biogard CBC (Italy)
Double Nickel 55WDG/LC™	*Bacillus amyloliquefaciens*	Certis (USA)
Companion®	*Bacillus subtilis* GB03	Growth products (USA)
Botokira Wettable Powder®	*Bacillus subtilis* IK-1080	(Idemitsu Kosan Inc., Japan)
Bio Arc®	*Bacillus megaterium*	Sphere Bio-Arc PVTLtd (India)
Mycostop®	*Streptomyces griseoviridis* Strain K61	Verdera Oy (Finland)
Actinovate®	*Streptomyces lydicus* WYEC 108	Novozymes (Denmark)

future research aiming to develop new bacterial biocontrol agents against *B. cinerea*.

Competition for space and nutrients

Competition occurs when biocontrol agents and pathogens require the same resources (Campbell, 1989). Efficient competition for the available nutrients and for niches represents an important mechanism accounting for bacterial protection of plants against various pathogens (Stockwell *et al*., 1998; Punja and Utkhede, 2003; Pal and McSpadden-Gardener, 2006; Cabrefiga *et al*., 2007; Lugtenberg and Kamilova, 2009). The suppression of *B. cinerea* infection through competition for niches and nutrients has been shown to be efficient in several *in situ* and *in vivo* studies (Table 2). *Botrytis cinerea* is highly susceptible to competition because external nutrients are required for conidial germination (Elad, 1996), germ tube growth and the successful completion of infection (Redmond *et al*., 1987; Elad and Stewart, 2004). Furthermore, this mechanism was suggested to be one of the major mechanisms in the control of post-harvest diseases (Duffy, 2001; Spadaro and Gullino, 2004; Sharma *et al*., 2009; Jamalizadeh *et al*., 2011). The ability of antagonists to rapidly colonize fruit wounds, prior to colonization by *B. cinerea*, is an important feature of post-harvest biocontrol agents that reduce grey mold incidence and/or severity in fruits (Nunes *et al*., 2001, 2002; Sharma *et al*., 2009; Jamalizadeh *et al*., 2011).

Given the limited nutritional resources at the leaf surface (Andrews, 1992; Huang and Erickson, 2005), the efficiency of phylosphere colonization with nutrient uptake by bacteria is a key feature for successful antagonism by exhausting the available substrates and thus, reducing *Botrytis* infection. For instance, in greenhouse conditions, *Pseudomonas putida* Cha94 and *Bacillus amyloliquefaciens* BL3 controlled *B. cinerea* infection on pepper by colonizing the floral and foliar canopies (Park *et al*., 1999). Similarly, in bean and tomato plants, the severity of the *B. cinerea* infection and sporulation was reduced by several saprophytic bacterial isolates including *Xanthomonas maltophilia, Bacillus pumilus, Lactobacillus* sp. and *Pseudomonas* sp. (Elad *et al*., 1994). The effect of these isolates was due to competition on detached leaves for the available nutrients. Similarly, competition for nutrients by bacteria near spores may result in increased inhibition of germination of *B. cinerea* spores on leaf surfaces (Sztejnberg and Blakeman, 1973; Brodie and Blakeman, 1975).

Table 2. Examples of bacteria providing biocontrol of *Botrytis cinerea*, through competition for space and/or nutrients.

Antagonistic bacteria	Plant/fruit/ conditions	Mechanism of inhibition	Reference
Pantoea agglomerans LRC 954, *Pseudomonas fluorescens* LRC 1788	Lentil seedling	Competition for space and nutrients	Huang and Erickson, 2005
Erwinia herbicola (*Pantoea agglomerans)*	Apple juice	Competition for nutrients	Bryk *et al*., 1998
Pseudomonas putida Cha94, *B. amyloliquefaciens* BL3	Pepper	Competition for space and nutrients	Park *et al*., 1999
Rahnella aquatilis	Apple fruit/*in vitro*	Competition for nutrients	Calvo *et al*., 2007
Pantoea agglomerans	Apple fruit	Competition for space and nutrients	Nunes *et al*., 2002
Bacillus sp.(isolate UYBC38)	*In vitro*/*in situ* (grape, peach, and apple)	Competition for nutrients	Rabosto *et al*., 2006
Paenibacillus polymyxa	Strawberry fruit pulp suspension	Competition for nutrients	Helbig, 2001
Xanthomonas maltophilia, Bacillus pumilus, Lactobacillus sp., *Pseudomonas* sp.	Bean and tomato	Competition for nutrients	Elad *et al*., 1994

In the rhizosphere, good establishment of introduced bacteria is also considered a critical factor that can limit their biocontrol efficacy (Lugtenberg and Kamilova, 2009). For example, the suppression of *B. cinerea* symptoms on lentil seedlings was demonstrated following rhizosphere colonization by *Pantoea agglomerans* LRC 954 and *Pseudomonas fluorescens* LRC 1788 (Huang and Erickson, 2002, 2005).

Although conidial germination of *B. cinerea* depends significantly on nutrient availability, interference with the subsequent infection process may also occur by utilizing antagonistic bacteria that use the available nutrients more efficiently than the pathogen. The application of competitive bacteria on floral organs, harbouring pollen grains, stigma exudates, and dead and/or senescent petals, deprives *B. cinerea* of important nutrient sources. Moreover, the exclusion of *B. cinerea* from an infection site by bacteria colonizing rapidly in this area might be a suitable method for protecting wounded host tissues, notably wounded fruits during maturation and post-harvest storage.

However, under post-harvest conditions, and regarding the rapid colonization potential of *B. cinerea,* growth and viability potential of introduced bacteria are required to enhance their efficacy and to ensure durable effects against the pathogen. It is important to note here that more BCA examples, involving this MoA, are found in yeasts. The capacity of yeasts to grow rapidly, with the rapid depletion of available nutrients, is associated with formation of biofilms covering wounds, and their tolerance to lower relative humidity levels make them highly efficient competing BCAs under postharvest conditions (Wilson and Wisnieswski, 1994; Liu *et al*., 2013; Spadaro and Droby, 2016). In general, yeasts produce fewer antibiotics than bacteria, so this may be an advantage for using yeasts as BCAs under post-harvest conditions (Wisniewski and Wilson, 1992; Liu *et al*., 2013).

Antibiosis

Antibiosis is a commonly assumed mechanism in biocontrol activity of bacteria on leaf surfaces, in the rhizosphere and in fruit wounds (Ghaouth *et al*., 2004). According to Thomashow *et al*. (1997), antibiotics encompass a chemically heterogeneous group of organic, low molecular weight compounds produced by microorganisms, that are deleterious to the growth or metabolic activities of other microorganisms.

Antibiotic-producing microorganisms have often been considered first in screening for BCAs, using *in vitro* tests performed on agar and/or in liquid culture. Many literature reports support the great potential of bacteria that produce antifungal metabolites to control *B. cinerea* both *in vitro* and on a wide range of host plant species. The potential antifungal metabolites of numerous and various bacterial genera and species (*Bacillus*, *Paenibacillus*, *Pseudomonads*, *Burkholderia* and *Streptomyces*) are illustrated in Table 3.

Extensive research programmes show that *Bacillus* is among the most effective bacterial genera for control of plant diseases (Nagorska *et al*., 2007; Ongena and Jacques, 2008; Raaijmakers *et al*., 2010; Kumar *et al*., 2011). *Paenibacillus*, originally included within *Bacillus*, has been reclassified as a separate genus (Ash *et al*., 1993). It is widely accepted that the *Bacillus* and *Paenibacillus* species produce various antifungal substances, including lipopeptide antibiotics, antifungal proteins, volatile compounds, lytic enzymes, other antibiotics and plant defense-related enzymes (Selim *et al*., 2005; Huang and Chen, 2008; Ongena and Jacques, 2008; Raza *et al*., 2008; Govindasamy *et al*., 2010; Malfanova *et al*., 2012; Zhang *et al*., 2013; Zhao *et al*., 2013). Although most of the secondary metabolites produced by *Bacillus* spp. are peptide antibiotics (Ongena and Jacques, 2008; Pérez-García *et al*., 2011; Falardeau *et al*., 2013), the production of many non-peptide antibiotics has been reported for several *Bacillus* spp. (Baruzzi *et al*., 2011; Hamdache *et al*., 2012).

Among these antimicrobial compounds, the cyclic lipopeptides (LPs) are well studied in the context of the biological control of *B. cinerea* by bacteria. The involvement of these compounds in the protective action of the *Bacillus* spp. against *B. cinerea* under pre- and post-harvest conditions has been widely reported. *Bacillus subtilis* is a key species, and it inhibits the growth of a wide range of plant pathogens by producing a great variety of powerful antifungal metabolites, including lipopeptides (Stein, 2005; Ongena *et al*., 2005). The cyclic lipopeptides belong to three major families, *i.e.,* surfactin, iturin and fengycin (or plipastatin). They have been highlighted for their potential use in biotechnological and biopharmaceutical applications because of their surfactant properties (Ongena and Jacques, 2008). Surfactin shows surfactant activity and bactericidal effects and also hemolytic, antiviral and antimycoplasma

Table 3. Overview of literature reporting inhibition of *Botrytis cinerea* by antifungal metabolites produced by bacterial species.

Antagonistic bacteria	Plant/fruit/ conditions	Antifungal metabolites	Effect	Reference
Pseudomonas cepacia strain LT412	Apple and pears	Pyrrolnitrin	Mycelial growth inhibition and disease reduction	Janisiewicz and Roitman, 1988
Pseudomonas corrugata strain P94	Tomato leaf	Secondary metabolites (bacteriocin)	Disease reduction	Guo *et al.*, 2007
Pseudomonas fluorescens, *Bacillus* sp.	Grapes	Not identified	Disease reduction	Krol, 1998
Pseudomonas fluorescens strain Pf1TZ	*In vitro* / *in planta* (vine vitroplants)	Not identified	Mycelial growth inhibition, and disease reduction	Kilani-Feki *et al.*, 2010
Pseudomonas sp., *Pseudomonas fluorescens*, *Pseudomonas putida* *Pseudomonas aeruginosa*	*In vitro*	Not identified	Mycelial growth inhibition	Trotel-Aziz *et al.*, 2006; Kruijt *et al.*, 2009; Kumar *et al.*, 2011; Patkowska and Konopiński, 2014; Hernández-León *et al.*, 2015
Burkholderia phytofirmans PsJN	*In vitro* / grapevine plantlets	Not identified	Mycelial growth inhibition and disease reduction, plant growth promotion	Ait Barka *et al.*, 2000; Ait Barka *et al.*, 2002
Burkholderia gladioli	*In vitro*/*In situ* (leaves of strawberry)	Not identified	Inhibition of conidial germination	Walker *et al.*, 1996; Walker *et al.*, 2001
Burkholderia cepacia Cs5	*Vitis vinifera plants*	Didecyl-phthalate and two methyl alkyl-quinolones	disease reduction	Kilani-Feki and Jaoua, 2011
Bacillus sp. PB10, *Bacillus licheniformis*, *Bacillus megaterium*, *Bacillus subtilis*, *Bacillus* sp.	*In vitro* / cut leaves of tomato	Not identified	Mycelial growth inhibition and disease reduction	Enya *et al.*, 2007
Bacillus licheniformis, *Bacillus megaterium*	*In vitro* / perilla plants	Not identified	Inhibition of mycelial growth and conidial germination, disease reduction	Son *et al.*, 2002
Bacillus licheniformis N1	tomato plants	Not identified	Disease reduction and plant growth promotion	Lee *et al.*, 2006
Bacillus subtilis CL27, *B. pumilus* CL45	*In vitro*	Antibiotic appeared not to be peptide	Mycelial growth and sporulation inhibition	Leifert *et al.*, 1995
Bacillus subtilis CL27	*Astilbe* seedlings	Antibiotic appeared not to be peptide	Disease reduction	Leifert *et al.*, 1995

(Continued)

Table 3. (Continued).

Antagonistic bacteria	Plant/fruit/ conditions	Antifungal metabolites	Effect	Reference
Bacillus subtilis *Brevibacterium linens*	*In vitro*/ tomato fruit	Antifungal compounds, including surfactins	Mycelial growth inhibition and disease reduction	On *et al*., 2015
Bacillus subtilis CU12	*In vitro*	Antimicrobial compound (acyclic dimer of 3-hydroxypropionaldehyde (HPA))	Mycelial growth inhibition	Wise *et al*., 2012
Bacillus subtilis GA1	Apple fruits	Fengycins	Mycelial growth inhibition and disease reduction	Touré *et al*., 2004
Bacillus subtilis BBG100	*In vitro*	Mycelial growth inhibition	Mycosubtilin and surfactin	Leclère *et al*., 2005
Bacillus subtilis M4	Apple fruits	Cyclolipopeptides like fengycins	Disease reduction	Ongena *et al*., 2005
Bacillus subtilis B-916	*In vitro*	Antifungal protein:Bacisubin	Mycelial growth inhibition	Liu *et al*., 2007
Bacillus atrophaeus CAB-1	*In vitro*	Lipopeptides: fengycin (C15–C17), a type of unidentified lipopeptide, and antifungal protein (putative phage-related pre-neck appendage protein)	Mycelial growth inhibition	Zhang *et al*., 2013
Bacillus sp. BS061	*In vitro*/tomato seedlings	Not identified	Mycelial growth inhibition and disease reduction	Kim *et al*., 2013
Bacillusamyloliquefaciens strain TF28	*In vitro*	Crude lipopeptides (iturin A)	Mycelial growth inhibition	Zhang *et al*., 2012
Bacillusamyloliquefaciens CNU114001	*In vitro*/tomato plants	Lipopeptide: iturin	Spore germ tube elongation inhibition and disease reduction	Ji *et al*., 2013
Bacillusamyloliquefaciens IMAUB1034	*In vitro*/tomato plants	Antifungal cyclic lipopeptide (analogue of the surfactin)	Mycelial growth inhibition and disease reduction	Wang *et al*., 2012
Brevibacillus brevis	*In vitro*/leaf sections of Chinese cabbage	Antibiotic (gramicidin S)	Germination and mycelial growth inhibition	Edwards and Seddon, 2001
Paenibacillus polymyxa, *Brevibacillus brevis*	*In vitro*/strawberry fruits and plants	Peptide polymyxin B (*P. polymyxa*) and gramicidin S (*B. brevis*)	Germination and mycelial growth inhibition, disease reduction	Haggag, 2008; Haggag *et al*., 2013

(Continued)

Table 3. (Continued).

Antagonistic bacteria	**Plant/fruit/ conditions**	**Antifungal metabolites**	**Effect**	**Reference**
Bacillus subtilis TS 01 and ZR 02, *Bacillus subtilis, Bacillus sp., Bacillus lentimorbus, Bacillusmegaterium, Bacilluspumilis, B. subtilis, Bacillus subtilis* CPA-8, *B. amyloliquefaciens, Bacillus* sp.; *Bacillus* sp.	*In vitro*	Not identified	Mycelial growth inhibition	Todorova and Kozhuharova, 2009; Walker *et al*., 1998; Ferreira, 1990; Yánez-Mendizábal *et al*., 2011; Hamdache *et al*., 2012; Cui *et al*., 2014; Patkowska and Konopiński, 2014
Streptomyces sp., *Micromonospora* sp.	*In vitro*/*in vitro* grapevine leaves and plantlets	Not identified	Morphological changes and severe structural alterations of the fungal mycelium	Loqman *et al*., 2009
Streptomyces araujoniae ASBV-1T	Strawberry pseudofruits	Multiantibiotic complex: macrotetralides class (including monactin, dinactin, trinactin, and tetranactin) and the cyclodepsipeptide valinomycin	Conidia germination inhibition and disease reduction	Silva *et al*., 2014
Streptomyces barakatei *Streptomyces beta-vulgaris*	*In vitro*/grapevine leaves	Secondary metabolites	Mycelial growth inhibition and disease reduction	Lebrihi *et al*., 2009 a,b
Streptomyces hygroscopicus, Streptomyces rimosus, Streptomyces anulatus	*In vitro*	Not identified	Mycelial growth inhibition	Liu *et al*., 2004; Ilic *et al*., 2007; Xin and Ming-shan, 2008; Svetlana *et al*., 2008; Postolaky *et al*., 2012 ; Couillerot *et al*., 2014
Streptomyces anulatus S37	*In vitro*, grapevine plantlets	streptochlorin, nigericin and piericidin A1.	Mycelial growth inhibition and disease reduction	Couillerot *et al*., 2014
Xenorhabdus nematophila TB	*In vitro, detachedtomatofruits*	Antimicrobialmetabolites	Mycelial growth inhibition, spore germinations inhibition and disease reduction	Fang *et al*., 2014

activities, but no marked fungitoxicity. Iturin and fengycin are cyclopeptides with antifungal activity (Leclère *et al*., 2005; Ongena and Jacques, 2008; Raaijmakers *et al*., 2010), particularly against pathogenic fungi and yeasts, but no antibacterial activity (Ongena and Jaques, 2008). In addition to these three main lipopeptide families, other lipopeptides, including kurstakin, maltacines, and polymyxins, have been identified in various *Bacillus* spp. (Raaijmakers *et al*., 2010; Borriss, 2015). The antimicrobial activity of lipopeptides is due to their ability to bind to lipid membrane bilayers in the pathogen cells, which causes permeability changes and/or structure damage. While fengycin and iturin produce pores in the plasmamembrane, surfactin is reported to dissolve this structure (Henry *et al*., 2011; Patel *et al.,* 2011; Pérez-García *et al*., 2011).

Previous studies demonstrated the important role of lipopeptides, not only in disease suppression (Thomashow and Weller, 1988; Keel *et al.,* 1989) but also in the ability of the *Bacillus* species to colonize plant rhizospheres (Cao *et al.,* 2011; Fan *et al*., 2011). Furthermore, these compounds play a key role in the beneficial interaction between *Bacillus* spp. and plants by acting as elicitors, stimulating plant immune-related responses and then suppressing diseases (Ongena and Jacques, 2008; Jourdan *et al*., 2009; Cawoy *et al*., 2014).

Pseudomonads possess many traits that make them well suited as biocontrol and growth-promoting agents. These include i) effective competition and colonization of plant surfaces, ii) the capacity to utilize seed and root exudates, and iii) rapid growth *in vitro* and the production of a wide range of bioactive metabolites, such as antibiotics, siderophores, volatiles compounds, and growth-promoting substances (Weller, 1988, 2007).

Many compounds produced by *Burkholderia sp*. exhibit antifungal activity, including lipopeptides, cepaciamides A and B, cepacidines, siderophores, altericidin, pyrrolnitrin, glidobactins and volatile compounds (Schmidt *et al*., 2009; Tenorio-Salgado *et al*., 2013).

Many species of actinomycetes are also of great interest, particularly Streptomycetes, because nearly two thirds of all known antibiotics are produced by *Streptomyces* (Taechowisan *et al*., 2012; Lucas *et al*., 2013; Mahajan and Balachandran, 2015). The genus includes well-known antifungal BCAs that inhibit various pathogenic fungi (El-Tarabily *et al*., 2000; Errakhi *et al.,* 2007; Loqman *et al*., 2009; Hamedi and Mohammadipanah, 2015).

The multiple antifungal activities of several antibiotics, their direct action on pathogens and the possible use of the antibiotic-rich bacterial culture supernatants makes antibiosis one of the most illustrated bacterial MoAs. There have been comprehensive overviews of the antibiotics produced by beneficial bacteria used as BCAs, their potential functions and their role in biocontrol (Raaijmakers *et al*., 2002; Raaijmakers and Mazzola, 2012). However, little information is available about bacterial production of antimicrobial compounds under field conditions. The impact of several abiotic parameters on this production, notably for lipopeptides, was reported by considering oxygen availability, temperature and nitrate sources (Tampakaki *et al*., 2009; Pretorius *et al.,* 2015). The potential wash-off by rainfall of the active compound(s) may also occur in the field. Antibiosis is considered an important MoA in the biological control of post-harvest diseases, but as discussed above, a BCA that does not produce antibiotics, or produces only a small amount of the compounds, might be more suitable under such conditions. Moreover, the resistance of the fungal pathogen, particularly *B. cinerea,* against antibiotics produced by bacterial control agents has already been reported (Schoonbeek *et al*., 2002; Duffy *et al.,* 2003; Bardin *et al*., 2015). Further investigations should address the environmental impacts and biosafety issues of antibiotic compounds produced by bacteria used as BCAs.

Production of lytic enzymes and the interference with pathogen activity and growth

In addition to antibiotics, some biocontrol bacterial strains produce other metabolites, such as enzymes that can interfere with the metabolic activities and/or growth of pathogens (Elad, 1996; Duffy *et al*., 2003; Compant *et al*., 2005). Some enzymes can degrade or detoxify virulence factors of plant pathogens. For example, oxalic acid contributes to the virulence of *B. cinerea* (Germeier *et al*., 1994). The degradation of oxalate by a bacterial strain closely related to *Cupriavidus campinensis* (named "oxB") reduced *B. cinerea* pathogenicity of *Arabidopsis thaliana* and crop plants (Schoonbeek *et al*., 2007). The production of extracellular cell wall-degrading enzymes is associated with the biocontrol abilities of bacteria.

Lytic enzymes, such as chitinases, glucanases, cellulases, proteases, and lipases that degrade cell wall components of pathogenic fungi, contribute to direct suppression of plant pathogens (Neeraja *et al*., 2010; Maksimov *et al*., 2011; Bouizgarne, 2013). Halophilic bacteria, such as *Virgibacillus marismortui*, *B. subtilis*, *B. pumilus*, *B. licheniformis*, *Terribacillus halophilus*, *Halomonas elongata*, *lanococcus rifietoensis*, *Staphylococcus equorum* and *Staphylococcus* sp., moderately suppressed growth of *B. cinerea in vitro*, by producing extracellular antifungal hydrolytic enzymes, including chitinase, β-1,3-glucanase, cellulase and protease (Essghaier *et al*., 2009). With respect to the control of *B. cinerea* by *Bacillus cereus*, the effect of strain IO8 was mediated by chitinase production (Hammami *et al*., 2013). However, for another strain, B-02, antifungal activity was caused by effects on DNA synthesis, mitochondrial membrane potential and the reactive oxygen quantity in the pathogen hyphae (Li *et al*., 2012). Similarly, the role of chitinases was also revealed, in *Bacillus thuringiensis* UM96, to account for the protection of *Medicago truncatula* from *B. cinerea* infection (Martínez-Absalón *et al*., 2014). Joo (2005) demonstrated antifungal activity of purified chitinase from *Streptomyces halstedii* AJ-7 against various red pepper fungal pathogens, including *B. cinerea*.

Two strains of *Pseudomonas* sp. (B194 and B224) and two strains of *Erwinia herbicola* lysed *B. cinerea* germ tubes and hyphae (Bryk *et al*., 1998, 2004). *Serratia plymuthica* and *S. marcescens* produced lytic enzymes, such as chitinases and proteases, and inhibited growth of pathogens, including *B. cinerea*, *Fusarium oxysporum*, *Sclerotinia sclerotiorum* and *Rhizoctonia solani* (Frankowski *et al*., 2001; Kamensky *et al*., 2003; Ningaraju, 2006).

Another MoA is the inhibition of hydrolytic enzyme synthesis in *B. cinerea* during the first phase of the host-pathogen interaction, which is crucial for infection success (Baarlen *et al*., 2007; Nakajima and Akutsu, 2014; Nafisi *et al*., 2015). Decreases in the activities of pectin lyase and polygalacturonase produced by *B. cinerea* were observed during biological control on vines by *Bacillus circulans* (Paul *et al*., 1997). Similarly, bacterial metabolites, such as siderophores, may control *B. cinerea* by inhibiting portions of pathogen virulence factors. As an example, enterochelin, from the enterobacterium *Rahnella aquatilis* BNM, inhibited pathogen production of polygalacturonase and laccase (Sansone *et al*., 2011; Sanz Ferramola *et al*., 2013). Thus, the inhibition of key *B. cinerea* enzymes enhances the inhibitory activities of the biocontrol agents (Table 4).

The *B. cinerea* antagonist enzymatic activity by the BCA rapidly takes place at the host organ surface before and/or at the pathogen's arrival. *Botrytis cinerea* is a fast-germinating pathogen which rapidly enters the host when there are wounds and/or when the host tissues are highly susceptible (Nair and Allen, 1993; Ciliberti *et al*., 2015). This MoA may be less efficient in the field because *B. cinerea* remains for only a short period at host surfaces before infection occurs. Compared to bacteria, yeasts also secrete lytic enzymes, and this is known to play an important role in their biocontrol activity (Wisniewski *et al*., 1991; Zimand *et al*., 1996; Kapat *et al*., 1998; Spadaro and Droby, 2016). Spadaro and Droby (2016) provided more information about the enzymes produced by yeasts, and their biocontrol roles in yeasts in postharvest situations. Although lytic enzymes might be effective against a wide spectrum of phytopathogens, their non-specificity may result in suppression of beneficial microorganisms existing in particular environments (Pretorius *et al*., 2015).

Pathogen growth inhibition can also be achieved indirectly by changing the growth conditions on plant surfaces, to make them unsuitable for successful infection. For example, *B. pumilus* NCIMB 13374 and *P. fluorescens* NCIMB 13373 inhibited *B. cinerea* growth in strawberries by increasing the pH from 6 to approx. 8. These bacterial strains also produce antifungal compounds (Swadling and Jeffries, 1998).

Production of volatile organic compounds

In recent years, the effects of bacterial volatile organic compounds on plants and pathogens have been increasingly studied. VOCs may be one of the key mechanisms for achieving successful biological control of plant pathogens (Ryu *et al*., 2004; Effmert *et al*., 2012). The emission of complex blends of VOCs by bacteria was reported in many studies (Kai *et al*., 2009; Effmert *et al*., 2012). Volatile bacterial substances, identified by gas chromatography combined with mass spectrometry (GC-MS), may vary in number and type, depending on the bacterial isolate (Wan *et al*., 2008; Kai *et al*., 2009; Arrebola *et al*., 2010). For example, more than 120 different VOCs were identified from 26 *Streptomyces* spp., comprising alkanes,

Table 4. Overview of literature reporting inhibition of *Botrytis cinerea* by bacteria producing enzymes and/or interfering with the activity and growth of this pathogen.

Antagonistic bacteria	Plant/fruit/ conditions	Enzymes	Anti-fungal effects	Reference
Bacillus cereus IO8	*In vitro*/ tomato plants	Chitinase	Mycelial growth inhibition and disease incidence reduction	Hammami *et al.*, 2013
Virgibacillus marismortui, *Bacillus subtilis*, *Bacillus pumilus*, *Bacillus licheniformis*, *Terribacillus halophilus*, *Halomonas elongata*, *lanococcus rifietoensis*, *Staphylococcus equorum*,*Staphylococcus* sp.	*In vitro*/strawberry fruits	Chitinase, β-1, 3-glucanase, cellulase and protease	Mycelial growth inhibition and disease incidence reduction	Essghaier *et al.*, 2009
Serratia plymuthica IC14	*In vitro*/cucumber leaves	Endochitinase	Mycelial growth inhibition and disease incidence reduction	Kamensky *et al.*, 2003
Serratia plymuthica HRO-C48	*In vitro*	Endochitinase (E.C. 3.2.1.14), CHIT60, one N-acetyl β -1,4-D-hexosaminidase (E.C. 3.2.1.52), CHIT100	Spore germination and germ tube elongation inhibition	Frankowski *et al.*, 2001
Pseudomonas sp. (B194 and B224) *Erwinia herbicola (Pantoea agglomerans)*	Apple juice	Not identified	Inhibition of germination and germ tube elongation	Bryk *et al.*, 1998, 2004
Bacillus thuringiensis UM96	*In vitro/in vitroMedicago truncatula* plants	Chitinases	Mycelial growth inhibition and disease reduction	Martínez-Absalón *et al.*, 2014
Bacillus cereus B-02	*In vitro*	Possible presence of bacteriocins, toxins and other metabolites	Spore Germination and hyphal growth inhibition; changes in cell morphology such as distortion, shrinking and swelling	Li *et al.*, 2012
Rahnella aquatilis BNM	*In vitro*/apple	Interference with activity and growth of the pathogen	Mycelial growth inhibition and disease reduction	Sansone *et al.*, 2011; Sanz Ferramola *et al.*, 2013
Bacillus circulans GI 070	*In vitro*/grapevine vitroplants	Interference with activity and growth of the pathogen	Mycelial growth inhibition and disease reduction	Paul *et al.*, 1997
Bacillus pumilus NCIMB 13374 *Pseudomonas fluorescens* NCIMB 13373	*In vitro*/strawberries	Interference with activity and growth of the pathogen	Conidial germination inhibition and disease reduction	Swadling and Jeffries, 1998

(Continued)

alkenes, alcohols, esters, ketones, sulfur compounds, and terpenoids (Schöller *et al*., 2002). Bacterial VOCs inhibit or prevent fungal growth, impair fungal spores and hyphae, and/or promote plant growth (Kai *et al*., 2007; Kai *et al*., 2009; Weisskopf, 2013). However, the VOCs from one bacterial strain do not cause the same inhibitory effect, or to the same degree, on different fungi. The responses may depend on the specific fungus–bacterial combination (Kai *et al*., 2009).

VOCs derived from the *Streptomyces* species can prevent growth of *B. cinerea*. For example, VOCs from *Streptomyces platensis* F-1 (phenylethyl alcohol and (+)-epi-bicyclesesquiphellandrene) suppressed pathogen growth. In addition to the reduction of *Botrytis* fruit rot in strawberry, they also decreased the level of leaf blight in rice and oilseed rape (Wan *et al*., 2008). In tomato fruit, the inhibitory effects of VOCs on growth of *B. cinerea* from VOCs produced by *Streptomyces globisporus* JK-1 grown on autoclaved wheat seeds has been demonstrated (Li *et al*., 2010).

Similarly, within the genera *Bacillus* and *Paenibacillus*, the potential role of different VOCs to inhibit *B. cinerea* infection has been demonstrated, but only as one of the MoAs of these bacteria (Berrada *et al*., 2012; Zhang *et al*., 2013). Different degrees of inhibitory effects of VOCS from *Paenibacillus polymyxa* and *Bacillus sp*. (*B. subtilis* BLO2, *B. pumilus* BSH-4 and ZB13) were observed *in vitro* on *S. sclerotiorum*, *B. cinerea* and *Cercospora kikuchii* (Liu *et al*., 2008). Similarly, Chen *et al*. (2008) showed the antagonistic effects of these compounds generated by *B. subtilis*, on mycelial growth and the conidial germination of *B. cinerea*. For *B. cereus* (strain C1L), the protective effect against *B. cinerea* in tobacco was achieved by inoculating *B. cereus* into the soil, or by drenching the soil with dimethyl disulfide (Huang *et al*., 2012). The volatiles 1-octen-3-ol, benzothiazol, and citronellol, produced by *P. polymyxa* (strain BMP-11), inhibited mycelial *in vitro* growth of eight fungal pathogens, including *B. cinerea* (Zhao *et al*., 2011).

In addition to their strong antimicrobial inhibitory potential, bacteria emit VOCs which can promote plant growth, enhance plant tolerance to abiotic stress, and elicit induced systemic resistance (ISR) (Ryu *et al*., 2003, 2004; Bhattacharyya *et al*., 2015; Kanchiswamy *et al*., 2015; Liu and Zhang, 2015). Because *B. cinerea* was recently considered an endophyte (Van Kan *et al*., 2014), a potential antagonistic interaction might take place between the VOCs pro-

Table 4. (Continued).

Antagonistic bacteria	**Plant/fruit/ conditions**	**Enzymes**	**Anti-fungal effects**	**Reference**
Gluconobacter cerinus	*In vitro*	Interference with activity and growth of the pathogen	Mycelial growth inhibition	Guzzon *et al*., 2014
OxB related to *Cupriavidus* sp. *Bacillus pumilus* B-30087	*A. Arabidopsis thaliana*, cucumber, grapevine, tomato	Degradation of virulence factors	Disease reduction	Schoonbeek *et al*., 2007
Streptomyces halstedii AJ-7	*In vitro*	Chitinase	Mycelial growth inhibition	Joo, 2005
Bacillus subtilis	grapevine leaf	N-acetyl glucosaminidase (Nagase), the chitin-1,4-chitobiosidase (Biase) and endochitinase	Disease reduction	Maachia *et al*., 2015

duced by endophytic bacteria and the pathogen during this endophytic stage. Furthermore, compared with diffusible compounds, VOCs may facilitate interactions between physically separated microorganisms. VOC-producing bacteria are well suited to control fungal decay under post-harvest storage conditions in controlled environment, as biofumigants, although safety issues associated with these biochemicals need to be evaluated.

Most studies concerning VOC effects on gray mold have been performed under controlled conditions, and thus, their advantages and drawbacks for field applications must be considered. The impacts of environmental parameters, particularly air movements, may be of major importance. Strong air currents could significantly decrease the concentration of produced VOCs, and limit their efficacy. Furthermore, adding nutrients into the soil, such as carbon sources, may promote bacterial production of VOCs (Fiddaman *et al.*, 1994). A possible drawback of this MoA is the inhibitory effects of certain VOCs at high concentrations on plant growth (Bailly and Weisskopf, 2012).

Induction of host plant resistance

In addition to these direct interactions, some plant growth-promoting bacteria are indirectly effective against plant pathogens by enhancing plant defense mechanisms, which is induced systemic resistance (ISR). This corresponds to a state of defense in the whole plant, preparing it to respond more quickly and intensely to a pathogen attack (Van Loon *et al*., 1998; Bloemberg and Lugtenberg, 2001). ISR involves the jasmonic acid (JA) and ethylene (ET) signaling pathways (Pieterse *et al*., 1996; Glick, 2012). Several examples of bacterial strains eliciting resistance against *B. cinerea* were reported in different cultivated plant species. The induction of systemic resistance in grapevine using beneficial microorganisms was reviewed by Compant *et al*. (2013).

Several compounds produced by bacteria, including volatiles, siderophores, flagellin, and lipopeptides are known to elicite ISR against *B. cinerea* in many plant species (Ongena *et al*., 2005; Ongena and Jacques, 2008; Wu *et al*., 2015). As for *P. aeruginosa,* the strain 7NSK2 produces a siderophore, pyochelin, and the antibiotic pyocyanin, which trigger the ISR in both tomato and bean against *B. cinerea* (De Meyer and Hofte, 1997; De Meyer *et al*., 1999; Audenaert *et al*., 2002). While the LPS, siderophores, and flagellin produced by *P. putida* WCS358 induce resistance in *Arabidopsis*, LPS and siderophores were the only active elicitors in bean and tomato to induce systemic resistance (ISR) (Meziane *et al*., 2005). Cawoy *et al*. (2014) found that adding 10 μM of pure surfactin reduced *B. cinerea* development on tobacco leaves. The ability of mycosubtilin (iturin family) from *B. subtilis* to trigger immune responses against *B. cinerea* in grapevine was reported by Farace *et al*. (2015). The ability of several bacteria, including *Micromonospora, Saccharothrix algeriensis* and *P. fluorescens*, has recently been shown to induce plant systemic resistance and then reduce *B. cinerea* infections (Muzammil *et al*., 2014; Gruau *et al*., 2015; Martínez-Hidalgo *et al*., 2015).

Considering field development in the future, different factors may influence induced resistance *in natura,* including the plant genotype, the plant growth stage, the environment and plant nutrition (Heil, 2001; Walter *et al*., 2013). For *B. cinerea,* the importance of this MoA on grape berries is limited to the early fruit stages. Stilbenic phytoalexins are induced mostly in the early growth stages in grape berries, which progressively lose their potential for stilbene synthesis towards fruit maturity (PR proteins are, however, possibly induced in such maturing tissues). Furthermore, although hypersensitive responses (HR) were reported to be effective against many pathogens, host cell death induced by *B. cinerea* in Arabidopsis promotes growth of the fungus (Govrin and Levine, 2000). Furthermore, this MoA is also associated with metabolic costs and energety trade-offs within host plants. These costs can include allocation from plant growth and development towards defense, as well as ecological costs, such as negative effects on symbiotic interactions (Walters and Heil, 2007; Walters *et al*., 2013). However, more research must be carried out to provide better understanding of the effects of biotic and abiotic factors on plant induction for plant health, growth, and productivity.

Discussion and future prospects

We have described the different MoAs of bacterial BCAs against *B. cinerea*, and some advantages and drawbacks of each have been cited for each MoA. It is important to emphasize that the lines between the different MoAs may be indistinct. Most bacterial biocontrol strains produce antibiotic compounds and enzymes by which they interfere with pathogen growth and metabolic activity. Meanwhile, many lipopeptides and VOCs also induce host plant resistance. In terms of future field applications, some MoAs are likely to be of prime importance depending on *B. cinerea* epidemiology. A key example is the competition MoA for suppressing *B. cinerea* at host floral phenological stages, which are highly susceptible to the pathogen because of the abundant nutrient sources (pollen grains, floral exudates, senescing petals). Another example of a potentially very well-suited MoA in relation to the pathogen infection pathway is the production of VOCs under post-harvest storage conditions. However, favouring one specific MoA at a precise epidemiological stage, even if perfectly adapted, may not be sufficient for insuring biocontrol efficacy. The bacterial BCAs must survive and multiply at host surfaces to interfere with the pathogen. For *B. cinerea*, we consider the pathogen to be of minor epidemiological importance in the biological phase within the soil, so bacterial BCA survival and development should be, above all, assured at the surface of aerial host organs (leaves, flowers, fruits). Abiotic parameters related to temperature and relative humidity directly affect the survival of microorganisms, including microbial BCAs on the surfaces of host plants (Kredics *et al.,* 2003). In general, bacteria are more sensitive to moisture and water availability than fungi. Bacteria may exhibit poor ability to survive in hot, dry summer conditions, with the exception of spore-forming bacteria (*Bacillales*) which survive as spores and resume active forms under favorable conditions. Natural bacterial populations on fruit surfaces are generally less than those of yeasts (Barata *el al.,* 2012). Repeated sprays as field treatments seem to be required for bacterial BCAs. Some bacteria penetrate through host stomata or *via* injuries in leaves and stems, and then live also as endophytes without being disturbed by external abiotic and/or biotic stresses. From this point of view, bacteria in the *Bacillale* , notably *Bacillus* spp., have been considered as BCAs of interest because of their potential endophytic aptitude (Bacon and Hinton, 2002). This is also why BCA bacterial strains isolated from the host plant to be protected are likely to be well-adapted for survival and development on and within that host. It should be noted that recent molecular methods are likely to be of prime importance for detection and quantification of specific BCA strains in particular environments. These technologies are also well-suited for assessing location, proliferation and/or survival of BCAs on and within host plants (Narayanasamy, 2013; Soto-Muñoz *et al.,* 2014).

Biological control with microorganisms presents inherent variability in efficacy, notably depending on the different MoAs and the host plants and organisms involved. Furthermore, the effects of external abiotic factors under field conditions represent another important source of variability in efficacy. Therefore, biological control of disease in the field, based on only one MoA, may result in moderate and highly variable efficacy and be of little significance from a commercial point of view. The combination of different MoAs is widely considered as a strategy to overcome the variability in the biocontrol of fruit pathogens, including *B. cinerea* (Elmer and Reglinski, 2006; Romanazzi *et al.*, 2016). Furthermore, there may be risk of loss of biocontrol durability, which has been little studied but is likely to be important in the near future. As for chemicals, a combination of different MoAs, particularly for synthetic fungicides, is a key strategy for reducing risks of development of resistance to pesticides . Thus, a similar strategy may be promoted in biocontrol (Bardin *et al.*, 2015).

When dealing with bacteria, a combination of different MoAs can be achieved in different ways. First, one species showing more than one MoA (Lahlali *et al.*, 2013) can be used. Production of several different antibiotic molecules by the one species may also be considered here. For example, *B. subtilis* strains produce several cyclic lipopeptides (Falardeau *et al.*, 2013). Second, two bacterial strains (from the same or from different species) can be used together, each presenting a different MoA (Magnin-Robert *et al.*, 2013). Third, different MoAs can be used at different times, depending the stage of the particular grey mold epidemic. Specific MoAs may be more appropriate at key epidemiological stages than others.

From practical perspectives, combinations with non-bacterial microorganisms and/or with natural products may also be worth considering, either in joint applications or focusing according to key epidemiological stages. Yeast and yeast-like fungi are complementary to bacteria by surviving in different conditions, or by being more efficient as saprophytic competitors (Nunes *et al.*, 2002). Natural products may improve the dispersion, persistence and survival on plant phylloplanes, but others also elicit natural plant defenses and/or increase the efficacy of biocontrol treatments by contributing to pathogen growth suppression (Teixidó *et al.*, 2001). Combinations with fungicide treatments can also be effective in conventional agriculture; however, compatibility with phytosanitary products can be another important consideration, as well as in combination with natural products (Francesco and Mari, 2014).

Some examples of MoA combinations have been considered in the literature. However, few combined field biocontrol programmes with trusted efficacy are yet to become available. Therefore, more applied research, focused on such combinations, is necessary,, especially in the field, combining commercialized products and also products in developmental stages for different crops. Public institutions and extension services may adapt combinational strategies to local conditions. Nonetheless, the private sector should also be involved in developing such strategies and supporting public research to improve the variable, and sometimes poor, efficacy of some of the biocontrol products already available. In parallel, new *in-vivo* and field screenings, associated with studies on the effects of BCAs on the more general microbiota, and on the particular MoAs of each effective strain, will allow for the design of new combinations and timings to be tested in the field. This should be based on *a priori* knowledge of complimentary MoAs, and this approach is likely to become more widely used and purposeful thanks to new tools provided by next generation sequencing technologies (Massart *et al.*, 2015).

Another constraint for biological control with bacteria is the necessity for adequate registration systems prior to commercialization. Most of the regulations are following the OECD guidance documents, particularly the #67 published in 2012. The EU through the EFSA assessment procedure integrates BCAs as "biopesticides" entering in the common registration process for all pesticides (Regulation EC 1107/2009). BCAs are considered as low risk according to their sustainable use, and can be included in safe integrated pest management (IPM) practices (Villaverde *et al.*, 2014). Regulations in the USA are more specific for biopesticides, depending on the Environmental Protection Agency (EPA). Registration is a long and difficult process that is common for every biological control product, limiting the development of bacterial or fungal BCAs. This has been discussed in several publications, where the constraints related to different modes of action are also outlined (Spadaro and Gullino, 2010; Walters *et al.*, 2012; Bashan *et al.*, 2014; OECD report, 2014). Nonetheless, there is a growing perspective for more appropriate consideration of the properties and hazards of BCAs, which may lead to simpler evaluations of the human and environmental safety of biocontrol products in the future (Sundh, 2014).

In conclusion, bacterial antagonists represent an important biocontrol option against diseases caused by *B. cinerea*, due to their rapid development and the variety of antifungal and defense elicitor compounds they produce. Some MoAs are likely to be more suitable than others to concrete conditions in pre- and/or postharvest stages. However, combination of different MoAs, and combination with other control strategies, is likely to provide opportunities to reduce variability in biocontrol efficacy. Basic and applied research is therefore needed to design more refined application programmes, which will provide reliable solutions for plant protection and production in conventional and organic agriculture in the near future.

Acknowledgments

The authors are grateful to the Syrian government for a Ph.D. grant to Rana Haidar and for financial support through the CASDAR project (V1302). We also thank the Conseil Interprofessionnel du Vin de Bordeaux for financial support. We are also grateful to the Agreenskills postdoctoral fellowship program for Carlos Calvo-Garrido and for financial support from the European Union. The manuscript was edited for English with the Elsevier web shop service before submission.

Literature cited

Ait Barka E., A. Belarbi, C. Hachet, J. Nowak and J.C. Audran, 2000. Enhancement of *in vitro* growth and resistance to gray mould of *Vitis vinifera* co-cultured with plant growth-promoting rhizobacteria. *FEMS Microbiology Letters* 186, 91–95.

Ait Barka E., S. Gognies, J. Nowak, J.C. Audran and A. Belarbi, 2002. Inhibitory effect of bacteria on *Botrytis cinerea* and its influence to promote the grapevine growth. *Biological Control* 24, 135–142.

Andrews J.H., 1992. Biological control in the phyllosphere. *Annual Review of Phytopathology* 30, 603–635.

Arrebola E., D. Sivakumar and L. Korsten, 2010. Effect of volatile compounds produced by *Bacillus* strains on postharvest decay in citrus. *Biological Control* 53, 122–128.

Ash C., F.G. Priest and M. D. Collins, 1993. Molecular identification of rRNA group 3 bacilli (Ash, Farrow, Wallbanks and Collins) using a PCR probe test. proposal for the creation of a new genus *Paenibacillus*. *Antonie Leeuwenhoek* 64, 253–260.

Audenaert K., T. Pattery, P. Cornelis and M. Höfte, 2002. Induction of systemic resistance to *Botrytis cinerea* in tomato by *Pseudomonas aeruginosa* 7NSK2: Role of salicylic acid, pyochelin, and pyocyanin. *Molecular Plant-Microbe Interactions* 15, 1147–1156.

Baarlen P.V., L. Legendre and J.A.L.V. Kan, 2007. Plant defence compounds against *Botrytis* infection. In: *Botrytis: Biology, Pathology and Control* (Y. Elad, B. Williamson, P. Tudzynski, N. Delen, ed.), Springer, Netherlands, 143–161.

BashanY., L. E. De Bashan, S. R. Prabhu and J.P. Hernandez, 2014. Advances in plant growth-promoting bacterial inoculant technology: formulations and practical perspectives (1998–2013). *Plant Soil* 378, 1–33.

Bacon C.W. and D.M. Hinton, 2002. Endophytic and biological control potential of *Bacillus mojavensis* and related species. *Biological Control* 23, 274–284.

Bailly A. and L. Weisskopf, 2012. The modulating effect of bacterial volatiles on plant growth: current knowledge and future challenges. *Plant Signaling and Behavior* 7, 79–85.

Barata A., M. Malfeito-Ferreira and V. Loureiro, 2012. The microbial ecology of wine grape berries. *International Journal of Food Microbiology* 153, 243–259.

Bardin M., S. Ajouz, M. Comby, M. Lopez-Ferber, B. Graillot, M. Siegwart and P.C. Nicot, 2015. Is the efficacy of biological control against plant diseases likely to be more durable than that of chemical pesticides?. *Frontiers in Plant Science* 6:566.

Baruzzi F., L. Quintieri, M. Morea and L. Caputo, 2011. Antimicrobial Compounds Produced by *Bacillus* spp. and Applications in Food. In: *Science against Microbial Pathogens: Communicating Current Research and Technological Advances*, (A.M. Vilas, ed.), Formatex: Badajoz, Spain, 1102–1111.

Berrada I., O. Benkhemmar, J. Swings, N. Bendaou and M. Amar, 2012. Selection of halophilic bacteria for biological control of tomato gray mould caused by *Botrytis cinerea*. *Phytopathologia Mediterranea* 51, 625–630.

Bhattacharyya P.N. and D.K. Jha, 2012. Plant growth-promoting rhizobacteria (PGPR): emergence in agriculture. *World Journal of Microbiology and Biotechnology* 28, 1327–1350.

Bhattacharyya D., S.M. Yu and Y.H. Lee, 2015. Volatile compounds from *Alcaligenes faecalis* JBCS1294 confer salt tolerance in *Arabidopsis thaliana* through the auxin and gibberellin pathways and differential modulation of gene expression in root and shoot tissues. *Plant Growth Regulation* 75, 297–306.

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

Borriss R., 2015. *Bacillus*, a plant-beneficial bacterium. In: *Principles of Plant-Microbe Interactions* (B. Lugtenberg, ed.), Springer International Publishing, Switzerland, 379–391.

Bouizgarne B., 2013. Bacteria for plant growth promotion and disease management. In *Bacteria in agrobiology: disease management* (D.K. Maheshwari, ed.), Springer, Berlin, Germany, 15–47.

Brent K.J. and D.W. Hollomon, 1998. *Fungicide Resistance: The Assessment of Risk*. Global Crop Protection Federation, Brussels, Belgium, pp.1–48.

Brodie I.D.S. and J.P. Blakeman, 1975. Competition for carbon compounds by a leaf surface bacterium and conidia of *Botrytis cinerea*. *Physiological Plant Pathology* 6, 125–136.

Bryk H., B. Dyki and P. Sobiczewski, 1998. Antagonistic effect of *Erwinia herbicola* on *in vitro* spore germination and germ tube elongation of *Botrytis cinerea* and *Penicillium expansum*. *BioControl* 43, 97–106.

Bryk H., B. Dyki and P. Sobiczewski, 2004. Inhibitory effect of *Pseudomonas* spp. on the development of *Botrytis cinerea* and *Penicillium expansum*. *Plant Protection Science* 40, 128–134.

Cabrefiga J., A. Bonaterra and E. Montesinos, 2007. Mechanisms of antagonism of *Pseudomonas fluorescens* EPS62e against *Erwinia amylovora*, the causal agent of fire blight. *International Microbiology* 10, 123–132.

Calvo J., V. Calvente, M.E. De Orellano, D. Benuzzi and M.I. Sanz De Tosetti, 2007. Biological control of postharvest spoilage caused by *Penicillium expansum* and *Botrytis cinerea* in apple by using the bacterium *Rahnella aquatilis. International Journal of Food Microbiology* 113, 251–257.

Campbell R., 1989. Biocontrol of postharvest diseases - Introduction. In: *Biological control of foliar and post-harvest diseases* (N.J. Fokkema, J. Kohl, Y. Elad, ed.), *IOBC/WPRS Bulletin* 16, 93–94.

Cao Y., Z.H. Zhang, N. Ling, Y.J. Yuan, X.Y. Zheng, B. Shen and Q.R. Shen, 2011. *Bacillus subtilis* SQR 9 can control *Fusarium* wilt in cucumber by colonizing plant roots. *Biology and Fertility of Soils* 47, 495–506.

Cawoy H., M. Mariutto, G. Henry, C. Fisher, N. Vasilyeva, P. Thonart, J. Dommes and M. Ongena, 2014. Plant defense stimulation by natural isolates of *Bacillus* depends on efficient surfactin production. *Molecular Plant-Microbe Interactions* 27, 87–100.

Chen H., X. Xiao, J. Wang, L.J. Wu, Z.M. Zheng and Z.L. Yu, 2008. Antagonistic effects of volatiles generated by *Bacillus subtilis* on spore germination and hyphal growth of the plant pathogen, *Botrytis cinerea*. *Biotechnology Letters* 30, 919–923.

Ciliberti N., M. Fermaud, L. Languasco and V. Rossi, 2015. Influence of fungal strain, temperature, and wetness duration on infection of grapevine inflorescences and young berry clusters by *Botrytis cinerea*. *Phytopathology* 105, 325–333.

Compant S., B. Duffy, J. Nowak, C. Clement and E.A. Barka, 2005. Use of plant growth-promoting bacteria for biocontrol of plant diseases: principles, mechanisms of action, and future prospects. *Applied and Environmental Microbiology* 71, 4951–4959.

Compant S., G. Brader, S. Muzammil, A. Sessitsch, A. Lebrihi and F. Mathieu, 2013. Use of beneficial bacteria and their secondary metabolites to control grapevine pathogen diseases. *BioControl* 58, 435–455.

Couillerot O., S. Loqman, A. Toribio, J. Hubert, L. Gandner, J.M. Nuzillard, Y. Ouhdouch, C. Clément, E.A. Barka and

J.H. Renault, 2014. Purification of antibiotics from the biocontrol agent *Streptomyces anulatus* S37 by centrifugal partition chromatography. *Journal of chromatography. B, Analytical technologies in the biomedical and life sciences* 944, 30–34.

Cui N., X.L. Wang, L.Y. Shen and Y.M. Mao, 2014. Diversity of endophytic bacteria in Jujube and their antimicrobial activity against pathogens. *Journal of Food, Agriculture and Environment* 12, 1314–1317.

De Meyer G. and M. Höfte, 1997. Salicylic acid produced by the rhizobacterium *Pseudomonas aeruginosa* 7NSK2 induces resistance to leaf infection by *Botrytis cinerea* on bean. *Phytopathology* 87, 588–593.

De Meyer G., K. Audenaert and M. Höfte, 1999. *Pseudomonas aeruginosa* 7NSK2-induced systemic resistance in tobacco depends on *in planta* salicylic acid accumulation, but is not associated with PR1a expression. *European Journal of Plant Pathology* 105, 513–517.

Duffy B.K., 2001. Competition, In: *Encyclopedia of plant pathology* (O.C. Maloy, T.D. Murray, ed.), Wiley, New York, 243–244.

Duffy B., A. Schouten and J.M. Raaijmakers, 2003. Pathogen self-defence: mechanisms to counteract microbial antagonism. *Annual Review of Phytopathology* 41, 501–538.

Edwards S.G. and B. Seddon, 2001. Mode of antagonism of *Brevibacillus brevis* against *Botrytis cinerea in vitro*. *Journal of Applied Microbiology* 91, 652–659.

Effmert U., J. Kalderas, R. Warnke and B. Piechulla, 2012. Volatile Mediated Interactions Between Bacteria and Fungi in the Soil. *Journal of Chemical Ecology* 38, 665–703.

Elad Y., J. Kohl and N.J. Fokkema, 1994. Control of infection and sporulation of *Botrytis cinerea* on bean and tomato by saprophytic yeasts. *European journal of plant pathology* 100, 315–336.

Elad Y., 1996. Mechanisms involved in the biological control of *Botrytis cinerea* incited diseases. *European Journal of Plant Pathology* 102, 719–732.

Elad Y. and A. Stewart, 2004. Microbial control of *Botrytis* spp.. In: *Botrytis: Biology, Pathology and Control.* (Y. Elad, B. Williamson, P. Tudzynski, N. Delen, ed.), Kluwer Academic Publishers, Dordrecht, Netherlands, 223–241.

Elmer P.A.G. and T. Reglinski, 2006. Biosuppression of *Botrytis cinerea* in grapes. *Plant Pathology* 55, 155–177.

El-Tarabily K.A, M.H. Soliman, A.H. Nassar, H.A. Al-Hassani, K. Sivasithamparam, F. McKenna and G.E.S.J. Hardy, 2000. Biological control of *Sclerotinia minor* using a chitinolytic bacterium and Actinomycetes. *Plant Pathology* 49, 573–583.

Enya J., H. Shinohara, S. Yoshida, T.T.H. Negishi, K. Suyama and S. Tsushima, 2007. Culturable leaf-associated bacteria on tomato plants and their potential as biological control agents. *Microbial Ecology* 53, 524–536.

Errakhi R., F. Bouteau, A. Lebrihi and M. Barakate, 2007. Evidences of biological control capacities of *Streptomyces* spp. against *Sclerotium rolfsii* responsible for damping-off disease in sugar beet (*Beta vulgaris* L.). *World Journal of Microbiology and Biotechnology* 23, 1503–1509.

Essghaier B., M.L. Fardeau, J.L. Cayol, M.R. Hajlaoui, A. Boudabous, H. Jijakli and N. Sadfi-Zouaoui, 2009. Biological control of grey mould in strawberry fruits by halophilic bacteria. *Journal of Applied Microbiology* 106, 833–846.

Falardeau J., C. Wise, L. Novitsky and T.J. Avis, 2013. Ecological and mechanistic insights into the direct and indirect antimicrobial properties of *Bacillus subtilis* lipopeptides on plant pathogens. *Journal of Chemical Ecology* 39, 869–878.

Fan B., X.H. Chen, A. Budiharjo, W. Bleiss, J. Vaterand and R. Borriss, 2011. Efficient colonization of plant roots by the plant growth promoting bacterium *Bacillus amyloliquefaciens* FZB42, engineered to express green fluorescent protein. *Journal of Biotechnology* 151, 303–311.

Fang X., M. Zhang, Q. Tang, Y. Wang and X. Zhang, 2014. In hibitory effect of *Xenorhabdus nematophila* TB on plant pathogens *Phytophthora capsici* and *Botrytis cinerea in vitro* and *in planta*. *Scientific Reports* 4, 4300.

Farace G., O. Fernandez, L. Jacquens, F. Coutte, F. Krier, P. Jacques, C. Clément, E.A. Barka, C. Jacquard and S. Dorey, 2015. Cyclic lipopeptides from *Bacillus subtilis* activate distinct patterns of defence responses in grapevine. *Molecular Plant Pathology* 16, 177–187.

Ferreira J.M.S., 1990. *In vitro* evaluation of epiphytic bacteria from table grapes for the suppression of *Botrytis cinerea*. *South African Journal of Enology and Viticulture* 11, 38–41.

Fiddaman P.J. and S. Rossall, 1994. Effect of substrate on the production of antifungal volatiles from *Bacillus subtilis*. *Journal of Applied Bacteriology* 76, 395–405.

Francesco A. and M. Mari, 2014. Use of biocontrol agents in combination with physical and chemical treatments: efficacy assessment. *Stewart Postharvest Review* 1, 2.

Frankowski J., M. Lorito, F. Scala, R. Schmid, G. Berg and H. Bahl, 2001. Purification and properties of two chitinolytic enzymes of *Serratia plymuthica* HRO-C48. *Archives of Microbiology* 176, 421–426.

Germeier C., K. Hedke and A.V. Tiedemann, 1994. The use of pH indicators in diagnostic media for acid-producing plant-pathogens. *Zeitschrift Pflanzenkrankheiten und Pflanzenschutz* 101, 498–507.

Ghaouth A.E., C. Wilson and M. Wisniewski, 2004. Biologically-based alternatives to synthetic fungicides for the control of postharvest diseases of fruit and vegetables. In *Diseases of Fruits and Vegetables*: *Volume II*, (S.A.M.H. Naqvi, ed.), Springer, Netherlands, 511–535.

Glick B.R., 2012. Plant growth-promoting bacteria: mechanisms and applications. *Scientifica* 1–15.

Govindasamy V., M. Senthilkumar, V. Magheshwaran, U. Kumar, P. Bose, V. Sharmaand and K. Annapurna, 2010. *Bacillus* and *Paenibacillus* spp.: potential PGPR for sustainable agriculture. In: *Plant growth and health promoting bacteria* (D.K. Maheshwari, ed.), Springer, Berlin, Germany, 333–364.

Govrin E.M. and A. Levine, 2002. Infection of *Arabidopsis* with a necrotrophic pathogen, *Botrytis cinerea*, elicits various defense responses but does not induce systemic acquired resistance (SAR). *Plant Molecular Biology* 48, 267–276.

Gruau C., P. Trotel-Aziz, S. Villaume, F. Rabenoelina, C. Clément, F. Baillieul and A. Aziz, 2015. *Pseudomonas fluorescens* PTA-CT2 triggers local and systemic immune response against *Botrytis cinerea* in grapevine. *Molecular Plant-Microbe Interactions* 28, 1117–1129.

Guo Y., H. Zheng, Y. Yangand and H. Wang, 2007. Characterization of *Pseudomonas corrugata* strain p94 isolated from soil in Beijing as a potential biocontrol agent. *Current Microbiology* 55, 247–253.

Gupta G., S.S. Parihar, N.K. Ahirwar, S.K. Snehi and V. Singh, 2015. Plant Growth Promoting Rhizobacteria (PGPR): Current and Future Prospects for Development of Sustainable Agriculture. *Microbial and Biochemical Technology* 7:2.

Guzzon R., E. Franciosi and R. Larcher, 2014. A new resource from traditional wines: characterisation of the microbiota of “Vino Santo” grapes as a biocontrol agent against *Botrytis cinerea*. *European Food Research and Technology* 239, 117–126.

Haggag W.M., 2008. Isolation of bioactive antibiotic peptides from *Bacillus brevis* and *Bacillus polymyxa* against *Botrytis* grey mould in strawberry. *Archives of Phytopathology and Plant Protection* 41, 477–491.

Haggag W.M., F. Abd-El-Kareem and S.D. Abou-Hussein, 2013. Bioprocessing of *Brevibacillus Brevis* and *Bacillus Polymyxa*: apotential biocontrol agent of gray mould disease of strawberry fruits. *International Journal of Engineering and Innovative Technology* 3, 509–518.

Hahn M., 2014. The rising threat of fungicide resistance in plant pathogenic fungi: *Botrytis* as a case study. *Journal of Chemical Biology* 7, 133–141.

Hamdache A., M. Ezziyyani, A. Badoc and A. Lamarti, 2012. Effect of pH, temperature and water activity on the inhibition of *Botrytis cinerea* by *Bacillus amyloliquefaciens* isolates. *African Journal of Biotechnology* 11, 2210–2217.

Hamedi J. and F. Mohammadipanah, 2015. Biotechnological application and taxonomical distribution of plant growth promoting actinobacteria. *Journal of Industrial Microbiology and Biotechnology* 42, 157–171.

Hammami I., R. Siala, M. Jridi, N. Ktari, M. Nasri and M.A. Triki, 2013. Partial purification and characterization of chiIO8, a novel antifungal chitinase produced by *Bacillus cereus* IO8. *Journal of Applied Microbiology* 115, 358–366.

Heil M., 2001. The ecological concept of costs of induced systemic resistance (ISR). *European Journal of Plant Pathology* 107, 137–146.

Helbig J., 2001. Biological control of *Botrytis cinerea* Pers.ex.Fr. in strawberry by *Paenibacillus polymyxa* (isolate 18191). *Journal of Phytopathology* 149, 265–273.

Henry G., M. Deleu, E. Jourdan, P. Thonart and M. Ongena, 2011. The bacterial lipopeptide surfactin targets the lipid fraction of the plant plasma membrane to trigger immune related responses. *Cell Microbiology* 13, 1824–1837.

Hernández-León R., D. Rojas-Solís, M. Contreras-Pérez, M.C. Orozco-Mosqueda, L.I. Macías-Rodríguez, H.R. De La Cruz, E. Valencia-Cantero and G. Santoyo, 2015. Characterization of the antifungal and plant growth-promoting effects of diffusible and volatile organic compounds produced by *Pseudomonas fluorescens* strains. *Biological Control* 81, 83–92.

Huang H. and R.S. Erickson, 2002. Biological control of *Botrytis* stem and blossom blight of lentil. *Plant Pathology Bulletin* 11, 7–14.

Huang H. and R.S. Erickson, 2005. Control of lentil seedling blight caused by *Botrytis cinerea* using microbial seed treatments. *Plant Pathology Bulletin* 14, 35–40.

Huang C.J. and C.Y. Chen, 2008. Synergistic interactions between chitinase ChicCW and fungicides against plant fungal pathogens. *Journal of Microbiology and Biotechnology* 18, 784–787.

Huang C.J., J.F. Tsay, S.Y. Chang, H.P. Yang, W.S. Wu and C.Y. Chen, 2012. Dimethyl disulfide is an induced systemic resistance elicitor produced by *Bacillus cereus* C1L. *Pest Management Science* 68, 1306–1310.

Ilic S.B., S.S. Konstantinovic, Z.B. Todorovic, M.L. Lazic, V.B. Veljkovic, N. Jokovic and B.C. Radovanovic, 2007. Characterization and antimicrobial activity of the bioactive metabolites in *Streptomycete* isolates. *Microbiology* 76, 421–428.

Ji S.H., N.C. Paul, J.X. Deng, Y.S. Kim, B.S. Yun and S.H. Yu, 2013. Biocontrol activity of *Bacillus amyloliquefaciens* CNU114001 against fungal plant diseases. *Mycobiology* 41, 234–242.

Jamalizadeh M., H. Etebarian, H. Aminian and A. Alizadeh, 2011. A review of mechanisms of action of biological control organisms against post-harvest fruits poilage. *Bulletin OEPP/EPPO* 41, 65–71.

Janisiewicz W.J. and J.N. Roitman, 1988. Biological control of blue mold and gray mold on apple and pear with *Pseudomonas cepacia*. *Phytopathology* 78, 1697–1700.

Joo G.J., 2005. Production of an anti-fungal substance for biological control of *Phytophthora capsici* causing phytophthora blight in red peppers by *Streptomyces halstedii*. *Biotechnology Letters* 27, 201–205.

Jourdan E., G. Henry, F. Duby, J. Dommes, J.P. Barthélemy, P. Thonart and M. Ongena, 2009. Insights into the defense-related events occurring in plant cells following perception of surfactin-type lipopeptide from *Bacillus subtilis*. *Molecular Plant-Microbe Interactions* 22, 456–468.

Jarvis W.R., 1977. *Botryotinia and Botrytis Species-Taxonomy, Physiology and Pathogenicity: A Guide to the Literature*. Ottawa: Research Branch, Canadian Department of Agriculture.

Kai M., U. Effmert, G. Berg and B. Piechulla, 2007. Volatiles of bacterial antagonists inhibit mycelial growth of the plant pathogen *Rhizoctonia solani*. *Archives of Microbiology* 187, 351–360.

Kai M., M. Haustein, F. Molina, A. Petri, B. Scholz and B. Piechulla, 2009. Bacterial volatiles and their action potential. *Applied Microbiology and Biotechnology* 81, 1001–1012.

Kamensky M., M. Ovadis, I. Chet and L. Chernin, 2003. Soil-borne strain IC14 of *Serratia plymuthica* with multiple mechanisms of antifungal activity provides biocontrol of *Botrytis cinerea* and *Sclerotinia sclerotiorum* diseases. *Soil Biology and Biochemistry* 35, 323–331.

Kanchiswamy C.N., M. Malnoy and M.E. Maffei, 2015. Chemical diversity of microbial volatiles and their potential for plant growth and productivity. *Frontiers in Plant Science* 6, 151.

Kapat A., G. Zimand and Y. Elad, 1998. Effect of two isolates of *Trichoderma harzianum* on the activity of hydrolytic enzymes produced by *Botrytis cinerea*. *Physiological and Molecular Plant Pathology* 52, 127–137.

Karunaratne A.M., 2011. Biocontrol mechanisms employed by PGPR and strategies of microbial antagonists in disease control on the post-harvest environment of fruits. In: *Ba-*

cteria in Agrobiology: Crop Ecosystems, (D. Maheshwari, ed.), Springer-Verlag, Berlin Heidelberg, Germany 131–164.

Keel C., C. Voisard, C.H. Berling, G. Kahir and G. Defago, 1989. Iron sufficiency is a prerequisite for suppression of tobacco black root rot by *Pseudomonas fluorescens* strain CHA0 under gnotobiotic conditions. *Phytopathology* 79, 584–589.

Kilani-Feki O., O. Khiari, G. Culioli, A. Ortalo-Magne, N. Zouari, Y. Blacheand and S. Jaoua, 2010. Antifungal activities of an endophytic *Pseudomonas fluorescens* strain Pf1TZ harbouring genes from pyoluteorin and phenazine clusters. *Biotechnology Letters* 32, 1279–1285.

Kilani-Feki O. and S. Jaoua, 2011. Biological control of *Botrytis cinerea* using the antagonistic and endophytic *Burkholderia cepacia* Cs5 for vine plantlet protection. *Canadian Journal of Microbiology* 57, 896–901.

Kim Y.S., J.G. Song, I.K. Lee, W.H. Yeo and B.S. Yun, 2013. *Bacillus* sp. BS061 suppresses powdery mildew and gray mold. *Mycobiology* 41, 108–111.

Köhl J., J. Postma, P. Nicot, M. Ruocco and B. Blum, 2011. Stepwise screening of microorganisms for commercial use in biological control of plant-pathogenic fungi and bacteria. *Biological Control* 57, 1–12.

Komárek M., E. Čadková, V. Chrastný, F. Bordas and J.C. Bollinger, 2010. Contamination of vineyard soils with fungicides: a review of environmental and toxicological aspects. *Environment International* 36, 138–51.

Kredics L., Z. Antal, L. Manczinger, A. Szekeres, F. Kevei and E. Nagy, 2003. Influence of environmental parameters on *Trichoderma* strains with biocontrol potential. *Food Technology and Biotechnology* 41, 37–42.

Krol E., 1998. Epiphytic bacteria isolated from grape leaves and its effect on *Botrytis cinerea* Pers. *Phytopathologia Polonica* 16, 53–61.

Kruijt M., H. Tran and J.M. Raaijmakers, 2009. Functional, genetic and chemical characterization of biosurfactants produced by plant growth-promoting *Pseudomonasputida* 267. *Journal of Applied Microbiology* 107, 546–556.

Kumar A., A. Prakash and B.N. Johri, 2011. Bacillus as PGPR in Crop Ecosystem. In: *Bacteria in Agrobiology: Crop Ecosystems* (D.K. Maheshwari, ed.), Springer-Verlag, Berlin Heidelberg, Germany, 37–59.

Labuschagne N., T. Pretorious and A.H. Idris, 2010. Plant growth promoting rhizobacteria as biocontrol agents against soil borne diseases. In: *Plant growth and health promoting bacteria* (D. K. Meheshwari, ed.), Springer-Verlag, Berlin Heidelberg, Germany, 211–230.

Lahlali R., G. Peng, B.D. Gossen, L. McGregor, F.Q Yu, R.K. Hynes, S. F. Hwang, M.R. McDonald and S.M. Boyetchko, 2013. Evidence that the biofungicide Serenade (*Bacillus subtilis*) suppresses clubroot on canola via antibiosis and induced host resistance. *Phytopathology* 103, 245–254.

Lebrihi A., R. Errakhiand and M. Barakate, 2009a. New *Streptomyces barakatei* strain, culture filtrate, derived active compounds and use thereof in the treatment of plants. Patent WO/2009/ 156687.

Lebrihi A., R. Errakhi and M. Barakate, 2009b. New *Streptomyces beta-vulgaris* strain, culture filtrate, derived active compounds and use thereof in the treatment of plants. Patent WO/2009/156688.

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

Lee J.P., S.W. Lee, C.S. Kim, J.H. Son, J.H. Song, K.Y. Lee, H.J. Kim, S.J. Jung and B.J. Moon, 2006. Evaluation of formulations of *Bacillus licheniformis* for the biological control of tomato gray mold caused by *Botrytis cinerea*. *Biological Control* 37, 329–337.

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

Leroux P., R. Frita, D. Debiu, C. Albertini, C. Lanen, J. Bach, M. Gredt and F. Chapeland, 2002. Mechanisms of resistance to fungicides in field strains of *Botrytis cinerea*. *Pest Management Science* 58, 876–888.

Leroux, P. 2004. Chemical control of Botrytis and its resistance to chemical fungicides. In: *Botrytis: Biology, Pathology and Control.* (Y. Elad, B. Williamson, P. Tudzynski, N. Delen, ed.), Kluwer Academic Publishers, Dordrecht, Netherlands, 195–222.

Li Q.L., P. Ning, L. Zheng, J.B. Huang, G.Q. Li and T. Hsiang, 2010. Fumigant activity of volatiles of *Streptomyces globisporus* JK-1 against *Penicillium italicum* on *Citrus microcarpa. Postharvest Biology and Technology* 58, 157–165.

Li F.X., H.Q. Ma, J. Liu and C. Zhang, 2012. Antagonistic effects of *Bacillus cereus* strain B-02 on morphology, ultrastructure and cytophysiology of *Botrytis cinerea*. *Polish Journal of Microbiology* 61, 119–128.

Liu Q., Y.H. Wu and J.C. Yu, 2004. Screening for antagonistic actionmyces isolates from greenhouse soil in northeast China. *Soil* 36, 573–575 (in Chinese).

Liu Y., Z. Chen, T.B. Ng, J. Zhang, M. Zhou, F. Song, F. Lu and Y. Liu, 2007. Bacisubin, an antifungal protein with ribonuclease and hemagglutinating activities from *Bacillus subtilis* strain B-916. *Peptides* 28, 553–559.

Liu W.W., W. Mu, B.Y. Zhu, Y.C. Du and F. Liu, 2008. Antagonistic activities of volatiles from four strains of *Bacillus* spp. and *Paenibacillus* spp. against soil-borne plant pathogens. *Agricultural Sciences in China* 7, 1104–1114.

Liu J., Y. Sui, M. Wisniewski, S. Droby and Y. Liu, 2013. Review: utilization of antagonistic yeasts to manage postharvest fungal diseases of fruit. *International Journal of Food Microbiology* 167,153–161.

Liu X.M. and H. Zhang, 2015.The effects of bacterial volatile emissions on plant abiotic stress tolerance. *Frontiers in Plant Science* 6, 774.

Loqman S., E. Barka, C. Clement and Y. Ouhdouch, 2009. Antagonistic actinomycetes from Moroccan soil to control the grapevine gray mold. *World Journal of Microbiology and Biotechnology* 25, 81–91.

Lucas X., C. Senger, A. Erxleben, B.A. Grüning, K. Döring, J. Mosch, S. Flemming and S. Günther, 2013. StreptomeDB: a resource for natural compounds isolated from *Streptomyces* species. *Nucleic Acids Research* 47, D1130–D1136.

Lugtenberg B. and F. Kamilova, 2009. Plant-growth-promoting rhizobacteria. *Annual Review of Microbiology* 63, 541–556.

Maachia B., E. Rafik, M. Chérif, P. Nandal, T. Mohapatra and P. Bernard, 2015. Biological control of the grapevine diseases 'grey mold' and 'powdery mildew' by *Bacillus* B27 and B29 strains. *Indian journal of experimental biology* 53, 109–115.

Magnin-Robert M., D. Quantinet, M. Couderchet, A. Aziz and P. Trotel-Aziz, 2013. Differential induction of grapevine resistance and defense reactions against *Botrytis cinerea* by bacterial mixtures in vineyards. *Biocontrol* 58, 117–131.

Mahajan G. and L. Balachandran, 2015. Biodiversity in production of antibiotics and other bioactive compounds. *Advances in Biochemical Engineering/Biotechnology Journal* 147, 37–58.

Maksimov I.V., R.R. Abizgildina and L.I. Pusenkova, 2011. Plant growth promoting microorganisms as alternanive to chemical protection from pathogens. *Applied Biochemistry and Microbiology* 47, 333–345.

Malfanova N., L. Franzil, B. Lugtenberg, V. Chebotar and M. Ongena, 2012. Cyclic lipopeptide profile of the plant-beneficial endophytic bacterium *Bacillus subtilis* HC8. *Archives of Microbiology* 194, 893–899.

Martínez-Absalón S., D. Rojas-Solis, R. Hernandez-Leon, C. Prieto-Barajas, M. Orozco-Mosqueda, J. Peria-Cabriales, S. Sakuda, E. Valencia-Cantero and G. Santoyo, 2014. Potential use and mode of action of the new strain *Bacillus thuringiensis* UM96 for the biological control of the grey mould phytopathogen *Botrytis cinerea*. *Biocontrol Science and Technology* 24, 1349–1362.

Martínez-Hidalgo P., J.M. García and M.J. Pozo, 2015. Induced systemic resistance against *Botrytis cinerea* by *Micromonospora* strains isolated from root nodules. *Frontiers in Microbiology* 6, 922.

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

Meziane H., I. Van Der Sluis, L.C. Van Loon, M. Höfte and P.A.H.M. Bakker, 2005. Determinants of *Pseudomonas putida* WCS358 involved in inducing systemic resistance in plants. *Molecular Plant Pathology* 6, 177–185.

Muzammil S., C. Graillon, R. Saria, F. Mathieu, A. Lebrihi and S. Compant, 2014. The Saharan isolate *Saccharothrix algeriensis* NRRL B-24137 induces systemic resistance in *Arabidopsis thaliana* seedlings against *Botrytis cinerea*. *Plant Soil* 374, 423–434.

Nafisi M., L. Fimognari and S. Yumiko, 2015. Interplays between the cell wall and phytohormones in interaction between plants and necrotrophic pathogens. *Phytochemistry* 112, 63–71.

Nagorska K., M. Bikowski and M. Obuchowskji, 2007. Multicellular behaviour and production of a wide variety of toxic substances support usage of *Bacillus subtilis* as a powerful biocontrol agent. *Acta biochimica Polonica* 54, 495–508.

Nair N. and R.N. Allen, 1993. Infection of grape flowers and berries by *Botrytis cinerea* as a function of time and temperature. *Mycological Research* 97, 1012–1014.

Nakajima M. and K. Akutsu, 2014. Virulence factors of *Botrytis cinerea*. *Journal of General Plant Pathology* 80, 15–23.

Narayanasamy P., 2013. *Biological Management of Diseases of Crops: Volume 1: Characteristics of Biological Control Agents*. Springer Science & Business Media.

Neeraja C., K. Anil, P. Purushotham, K. Suma, P. Sarma, B.M. Moerschbacher and A.R. Podile, 2010. Biotechnological approaches to develop bacterial chitinases as a bioshield against fungal diseases of plants. *Critical Reviews in Biotechnology* 30, 231–241.

Nicot P., M. Bardin, C. Alabouvette, J. Köhl and M. Ruocco, 2011. Potential of biological control based on published research. 1. Protection against plant pathogens of selected crops. In: *Classical and augmentative biological control against diseases and pests: critical status analysis and review of factors influencing their success* (P. Nicot, ed.), *IOBC/WPRS*, Zurich, 1–11.

Ningaraju T.M., 2006. *Cloning and characterization of chitinase gene/s from native isolates of Serratia marcescens*. PhD Thesis, University of Dharwad, India.

Nunes C., J. Usall, N. Teixido and I. Vinas, 2001. Biological control of postharvest pear diseases using a bacterium, *Pantoea agglomerans* CPA-2. *International Journal of Food Microbiology* 70, 53–61.

Nunes C., J. Usall, N. Teixido, E. Fons and I. Vinas, 2002. Postharvest biological control by *Pantoea agglomerans* (CPA-2) on Golden Delicious apples. *Journal of Applied Microbiology* 92, 247–255.

OECD, 2012. Guidance to the environmental safety evaluation of microbial biocontrol agents. Series on Pesticides No.67 ENV/JM/MONO 1, 17 feb. 2012

OECD, 2014. Report of the OECD/KEM/EU workshop on microbial pesticides assesment and management of risks. Series on Pesticides No. 76

On A., F. Wong, Q. Ko, R.J. Tweddell, H. Antoun and T.J. Avis, 2015. Antifungal effects of compost tea microorganisms on tomato pathogens. *Biological Control* 80, 63–69.

Ongena M., P. Jacques, Y. Toure, J. Destain, A. Jabrane and P. Thonart, 2005. Involvement of fengycin-type lipopeptides in the multifaceted biocontrol potential of *Bacillus subtilis*. *Applied Microbiology and Biotechnology* 69, 29–38.

Ongena M. and P. Jacques, 2008. *Bacillus* lipopeptides: versatile weapons for plant disease biocontrol. *Trends in Microbiology* 16, 115–125.

Pal K.K. and B. McSpadden-Gardener, 2006. Biological control of plant pathogens. *The Plant Health Instructor*. DOI:10.1094/PHI-A-2006-1117–02.

Pan S. and S. Bhagat, 2011. Biological control of plant diseases. *The Journal of Plant Protection Sciences* 3, 1–14.

Park S., D. Bae, J. Lee, S. Chung and H. Kim, 1999. integration of biological and chemical methods for the control of pepper gray mold rot under commercial greenhouse conditions *Plant Pathology Journal* 15, 162–167.

Patel H., C. Tscheka, K. Edwards, G. Karlsson and H. Heerkotz, 2011. All-or-none membrane permeabilization by fengycin-type lipopeptides from *Bacillus subtilis* QST713. *Biochimica et Biophysica Acta* 1808, 2000–2008.

Patkowska E. and M. Konopiński, 2014. Antagonistic activity of selected bacteria occurring in the soil after root chicory cultivation. *Plant Soil and Environment* 60, 320–324.

Paul B., I. Girard, T. Bhatnagar and P. Bouchet, 1997. Suppression of *Botrytis cinerea* causing grey mould disease of grape vine (*Vitis vinifera*) and its pectinolytic activities by a soil bacterium. *Microbiological Research* 152, 413–420.

Pérez-García A., D. Romero and A. DeVicente, 2011. Plant protection and growth stimulation by microorganisms: biotechnological applications of bacilli in agriculture. *Current Opinion in Biotechnology* 22, 187–193.

Pieterse C.M., S.C. Van Wees, E. Hoffland, J.A. Van Pelt, and L.C. Van Loon, 1996. Systemic resistance in *Arabidopsis* induced by biocontrol bacteria is independent of salicylic acid accumulation and pathogenesis-related gene expression. *Plant Cell* 8, 1225–1237.

Postolaky O., T. Syrbu, N. Poiras, K. Baltsat, S. Maslobrod and S. Boortseva, 2012. *Streptomycetes* and *micromycetes* as perspective antagonists of fungal phytopathogens. *Communications in agricultural and applied biological sciences* 77, 249–257.

Pretorius D., J. Van Rooyen and K.G. Clarke, 2015. Enhanced production of antifungal lipopeptides by *Bacillus amyloliquefaciens* for biocontrol of postharvest disease. *New Biotechnology* 32, 243–252.

Punja Z.K. and R.S. Utkhede, 2003. Using fungi and yeasts to manage vegetable crop diseases. *Trends in Biotechnology* 21, 400–407.

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

Raaijmakers J.M., I. De Bruijn, O. Nybroe and M. Ongena, 2010. Natural functions of lipopeptides from *Bacillus* and *Pseudomonas*: more than surfactants and antibiotics. *FEMS Microbiology Reviews* 34, 1037–1062.

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

Rabosto X., M. Garrau, A. Paz, E. Boido, E. Dellacassa and F. Carrau, 2006. Grapes and vineyard soils as source of microorganisms for biological control of *Botrytis cinerea*. *American Journal of Enology and viticulture* 57, 332–338.

Raza W., W. Yang and Q.R. Shen, 2008. *Paenibacillus polymyxa:* antibiotics, hydrolytic enzymes and hazard assessment. *Journal of Plant Pathology* 90, 419–430.

Redmond J.C., J.J. Marois and J.D. Macdonald, 1987. Biological control of *Botrytis cinerea* on roses with epiphytic microorganisms. *Plant Disease* 71,799–802.

Romanazzi G. and E. Feliziani, 2014. *Botrytis cinerea.* In: *Postharvest Decay: Control Strategies* (S. Bautista-Baños, ed.), Elsevier, London, 131–146.

Romanazzi G., J.L. Smilanick, E. Feliziani and S. Droby, 2016. Integrated management of postharvest gray mold on fruit crops. *Postharvest Biology and Technology* 113, 69–76.

Ryu C.M., M.A. Farag, C.H. Hu, M.S. Reddy, H.X. Wei, P.W. Pare and J.W. Kloepper, 2003. Bacterial volatiles promote growth in *Arabidopsis*. *Proceedings of the National Academy of Sciences of the United States of America* 100, 4927–4932.

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

Sansone G., I. Rezza, V. Calvente, D. Benuzzi and M.I. Sanz Ferramola, 2011. Inhibitors of polygalacturonase and laccase of *Botrytis cinerea* and their application to the control of the fungus. *International Biodeterioration and Biodegradation* 65, 243–247.

Sanz Ferramola M.I., D. Benuzzi, V. Calvente, J. Calvo, G. Sansone, S. Cerutti and J. Raba, 2013. The use of siderophores for improving the control of postharvest diseases in stored fruits and vegetables. In: *Microbial pathogens and strategies for combating them: science, technology and education* (A. éndez-Vilas, ed.), Formatex: Badajoz, Spain N Biotechnol, 1385–1394.

Schmidt S., J.F. Blom, J. Pernthaler, G. Berg, A. Baldwin, E. Mahenthiralingam and L. Eberl, 2009. Production of the antifungal compound pyrrolnitrin is quorum sensing-regulated in members of the *Burkholderia cepacia* complex. *Environmental Microbiology* 11, 1422–1437.

Schöller C.E.G., H. Gürtler, R. Pedersen, S. Molin and K. Wilkins, 2002. Volatile metabolites from actinomycetes. *Journal of Agricultural and Food Chemistry* 50, 2615–2621.

Schoonbeek H.J., J.M. Raaijmakers and M.A. De Waard, 2002. Fungal ABC transporters and microbial interactions in natural environments. *Molecular Plant-Microbe Interactions* 15, 1165–1172.

Schoonbeek H.J., A.C. Jacquat-Bovet, F. Mascher and J.P. Métraux, 2007. Oxalate-degrading bacteria can protect *Arabidopsis thaliana* and crop plants against *Botrytis cinerea*. *Molecular Plant-Microbe Interactions* 20, 1535–1544.

Selim S., J. Negrel, C. Govaerts, S. Gianinazzi and D.V. Tuinen, 2005. Isolation and partial characterization of antagonistic peptides produced by *Paenibacillus* sp. Strain B2 isolated from the sorghum mycorhizosphere. *Applied and Environmental Microbiology* 71, 6501–6507.

Sharma R.R., D. Singh and R. Singh, 2009. Biological control of postharvest diseases of fruits and vegetables by microbial antagonists: A review. *Biological Control* 50, 205–221.

Silva L.J., E.J. Crevelin, W.R. Souza, L.A. Moraes, I.S. DeMelo and T.D. Zucchi, 2014. *Streptomyces araujoniae*produces a multiantibiotic complex with ionophoric properties to control *Botrytis cinerea*. *Phytopathology* 104, 1298–1305.

Son Y.J., J.P. Lee, C.S. Kim, J.H. Song, H.J. Kim, W.J. Kim, D.H. Kim, H.C. Park and B.J. Moon, 2002. Biological control of gray mold rot of perilla caused by *Botrytis cinerea*. Resistance of perilla cultivars and selection of antagonistic bacteria. *Journal of Plant Pathology* 18, 36–42.

Soto-Muñoz L., N. Teixidó, J. Usall, I. Viñas and R. Torres, 2014. Detection and quantification by PCR assay of the biocontrol agent *Pantoea agglomerans* CPA-2 on apples. *International Journal of Food Microbiology* 175, 45–52.

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

Spadaro D. and M.L. Gullino, 2010. Opportunities and constraints in the development of antagonistic yeasts for the control of postharvest diseases of fruit. *Stewart Postharvest Review* 3, 1–8.

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

Stein T., 2005. *Bacillus subtilis* antibiotics: structures, syntheses and specific functions. *Molecular Microbiology* 56, 845–857.

Stockwell V.O., K.B. Johnson and J.E. Loper, 1998. Establishment of bacterial antagonists of *Erwinia amylovora* on pear and apple blossoms as influenced by inoculum preparation. *Phytopathology* 88, 506–513.

Sundh I., 2014. Regulation of microbial biocontrol agents in the Euroupean Union: A microbiologist's view. In: *Abstracts, XIII Meeting of the Working Group Biological control of fungal and bacterial plant pathogens. Biocontrol of Plant Diseases:"From the field to the laboratory and back again"*, 15–18 June, 2014, Uppsala, Sweden.

Svetlana B., T. Sirbu, O. Postolachi and V. Subina, 2008. Antimicrobial properties of *micromycetes* and *streptomycetes* from Moldovan soils. *Bulletin of University of Agricultural Sciences and Veterinary Medicine Cluj Napocaculture* 1, 389.

Swadling I.R. and P. Jeffries, 1998. Antagonistic Properties of two bacterial biocontrol agents of grey mould disease. *Biocontrol Science and Technology* 8, 439–448.

Sztejnberg A. and J.P. Blakeman, 1973. Studies on leaching of *Botrytis cinerea* conidia and dye absorption by bacteria in relation to competition for nutrients on leaves. *Journal of general microbiology* 78, 15–22.

Taechowisan T., S. Chanaphat, W. Ruensamran and W.S. Phutdhawong, 2012. Antifungal activity of 3-methylcarbazoles from *Streptomyces* sp. LJK109; an endophyte in *Alpinia galanga*. *Journal of Applied Pharmaceutical Science* 2, 124–128.

Tampakaki A.P., E. Hatziloukas and N.J. Panopoulos, 2009. *Plant pathogens, bacteria. Encyclopedia of Microbiology*. 3rd ed. Elsevier, 655–677.

Teixidó N., J. Usall, L. Palou, A. Asensio, C. Nunes and I. Viñas, 2001. Improving control of green and blue molds of oranges by combining *Pantoea agglomerans* (CPA-2) and sodium bicarbonate. *European Journal of Plant Pathology* 107, 685–694.

Tenorio-Salgado S., R. Tinoco, R. Vazquez-Duhalt, J. Caballero Melladoand and E. Perez-Rueda, 2013. Identification of volatile compounds produced by the bacterium *Burkholderia tropica* that inhibit the growth of fungal pathogens. *Bioengineering* 4, 1–8.

Thomashow L.S. and D.M. Weller, 1988. Role of a phenazine antibiotic from *Pseudomonas fluorescens* in biological control of *Gaeumannonas graminis* var. *tritici*. *Journal of Bacteriology* 170, 3499–3508.

Thomashow L.S., R.F. Bonsall and D.M. Weller, 1997. Antibiotic production by soil and rhizosphere microbes in situ. In: *Manual of Environmental Microbiology* (C.J. Hurst, G.R. Knudsen, M.J. Mclnerney, L.D. Stetzerbach, M.V. Walter, ed.), American Society for Microbiology, Washington, DC, 493–499.

Todorova S. and L. Kozhuharova, 2009. Characteristics and antimicrobial activity of *Bacillus subtilis* strains isolated from soil. *World Journal of Microbiology and Biotechnology* 26, 1207–1216.

Touré Y., M. Ongena, P. Jacques, A. Guiroand and P. Thonart, 2004. Role of lipopeptides produced by *Bacillus subtilis* GA1 in the reduction of grey mould disease caused by *Botrytis cinerea* on apple. *Journal of Applied Microbiology* 96, 1151–1160.

Trotel-Aziz P., A. Aziz, M. Magnin-Robert, E. Aït Barka and S. Gogniès, 2006. Bactéries présentant une activité protectrice de la vigne contre *Botrytis cinerea*. *French patent* 06.06.513.

Van Kan J.A., M.W. Shaw and R.T. Grant-Downton, 2014. Botrytis Species: Relentless Necrotrophic Thugs or Endophytes Gone Rogue?. *Molecular Plant Pathology* 15, 957–961.

Van Loon L.C., P.A.H.M. Bakker and C.M.J. Pieterse, 1998. Systemic resistance induced by rhizosphere bacteria. *Annual Review of Phytopathology* 36, 453–483.

Villaverde J.J., B. Sevilla-Morán, P. Sandín-España, C. López-Goti and J.L. Alonso-Prados, 2014. Biopesticides in the framework of the European pesticide regulation (EC) No. 1107/2009. *Pest Management Science* 70, 2–5.

Walker R., K.A. Emslie and E.J. Allan, 1996. Bioassay methods for the detection of antifungal activity by *Pseudomonas antimicrobica* against the grey mould pathogen *Botrytis cinerea*. *Journal of Applied Bacteriology* 81, 531–537.

Walker R., A.A. Powell and B. Seddon, 1998. *Bacillus* isolates from the spermosphere of peas and dwarf French beans with antifungal activity against *Botrytis cinerea* and *Pythium* species. *Journal of Applied Microbiology* 84, 791–801.

Walker R., C.M.J. Innes and E.J. Allan, 2001. The potential biocontrol agent *Pseudomonas antimicrobica* inhibits germination of conidia and outgrowth of *Botrytis cinerea*. *Letters in Applied Microbiology* 32, 346–348.

Walker A.S., A. Micoud, F. Rémuson, J. Grosman, M. Gredt and P. Leroux, 2013. French vineyards provide information that opens ways for effective resistance management of *Botrytis cinerea* (grey mould). *Pest Management Science* 69, 667–678.

Walters D. and M. Heil, 2007. Costs and trade-offs associated with induced resistance. *Physiological and Molecular Plant Pathology* 71, 3–17.

Walters D.R., A. Avrova, I.J. Bingham, F.J. Burnett, J. Fountaine, N.D. Havis, S.P. Hoad, G. Hughes, M. Loosely, S.J.P. Oxley, A. Renwick, C.F.E. Topp and A.C. Newton, 2012. Control of foliar diseases in barley: towards an integrated approach. *European Journal of Plant Pathology* 133, 33–73.

Walters D.R., J. Ratsep and N.D. Havis, 2013. Controlling crop diseases using induced resistance: challenges for the future. *Journal of Experimental Botany* 64, 1263–1280.

Wan M., G. Li, J. Zhang, D. Jiang and H.C. Huang, 2008. Effect of volatile substances of *Streptomyces platensis* F-1 on control of plant fungal diseases. *Biological Control* 46, 552–559.

Wang J.L., Z.Y. Zong, W. Shang, W. Qi and H.K. Wang, 2012. Activity against *Botrytis cinerea* of *Bacillus amyloliquefaciens* IMAUB1034 isolated from naturally fermented congee. *Journal of Food Agriculture and Environment* 10, 534–542.

Weisskopf L., 2013. The potential of bacterial volatiles for crop protection against phytopathogenic fungi. In: *Microbial pathogens and strategies for combating them: science, technology and education* (A. Méndez-Vilas, ed.), Formatex: Badajoz, Spain N Biotechnol, 1352–1363.

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

Weller D.M., 2007. *Pseudomonas* biocontrol agents of soilborne pathogens: Looking back over 30 years. *Phytopathology* 97, 250–256.

Williamson B., B. Tudzynski, P. Tudzynski and J.A.L. Van Kan, 2007. *Botrytis cinerea*: the cause of grey mould disease. *Molecular Plant Pathology* 8, 561–580.

Wilson, C.L., Wisniewski M., 1994. *Biological Control of Postharvest Diseases: Theory and Practice.* CRC Press, Boca Raton, Florida, 182 pp.

Wise C., L. Novitsky, A. Tsopmo and T.J. Avis, 2012. Production and antimicrobial activity of 3-hydroxypropionaldehyde from *Bacillus subtilis* strain CU12. *Journal of Chemical Ecology* 38, 1521–1527.

Wisniewski M., C. Biles, S. Droby, R. McLaughlin, C. Wilson and E. Chalutz, 1991. Mode of action of the postharvest biocontrol yeast, *Pichia guilliermondii*. I. Characterization of attachment to *Botrytis cinerea*. *Physiological and Molecular Plant Pathology* 39, 245–258.

Wisniewski M. and C. Wilson, 1992. Biological control of postharvest diseases of fruits and vegetables: recent advances. *HortScience* 27, 94–98.

Wu L., H.J. Wu, J. Qiao, X. Gao and R. Borriss, 2015. Novel routes for improving biocontrol activity of *Bacillus* based bioinoculants. *Frontiers in Microbiology* 6, 1395.

Xin I. and J.I. Ming-Shan, 2008. Screening of antagonistic Actinomycetes from soil. *Journal of Henan Agricultural Sciences* 2008–01.

Yánez-Mendizábal V., J. Usall, I. Viñas, C. Casals, S. Marín, C. Solsona and N. Teixidó, 2011. Potential of a new strain of *Bacillus subtilis* CPA-8 to control the major postharvest diseases of fruit. *Biocontrol Science and Technology* 21, 409–426.

Zhang S.M., Y.X. Wang, L.Q. Meng, J. Li, X.Y. Zhao, X. Cao, X.L. Chen, A.X. Wang and J.F. Li, 2012. Isolation and characterization of antifungal lipopeptides produced by endophytic *Bacillus amyloliquefaciens* TF28. *African Journal of Microbiology Research* 6, 1747–1755.

Zhang X., B. Li, Y. Wang, Q. Guo, X. Lu, S. Li and P. Ma, 2013. Lipopeptides, a novel protein, and volatile compounds contribute to the antifungal activity of the biocontrol agent *Bacillus atrophaeus* CAB-1. *Applied Microbiology and Biotechnology* 97, 9525–9534.

Zhao H., Y.K. Kim, L.Huang and C.L. Xiao, 2010. Resistance to thiabendazole and baseline sensitivity to fludioxonil and pyrimethanil in *Botrytis cinerea* populations from apple and pear in Washington State. *Postharvest Biology and Technology* 56, 12–18.

Zhao L.J., X.N. Yang, X.Y. Li, W. Mu and F. Liu, 2011. Antifungal, insecticidal and herbicidal properties of volatile components from *Paenibacillus polymyxa* Strain BMP-11. *Agricultural Sciences in China* 10, 728–736.

Zhao X., Z.J. Zhou, Y. Han, Z.Z. Wang, J. Fan and H.Z. Xiao, 2013. Isolation and identification of antifungal peptides from *Bacillus* BH072, a novel bacterium isolated from honey. *Microbiological Research* 168, 598–606.

Zimand G., Y. Elad and I. Chet, 1996. Effect of *Trichoderma harzianum* on *Botrytis cinerea* pathogenicity. *Phytopathology* 86, 1255–1260.

Accepted for publication: June 13, 2016