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REVIEW

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

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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

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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 antagonize 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 nutrients 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®	<i>Pantoea agglomerans</i>	IRTA (Spain)
Serenade Max®	<i>Bacillus subtilis</i>	Bayer, formerly BASF (Germany)
Bio-save®	<i>Pseudomonas syringae</i>	Jet harvest solutions (USA)
Amylo-X®	<i>Bacillus amyloliquefaciens</i>	Biogard CBC (Italy)
Double Nickel 55WDG/LC™	<i>Bacillus amyloliquefaciens</i>	Certis (USA)
Companion®	<i>Bacillus subtilis</i> GB03	Growth products (USA)
Botokira Wettable Powder®	<i>Bacillus subtilis</i> IK-1080	(Idemitsu Kosan Inc., Japan)
Bio Arc®	<i>Bacillus megaterium</i>	Sphere Bio-Arc PVT Ltd (India)
Mycostop®	<i>Streptomyces griseoviridis</i> Strain K61	Verdera Oy (Finland)
Actinovate®	<i>Streptomyces lydicus</i> 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-Gardner, 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 phyllosphere 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
<i>Pantoea agglomerans</i> LRC 954, <i>Pseudomonas fluorescens</i> LRC 1788	Lentil seedling	Competition for space and nutrients	Huang and Erickson, 2005
<i>Erwinia herbicola</i> (<i>Pantoea agglomerans</i>)	Apple juice	Competition for nutrients	Bryk <i>et al.</i> , 1998
<i>Pseudomonas putida</i> Cha94, <i>B. amyloliquefaciens</i> BL3	Pepper	Competition for space and nutrients	Park <i>et al.</i> , 1999
<i>Rahnella aquatilis</i>	Apple fruit/ <i>in vitro</i>	Competition for nutrients	Calvo <i>et al.</i> , 2007
<i>Pantoea agglomerans</i>	Apple fruit	Competition for space and nutrients	Nunes <i>et al.</i> , 2002
<i>Bacillus</i> sp. (isolate UYBC38)	<i>In vitro</i> / <i>in situ</i> (grape, peach, and apple)	Competition for nutrients	Rabosto <i>et al.</i> , 2006
<i>Paenibacillus polymyxa</i>	Strawberry fruit pulp suspension	Competition for nutrients	Helbig, 2001
<i>Xanthomonas maltophilia</i> , <i>Bacillus pumilus</i> , <i>Lactobacillus</i> sp., <i>Pseudomonas</i> sp.	Bean and tomato	Competition for nutrients	Elad <i>et al.</i> , 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 Wisniewski, 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*, *Pseudomonas*, *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
<i>Pseudomonas cepacia</i> strain LT412	Apple and pears	Pyrolnitrin	Mycelial growth inhibition and disease reduction	Janisiewicz and Roitman, 1988
<i>Pseudomonas corrugata</i> strain P94	Tomato leaf	Secondary metabolites (bacteriocin)	Disease reduction	Guo <i>et al.</i> , 2007
<i>Pseudomonas fluorescens</i> , <i>Bacillus</i> sp.	Grapes	Not identified	Disease reduction	Krol, 1998
<i>Pseudomonas fluorescens</i> strain PflTZ	<i>In vitro</i> / <i>in planta</i> (vine vitropplants)	Not identified	Mycelial growth inhibition, and disease reduction	Kilani-Feki <i>et al.</i> , 2010
<i>Pseudomonas</i> sp., <i>Pseudomonas fluorescens</i> , <i>Pseudomonas putida</i> , <i>Pseudomonas aeruginosa</i>	<i>In vitro</i>	Not identified	Mycelial growth inhibition	Trotel-Aziz <i>et al.</i> , 2006; Kruijt <i>et al.</i> , 2009; Kumar <i>et al.</i> , 2011; Patkowska and Konopiński, 2014; Hernández-León <i>et al.</i> , 2015
<i>Burkholderia phytofirmans</i> PsjN	<i>In vitro</i> / grapevine plantlets	Not identified	Mycelial growth inhibition and disease reduction, plant growth promotion	Ait Barka <i>et al.</i> , 2000; Ait Barka <i>et al.</i> , 2002
<i>Burkholderia gladioli</i>	<i>In vitro</i> / <i>In situ</i> (leaves of strawberry)	Not identified	Inhibition of conidial germination	Walker <i>et al.</i> , 1996; Walker <i>et al.</i> , 2001
<i>Burkholderia cepacia</i> Cs5	<i>Vitis vinifera</i> plants	Didecyl-phthalate and two methyl alkyl-quinolones	disease reduction	Kilani-Feki and Jaoua, 2011
<i>Bacillus</i> sp. PB10, <i>Bacillus licheniformis</i> , <i>Bacillus megaterium</i> , <i>Bacillus subtilis</i> , <i>Bacillus</i> sp.	<i>In vitro</i> / cut leaves of tomato	Not identified	Mycelial growth inhibition and disease reduction	Enya <i>et al.</i> , 2007
<i>Bacillus licheniformis</i> , <i>Bacillus megaterium</i>	<i>In vitro</i> / perilla plants	Not identified	Inhibition of mycelial growth and conidial germination, disease reduction	Son <i>et al.</i> , 2002
<i>Bacillus licheniformis</i> N1	tomato plants	Not identified	Disease reduction and plant growth promotion	Lee <i>et al.</i> , 2006
<i>Bacillus subtilis</i> CL27, <i>B. pumilus</i> CL45	<i>In vitro</i>	Antibiotic appeared not to be peptide	Mycelial growth and sporulation inhibition	Leifert <i>et al.</i> , 1995
<i>Bacillus subtilis</i> CL27	<i>Astilbe</i> seedlings	Antibiotic appeared not to be peptide	Disease reduction	Leifert <i>et al.</i> , 1995

(Continued)

Table 3. (Continued).

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

(Continued)

Table 3. (Continued).

Antagonistic bacteria	Plant/fruit/ conditions	Antifungal metabolites	Effect	Reference
<i>Bacillus subtilis</i> TS 01 and ZR 02, <i>Bacillus subtilis</i> , <i>Bacillus</i> sp., <i>Bacillus lentimorbus</i> , <i>Bacillus megaterium</i> , <i>Bacillus pumilus</i> , <i>B. subtilis</i> , <i>Bacillus subtilis</i> CPA-8, <i>B. amyloliquefaciens</i> , <i>Bacillus</i> sp.; <i>Bacillus</i> sp.	<i>In vitro</i>	Not identified	Mycelial growth inhibition	Todorova and Kozhuharova, 2009; Walker <i>et al.</i> , 1998; Ferreira, 1990; Yáñez-Mendizábal <i>et al.</i> , 2011; Hamdache <i>et al.</i> , 2012; Cui <i>et al.</i> , 2014; Patkowska and Konopiński, 2014
<i>Streptomyces</i> sp., <i>Micromonospora</i> sp.	<i>In vitro</i> / <i>in vitro</i> grapevine leaves and plantlets	Not identified	Morphological changes and severe structural alterations of the fungal mycelium	Loqman <i>et al.</i> , 2009
<i>Streptomyces araujoniae</i> 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 <i>et al.</i> , 2014
<i>Streptomyces barakatei</i> <i>Streptomyces beta-vulgaris</i>	<i>In vitro</i> / grapevine leaves	Secondary metabolites	Mycelial growth inhibition and disease reduction	Lebrihi <i>et al.</i> , 2009 a,b
<i>Streptomyces hygrosopicus</i> , <i>Streptomyces rimosus</i> , <i>Streptomyces anulatus</i>	<i>In vitro</i>	Not identified	Mycelial growth inhibition	Liu <i>et al.</i> , 2004; Ilic <i>et al.</i> , 2007; Xin and Ming-shan, 2008; Svetlana <i>et al.</i> , 2008; Postolaky <i>et al.</i> , 2012 ; Couillerot <i>et al.</i> , 2014
<i>Streptomyces anulatus</i> S37	<i>In vitro</i> , grapevine plantlets	streptochlorin, nigericin and piericidin A1.	Mycelial growth inhibition and disease reduction	Couillerot <i>et al.</i> , 2014
<i>Xenorhabdus nematophila</i> TB	<i>In vitro</i> , detached tomato fruits	Antimicrobial metabolites	Mycelial growth inhibition, spore germinations inhibition and disease reduction	Fang <i>et al.</i> , 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 Jacques, 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; Er-

rakhi *et al.*, 2007; Loqman *et al.*, 2009; Hamed 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 post-harvest 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
<i>Bacillus cereus</i> IO8	<i>In vitro</i> / tomato plants	Chitinase	Mycelial growth inhibition and disease incidence reduction	Hammami <i>et al.</i> , 2013
<i>Virgibacillus marismortui</i> , <i>Bacillus subtilis</i> , <i>Bacillus pumilus</i> , <i>Bacillus licheniformis</i> , <i>Terribacillus halophilus</i> , <i>Halomonas elongata</i> , <i>Lanococcus rifietoensis</i> , <i>Staphylococcus equorum</i> , <i>Staphylococcus</i> sp.	<i>In vitro</i> / strawberry fruits	Chitinase, β -1, 3-glucanase, cellulase and protease	Mycelial growth inhibition and disease incidence reduction	Essghaier <i>et al.</i> , 2009
<i>Serratia plymuthica</i> IC14	<i>In vitro</i> / cucumber leaves	Endochitinase	Mycelial growth inhibition and disease incidence reduction	Kamensky <i>et al.</i> , 2003
<i>Serratia plymuthica</i> HRO-C48	<i>In vitro</i>	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 <i>et al.</i> , 2001
<i>Pseudomonas</i> sp. (B194 and B224) <i>Erwinia herbicola</i> (<i>Pantoea agglomerans</i>)	Apple juice	Not identified	Inhibition of germination and germ tube elongation	Bryk <i>et al.</i> , 1998, 2004
<i>Bacillus thuringiensis</i> UM96	<i>In vitro</i> / <i>in vitro</i> Medicago truncatula plants	Chitinases	Mycelial growth inhibition and disease reduction	Martínez-Absalón <i>et al.</i> , 2014
<i>Bacillus cereus</i> B-02	<i>In vitro</i>	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 <i>et al.</i> , 2012
<i>Rahnella aquatilis</i> BNM	<i>In vitro</i> / apple	Interference with activity and growth of the pathogen	Mycelial growth inhibition and disease reduction	Sansone <i>et al.</i> , 2011; Sanz Ferramola <i>et al.</i> , 2013
<i>Bacillus circulans</i> GI 070	<i>In vitro</i> / grapevine vitropplants	Interference with activity and growth of the pathogen	Mycelial growth inhibition and disease reduction	Paul <i>et al.</i> , 1997
<i>Bacillus pumilus</i> NCIMB 13374 <i>Pseudomonas fluorescens</i> NCIMB 13373	<i>In vitro</i> / strawberries	Interference with activity and growth of the pathogen	Conidial germination inhibition and disease reduction	Swadling and Jeffries, 1998

(Continued)

Table 4. (Continued).

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

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-

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 Weiskopf, 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 elicit 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 μ M 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 energy 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 *et 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.

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