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Bacillus thuringiensis beyond insect biocontrol: plant growth promotion and biosafety of polyvalent strains

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Abstract - The entomopathogenic bacterium *Bacillus thuringiensis* is widely used for the control of many agricultural insect pests and vectors of human diseases. Several studies reported also on its antibacterial and antifungal activities. However, to our knowledge there were no studies dealing with its capacity to act as a plant growth promoting bacterium. This review surveys the potential of *B. thuringiensis* as a polyvalent biocontrol agent, a biostimulator and biofertiliser bacterium that could promote the plant growth. Also, discussed is the safety of *B. thuringiensis* as a bacterium phylogenetically closely related to *Bacillus cereus* the opportunistic human pathogen and *Bacillus anthracis*, the etiological agent of anthrax.

Key words: *Bacillus thuringiensis*, PGPR, biocontrol, biostimulation, biofertilisation, safety.

INTRODUCTION

The entomopathogenic bacterium *Bacillus thuringiensis* is a Gram-positive spore-forming bacterium that belongs to the *Bacillus cereus* group which encompasses six validly described species (Daffonchio *et al*., 2000; Cherif *et al*., 2003a). This bacterium is ubiquitous and widely diffused in the environment including soil; insects and their habitats; stored products and warehouses; plant materials; and aquatic environments (Glare and O'Callaghan, 2000; Hernández *et al*., 2005; Bizzarri and Bishop, 2007). It is widely used as bioinsecticide for the control of many agricultural insect pests and vectors of human diseases, and constitues the basis of over 90% of commercially available biopesticides (Chattopadhyay *et al*., 2004). This is owing to its ability to produce characteristic proteinaceous crystalline toxins (δ-endotoxins) with a specific activity against certain insect species (for review see Schnepf *et al*., 1998). The *cry* genes are expressed in many plants allowing their protection against insect pathogens and genetically modified plants (GMP) based on *B. thuringiensis* toxin genes represent about 19 % of the total transgenic acreage in the world (James, 2005).

Plant growth-promoting bacteria are endophytic and free-living soil bacteria that can either directly or indirectly facilitate the growth of plants. Indirect stimulation of plant growth includes a variety of mechanisms by which the bacteria prevent phytopathogenic microorganisms from inhibiting plant growth and development. This biocontrol activity is accomplished owing to the production of bacteriocins (Cherif *et al*., 2003b), autolysins (Raddadi *et al*., 2004, 2005), lactonases (Dong *et al*., 2002), siderophores, β-1,3-glucanase, chitinases, antibiotics and hydrogene cyanide and to the ability to degrade indole-3-acetic acid (IAA) (protect the plant from high-IAA-producing bacteria) (Leveau and Lindow, 2005). Direct stimulation may include providing plants with fixed nitrogen, iron that has been sequestered by bacterial siderophores, soluble phosphate and other nutrients, and the ability to produce right amounts of the plant hormones such as IAA, gibberellic acid and cytokinins (Bloemberg and Lugtenberg, 2001) and to lower the levels of the plant ethylene hormone mediating 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase activity (Glick, 2005).

This review surveys the potential of *B. thuringiensis* as a polyvalent biocontrol agent, a biostimulator and biofertiliser bacterium that could promote the plant growth. Also, discussed is the safety of *B. thuringiensis* as a bacterium which could be considered a *B. cereus* (opportunistic human pathogen) that produces insecticidal crystal proteins, on the light of the genomic data.

Bacillus thuringiensis A POLYVALENT BIOCONTROL AGENT

Entomopathogenic activity

The δ-endotoxins

Bacillus thuringiensis has been used commercially in the biological control of insect pests for the last four decades due

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to its insecticidal properties. The insecticidal activity of *B. thuringiensis* is due mainly to its ability to synthesize, during the sporulation phase, large amounts of proteins (about 130-140 kDa) that form a parasporal crystal. When a susceptible insect ingests these crystalline (Cry) protoxins, known as δ-endotoxins, they are solubilized and proteolytically digested to yield the active toxic form of about 60 kDa. The activated toxins bind to specific receptors in the epithelial insect midgut (Luthy and Wolfersberger, 2000). Previously, two types of receptors for the Lepidoptera-specific Cry1A toxins have been characterised, the aminopeptidases N (APN) and the cadherin-like proteins, which are all glycoproteins (Knight *et al*., 1994; Vadlamudi *et al*., 1995). In a recent study, it has been demonstrated that also glycolipids serve as general host cell receptors for Cry1A toxins and for the nematode-specific Cry5B toxins (Griffitts *et al*., 2005). Toxin binding produces pores which leads to the loss of normal membrane function (Schwart and Laprade, 2000). As a result of membrane permeability, epithelial cells lyse and feeding activity is paralyzed. Finally, insects die of starvation, septicemia or a combination of both (Porcar and Juarez-Perez, 2003). Recently it has been reported that the presence of indigenous midgut bacteria is necessary for the *B. thuringiensis* insect killing (Broderick *et al.,* 2006). So far, more than 350 *cry* genes have been described and classified into more than 46 families according to the degree of amino acid sequence homology shared by their corresponding proteins (Crickmore *et al*., 2007). Cry proteins are active against lepidopteran, dipteran and coleopteran insect larvae and have now been shown to target nematodes as well, including the intestinal parasite *Nippostrongylus brasiliensis* (Schnepf *et al*., 1998; Wei *et al*., 2003; Kotze *et al*., 2005). In addition to the crystal toxins, some *B. thuringiensis* strains produce Cry1I (also referred as to CryV in the literature), another insecticidal toxin secreted during early stationary phase. It is active against certain lepidopteran and coleopteran insect larvae (Kostichka *et al*., 1996).

The cytolytic toxins

The second group of *B. thuringiensis* insecticidal crystal proteins is represented by the Cyt (cytolytic) toxins produced by *B. thuringiensis* ssp. *israelensis* and a few other subspecies (Wirth *et al*., 2001 and references therein). Cyt proteins are toxic in vivo to the larvae of members of the order Diptera, such as mosquitoes and black flies. These proteins, characterised by molecular weights ranging between 25 and 28 kDa (Glare and O'Callaghan, 2000) are produced during the sporulation phase and are deposited together with the Cry (δ-endotoxins) in the crystalline inclusion bodies where they can constitute about 40% of the crystal (Wirth *et al*, 2001). Five Cyt families are currently known (Wirth *et al*., 2001 and references therin; Crickmore *et al*., 2007). In contrast to the Cry toxins which are highly specific and which act via specific receptors, the Cyt toxins do not bind to protein receptors and directly interact with membrane lipids, inserting into the membrane and forming pores (Porcar and Juarez-Perez, 2003) or destroying the membrane via a detergent-like interaction (Manceva *et al*., 2005).

The vegetative insecticidal proteins (VIPs)

In addition to the crystal-associated toxic polypeptides, many *B. thuringiensis* strains secrete vegetative insecticidal proteins during vegetative growth (Warren, 1997). Two classes of VIP toxins have been described. The first consists of a binary system composed of two proteins, Vip1 and Vip2, which are 100 kDa and 52 kDa in size, respectively and are highly toxic to certain coleopteran species (Warren, 1997; Shi *et al*., 2004). The second class consists of an 82.5-kDa protein, Vip3, which is active against a wide spectrum of lepidopteran insects (Estruch *et al*., 1996, Chen *et al*., 2003). With regard to their mode of action, it has been shown that Vip1-Vip2 are both necessary for toxicity against susceptible insects with the membrane-binding Vip1 multimer providing a pathway for Vip2 ADP-ribosylase to enter the cytoplasm of target cells (Shi *et al*., 2004). Vip3A was shown to form stable ion channels in the absence of any receptors, supporting pore formation as an inherent property of this protein. Vip3A channels were voltage independent and highly cation selective as for Cry1Ab channels; however, they differed considerably in their principal conductance state and cation specificity (Lee *et al*., 2003). Thus, the VIPs represent a structurally different group of insecticidal toxins produced by the strains of *B. thuringiensis*. With several laboratories reporting development of resistance in insects against insecticidal crystal proteins of *B. thuringiensis*, these toxins offer a promise of extending the usefulness of *B. thuringiensis* toxins to delay the onset of resistance in insects owing to a different mode of action (Fang *et al.,* 2007; Wu *et al.,* 2007).

Chitinases

Chitin, is an insoluble linear homopolymer of N-acetylglucosamine (GlcNAc) connected by β–1,4-linkages which is utilised as a structural polysaccharide in nature (Gooday, 1994). Chitin occurs in insects as a major component of the cuticle and is also present (between 3% and 13%) in the peritrophic membrane (PM), a protective sleeve lining the gut of many insects (Binnington *et al*., 1998; Tellam *et al*., 1999; Terra, 2001). Hence, it is reasonable to speculate that chitinase activities may play key roles in the virulence of some pathogens that infect insects via the peritrophic membrane since pathogens that infect through the gut must penetrate this chitin-containing barrier. In this view, chitinase has been used together with *B. thuringiensis* to enhance larvicidal activity since the early 1970s. Initial experiments were conducted by mixing exogenous chitinase produced by *Bacillus circulans* or *Serratia marcescens* with *B. thuringiensis* (Regev *et al*., 1996; Sampson and Gooday, 1998 and references therein). *Bacillus thuringiensis* itself produces chitinases and the role of these endogenous chitinases has recently come under investigation. Wiwat *et al.* (2000) reported that the toxicity of *B. thuringiensis* ssp. *kurstaki* HD-1(G) for *Plutella xylostella* (diamondback moth) larvae is increased when in combination with its supernatant containing chitinase. Arora *et al.* (2003) reported a synergistic action of chitinase Chi36 from Bt HD-1 along with the vegetative insecticidal protein (Vip) against *Spodoptera litura* larvae. The presence of endochitinase and exochitinase genes was detected via PCR screening of 16 *B. thuringiensis* isolates which showed also an important chtinolytic activity on plates containing colloidal chitin as a major or unique carbon source (Raddadi *et al*., unpublished data). The observed potentiation of insecticidal activity of Cry and Vip in the presence of chitinase offers another tool to enhance the application of *B. thuringiensis* proteins and highlights the importance of these synergistic proteins as a tool to delay development of insect resistance to *B. thuringiensis*.

Proteases, phospholipases

Bacillus thuringiensis is highly resistant to the humoral defence system of the host, especially to cecropins and attacins, which are the main classes of inducible antibacterial peptides in various lepidopterans and dipterans (Hultmark *et al*., 1982; Inagaki *et al*., 1992). An extracellular zinc metalloprotease, termed InhA or InA (immune inhibitor A) which specifically hydrolyzes antibacterial proteins produced by the insect host, in vitro, was suggested to partly explain the success of the bacterium in invading hemocoel (Dalhammar and Steiner, 1984). Recently a new *B. thuringiensis* virulence factor, InhA2 that is highly homologous to InhA, has been characterised (Fedhila *et al*., 2002) and shown to play a major role in potentiating the toxicity of Cry proteins in orally infected insects. *inhA2* is a PlcR regulated gene essential for *B. thuringiensis* virulence (Fedhila *et al*., 2003). Also, the insect peritrophic membrane is formed by four classes of proteins (Tellam *et al*., 1999), in addition to chitin, glycoproteins and proteoglycans, which confers strength and elasticity to the PM and influences its permeability properties (Terra, 2001). Hence production of proteases among other secreted proteins could have a synergistic effect on the entomopathogenic effect of *B. thuringiensis*. The expression of several virulence genes, at the end of the exponential growth phase, that encode secreted proteins, including phospholipases C, haemolysins, enterotoxins, and proteases is regulated by PlcR (Gominet *et al*., 2001). PlcR-regulated toxins and degradative enzymes may facilitate the spread of the bacterium through host tissues, thus allowing bacterial cells to gain access to alternative sources of nutrients and to cause septicaemia (Fedhila *et al*., 2003). In addition, previous work suggested that phopholipases C are involved in the entomopathogenic properties of the bacteria (Zhang *et al*., 1993).

Other entomopathogenic factors: zwittermicin A, urease and HCN

Zwittermicin A (ZwA) is a linear aminopolyol new antibiotic that was first identified for its role in suppression of fungal plant disease by *B. cereus* UW85 (Silo-Suh *et al*., 1994). ZwA was also shown to be produced by Bt (see paragraph *Antifungal activity*). However, studies on the synergy between this antibiotic and the Bt insecticidal proteins have been carried out using purified *B. cereus* ZwA. They showed that it potentiates the insecticidal activity of the protein toxin produced by *B. thuringiensis*, increasing mortality of insects that are typically resistant to this toxin (Broderick *et al*., 2000; 2003). Hence, production of ZwA could constitute a potential additional factor for enhancing efficacy of *B. thuringiensis* and delaying development of insect resistance.

With regard to the urease and HCN production as factors that could enhance the insect biocontrol activity, there are no reports in the literature dealing with this. However, it has been reported that canatoxin, a variant form of urease isolated from jackbean seeds was shown to be proteolytically activated by insect cathepsin-like enzymes (mainly cathepsins B and D) to produce entomotoxic peptide(s). Canatoxin-derived peptide (MW 10 kDa) displays insecticidal activity against insects of Coleoptera (beetles) and Hemiptera (bugs) orders, such as the cowpea weevil, *Callosobruchus maculatus*, the kissing bug , *Rhodnius prolixus*, the cotton stainer bug, *Dysdercus peruvianus* and the green soybean stink bug, *Nezara viridula* (Carlini and Grossi-de-Sa, 2002; Staniscuaski *et al*., 2005). Also, ureases from soybean and jackbean plants exhibited an important insecticidal activity on the cotton stainer bug *Dysdercus peruvianus* independently of their ureolytic activity (Follmer *et al*., 2004). On the contrary, urease from *Bacillus pasteurii* did not show an insecticidal activity, and the authors hypothesised that the lack of such activity is due to its three-chain structure.

With regard to hydrogen cyanide production, it has been reported that cyanide is a potent poison expected to be active against most eukaryotic species (Blumer and Haas, 2000), and experiments on the investigation of the mechanism by which *Pseudomonas aeruginosa* PAO1 rapidly paralyzes and kills *Caenorhabditis elegans*, showed that the poison hydrogen cyanide is the sole or primary bacterial factor responsible for killing of the nematode (Gallagher and Manuel, 2001). *Bacillus thuringiensis* was recently shown to target this model invertebrate organism mediating its Cry5 toxins (Griffitts *et al*., 2005). Hence, it can be hypothesised that hydrogen cyanide could act as a synergistic factor of the insecticidal proteins, but more studies are needed to verify this hypothesis.

Antibacterial activity

Although the main biocontrol activity of *B. thuringiensis* is due to its entomopathogenic potential, different strains in this species have been shown to produce many potential factors that could be of great interest in the biocontrol of phytopathogenic bacteria. This makes from *B. thuringiensis* a polyvalent biocontrol agent that allows a better protection of the plants and could lead to decrease the use of chemical pesticides which have usually harmful impact on the environment.

Autolysins

Autolysins are endogenous peptidoglycan hydrolases that digest cell wall peptidoglycans of the producer bacterium and of other bacteria. According to the chemical bond cleaved in the peptidoglycan molecule, four different specificities have been defined: N-acetylmuramidase, N-acetylglucosaminidase, N-acetylmuramyl-L-alanine amidase and endopeptidase (Cibik and Chapot-Chartier, 2000). Such peptidoglycan hydrolases are synthesized during cellular growth and are involved in various fundamental steps of the bacterial life cycle: cell separation, cell wall turnover, peptidoglycan maturation and cell differentiation (mother cell lysis and spore outgrowth) in spore-forming bacteria (Smith *et al*., 2000).

The characterisation of the autolytic phenotype of 112 *B. thuringiensis* strains showed seven major proteins of molecular weights ranging between 25 and 90 kDa which exhibited peptidoglycan hydrolase activity, particularly at alkaline pH. Several of these proteins retained lytic activity against other bacterial species such as *Micrococcus lysodeikticus*, *Listeria monocytogenes* and *Staphylococcus aureus* (Raddadi *et al*., 2004, 2005). These proteins could be of great interest in field application of *B. thuringiensis* e.g. for improving bacterial or insect biocontrol by coupling with other antagonistic factors such as bacteriocins (Mora *et al*., 2003) or chitinases since the products of chitinase action are degraded to N-acetylglucosamine by N-acetylglucosaminidases (Sampson and Gooday, 1998).

Bacteriocins

Bacteriocins are ribosomally synthesized antimicrobial compounds that have a relatively narrow killing spectrum and are usually toxic to bacteria closely related to the producing strain or within the same ecological niches. Bacteriocins have been found in all major lineages of Bacteria and, more recently, have been described as universally produced by some members of the Archaea (Torreblanca *et al*., 1994; Riley and Wertz, 2002). The classification of bacteriocins put forward by Klaenhammer (1993) takes into account the chemical structure, heat stability, molecular mass, enzymatic sensitivity, presence of modified amino acids and mode of action of these chemicals. Four classes of bacteriocins can be distinguished. (i) Lanthibiotics containing the modified amino acid lanthionine. Bacteriocins such as nisin, epidermin, subtilin and mersacidin, belong to this group. (ii) Low-molecular weight bacteriocins (smaller than 10 kDa) formed exclusively by unmodified amino acids. Within this group specific antilisterial compounds (cystibiotics), bacteriocins formed by two peptides acting synergistically and thiol-activated peptides (thiolbiotics) can be found. (iii) High-molecular weight bacteriocins: heat-labile proteins larger than 30 kDa belong to this group. (iv) Bacteriocins carrying lipid or carbohydrate moieties. Little is known about the structure and function of this fourth proposed class. The antibiotic activity of bacteriocins from Gram-positive bacteria, is based on interaction with the bacterial membrane and its disruption in a specific and/or non-specific way (Héchard and Sahl, 2002 and references therein).

Several bacteriocins associated with the *B. cereus* group have been described and partially characterised. These include five bacteriocins produced by the *B. cereus* species such as cerein (9 kDa) from strains GN105 (Naclerio *et al*., 1993), cerein 7 (3.9 kDa) produced by strain BC7 (Oscáriz *et al*., 1999), cerein 8A from strain 8A (Bizani *et al*., 2005), cerein BS229 produced by *B. cereus* 229 (8.2 kDa) (Paik *et al*., 2000) and the recently described bacteriocin-like inhibitory substance (BLIS) (ca 3,4 kDa) from the *B. cereus* type strain ATCC 14579T (Risøen *et al*., 2004). Also six bacteriocins have been partially characterised from *B. thuringiensis*: thuricin (950 kDa) from strain HD2 (Favret and Yousten, 1989), tochicin (10.5 kDa) from strain HD868 (Paik *et al*., 1997), thuricin 7 (11.6 kDa) from strain BMG1.7 (Cherif *et al*., 2001), thuricin 439 (two active compounds thuricin 439A and thuricin 439B of 2.9 and 2.8 kDa, respectively) produced by *B. thuringiensis* B493 (Ahern *et al*., 2003:), entomocin 9 from *B. thuringiensis* strain *entomocidus* HD9 (Cherif *et al*., 2003b) and bacthuricin F4 (ca 3.16 kDa) from strain *B. thuringiensis* ssp*. kurstaki* BUPM4 (Kmoun *et al*., 2005). Also 13 *B. thuringiensis* isolates (wild isolates and reference strains) were found to produce bacteriocins and among them entomocin HD110 produced by *B. thuringiensis* strain *entomocidus* HD110 was characterised and partially purified (Cherif *et al*., 2006). Among all these bacteriocins, N-terminal amino acid sequence is available only for cerein 7 which was classified as class II bacteriocin (Oscáriz and Pisabarro, 2000), thuricin 439 and bacthuricin F4 that could not be classified in any of the groups described for bacteriocins produced by lactic acid bacteria. However, no data on bacteriocin structural genes and their regulatory elements are available until now.

AHL-Lactonases

Many bacterial species use complex communication systems that link cell density and gene expression to regulate a broad range of biological functions. Such cell-to-cell communication, termed quorum sensing (QS), depends on the production, diffusion, and recognition of small signal molecules or autoinducers (Miller and Bassler, 2001; Fuqua *et al*., 2001). In Gram-negative bacteria, the most intensively studied QS systems rely on the interaction of N-acylhomoserine lactones (AHLs), molecules that share identical homoserine lactone rings but vary in length and the substitution of the acyl side chain. AHL signals are involved in the regulation of a range of important biological functions, including luminescence, antibiotic production, plasmid transfer, motility, virulence, biofilm formation and functional coordination among microbial communities (Whitehead *et al*., 2001; Zhang, 2003; Federle and Bassler, 2003).

The quorum-sensing pathways could be subverted by production of natural products that act as AHL antagonists (Ren *et al*., 2005) and by expressing ''quorum-quenching'' enzymes that can hydrolyze AHL-signaling molecules. Two groups of AHL-degrading enzymes, classified according to the AHL cleavage site, are produced by soil bacteria. (i) AHL-acylases hydrolyse the amide bond of AHLs releasing the acyl chain and homoserine lactone (HSL) which are further metabolised and used as growth nutrients by *Variovorax paradoxus* and *Arthrobacter* respectively (Leadbetter and Greenberg, 2000; Flagan *et al*., 2003). To date, six AHL-acylase genes have been identified, four from the Gram-negative bacteria *Ralstonia* isolate (Lin *et al*., 2003), *Pseudomonas aeruginosa* PAO1 (Huang *et al*., 2003, 2006) and *Comamonas* sp. strain D1 (Uroz *et al.*, 2007), and two from the Gram-positive *Streptomyces* sp. (Park *et al*., 2005a) and *Rhodococcus erythropolis* (Uroz *et al.*, 2005). (ii) In an other enzymatic mechanism for AHLs inactivation, AHL-lactonases, hydrolyse the lactone rings and produce the corresponding acylhomoserine molecules that can no longer be used for signalling (Dong *et al*., 2000) but is used by *Arthrobacter* as nutrient for growth (Flagan *et al*., 2003). Two AHL-lactonases AiiA and AiiB produced by many *Bacillus thuringiensis* and *Agrobacterium tumifaciens* strains have been identified respectively (Dong *et al*., 2002; Lee *et al*., 2002; Liu *et al*., 2007; Raddadi *et al.*, unpublished). Biochemical characterisation of AiiA and AiiB AHL-lactonase showed that they are metallo-β–lactamase enzymes (Thomas *et al*., 2005; Liu *et al*., 2007). The *aiiA* gene was first identified from the soil bacterial isolate *Bacillus* sp. 240B1. Expression of the *aiiA* gene in *Erwinia carotovora* significantly reduced its virulence on five plants tested. Transgenic plants expressing AHL-lactonase can effectively quench bacterial QS signalling and disintegrate bacterial population density-dependent infections, whereas untransformed control plants develop severe disease symptoms (Dong *et al*., 2000, 2001). Further studies by Dong *et al*. (2004) have shown that *B. thuringiensis* strains, which produce AHL-lactonase suppress the QS-dependent virulence of the plant bacterial pathogen *Erwinia carotovora* through signal interference. These findings, illustrate the promising potential to explore the microbial antagonistic mechanisms such as signal interference, for the control and prevention of infectious diseases.

Antifungal activity

Chitinases and β-1,3-glucanases

The fungal cell wall accounts for ~20-30% of the dry weight of fungal cells. It protects the cell from physical damage and is responsible for its shape. The fungal cell wall with its skeletal layer composed of chitin and β-1,3-glucan is a target for a wide range of antifungal proteins. These include essentially chitinases and glucanases which degrade chitin and glucans respectively leading to fungal cell lysis (Theis and Stahl, 2004). Chitinases (EC 3.2.1.14) are found in a broad range of organisms, including bacteria, fungi, and higher plants, and play different roles in their origin (Felse and Panda, 1999). Chitinase-producing microorganisms have been reported as biocontrol agents for different kinds of fungal diseases of plants (Chernin *et al*., 1995; Kobayashi *et al*., 2002; Freeman *et al*., 2004). In the *B. cereus* group, chitinase-producing *B. cereus* strains were found to be effective for the biocontrol of phytopathogenic fungi. Indeed, an endophytic *B. cereus* strain 65 producing a chitobiosidase was found effective against *Ralstonia solani* in cotton (Pleban *et al*., 1997). Recently, it has been reported (Huang and Chen*,* 2004; Huang *et al.,* 2005) that *B. cereus* 28-9 strain exhibited biocontrol potential on the fungal pathogen *Botrytis elliptica* the causative agent of lily leaf blight, the most severe and destructive disease of the field-grown lilies. Although chitinases are widely produced by the different *B. thuringiensis* serovars (Liu *et al*., 2002), there are a few reports on the fungal biocontrol potential by these enzymes. Reyes-Ramirez *et al.* (2004) reported that a chitinase produced by a *B. thuringiensis* ssp. *israelensis* strain showed fungal inhibition between 45 and 100% when tested in growing cultures. The addition of this chitinase to soybean seeds infected with *Sclerotium rolfsii* increased the germination from 25 to 90%. Thus, in addition to their important role as synergistic factors for the enhancement of the *B. thuringiensis* insecticidal potential (see paragraph *Chitinases* in Entomopathogenic activity), chitinases from *B. thuringiensis* are promising in the biocontrol of phytopathogenic fungi and for preservation of stored seeds.

With regard to glucanases, several studies reported the production of these enzymes by different species in the genus *Bacillus* such as *B. subtilis* (Tang *et al*., 2004; Liu *et al*., 2006), *B. circulans* (Kim, 2003), *B. clausii* (Miyanishi *et al*., 2003) and *B. amyloliquefaciens* (Il Kim and Chang, 2004). Until now, no investigation of this activity in the *B. cereus* group and especially in *B. thuringiensis*, is reported in the literature. In a study aiming to screen the antifungal potential of 16 *B. thuringiensis* isolates, mediating PCR amplification of β-1,3-glucanase using degenerate primers, three strains gave an amplicon of the expected molecular weight and are probably glucanase producers. Also all the strains were chitinase producers and showed antagonistic activity against different fungal species in vitro (Raddadi *et al*., unpublished data).

Zwittermicin A

The linear aminopolyol antibiotic zwittermicin A (ZwA) was first identified for its contribution to the ability of *B. cereus* UW85 to suppress alfalfa damping-off (Silo-Suh *et al*., 1994) and may be important for other biological activities of UW85, such as the control of fruit rot of cucumber (Smith *et al*., 1993) or the suppression of other plant diseases in the lab and in the field (Handelsman *et al*., 1991; Osburn *et al*., 1995). In a further study, ZwA was shown to have a broad target range inhibiting diverse protists, Oomycetes, fungi, and bacteria (Silo-Sah *et al*., 1998). The inhibitory activity of ZwA against Oomycetes could be of great interest for the control of these filamentous phytopathogenic fungi (Shang *et al*., 1999), on which chitinases would have no activity since they lack chitin in their cell walls (Theis and Stahl., 2004). The mode of action of ZwA is not yet fully understood, however an association between effects on membrane potential (DY) and RNA polymerase activity, and ZwA sensitivity have been suggested (Stabb and Handelsman, 1999). The ZwA antibiotic was also shown to be produced by Bt (Raffel *et al*., 1996; Nair *et al*., 2004, Raddadi *et al*., unpublished data). Recent studies showed that the 38.6 kb ZwA biosynthesis cluster of *B. thuringiensis* subsp. *kurstaki* strain YBT-1520 has similar organization to that of *B. cereus* UW85 and is located on the chromosome (Zhao *et al.,* 2007). Based on the structural and genetic information, it is hypothesized that the premature ZwA is synthesized by a nonribosomal peptide synthetase and polyketide synthetase (PKS) hybrid pathway, then a carbamoyltransferase catalyzes the premature ZwA into ZwA (Ansari et al., 2004; Emmert et al., 2004; Zhao *et al.,* 2007).

Hydrogen cyanide (HCN)

It is a secondary metabolite typically produced from glycine by fungi, and bacteria during early stationary growth phase (Faramarzi *et al*., 2004). This metabolite has been long recognized to contribute to bacterial pathogenicity (Gallagher and Manoil, 2001; Firoved and Diretic, 2003), and is considered as a broad-spectrum antimicrobial compound involved in biological control of root diseases by many plant-associated fluorescent pseudomonads (Sharifi-Tehrani *et al*., 1998; Blumer and Haas, 2000; Ramette *et al*., 2003).

Recently, bacteria from the genus *Bacillus* were shown to produce a relevant quantity of HCN *in vitro*, and to represent a large part (up to 50%) of the soil microbial community. However, in this case, HCN^+ *Bacillus* were supposed to be implicated in the plant pathogenicity (Benizri *et al*., 2005). Until today, no reports on the relationship between *Bacillus* HCN production and biocontrol activity is found in literature. However, our preliminary screening for HCN production *in vitro*, of 16 *B. thuringiensis* isolates showed the development of the characteristic brown colour using HCN-indicator paper of Lorck (1948) in seven strains. Most of the HCN producer strains were zwittermicin A-positive and have fungal antagonistic activities in vitro that could be explained by the synergy between HCN and antibiotic (Raddadi *et al*., unpublished data). Also, in a study of the antagonistic effects on *Verticillium dahliae Klebahn* of 89 bacterial isolates collected from cotton rhizosphere, three *Bacillus sp*. isolates inhibited the mycelial growth of the fungus through production of volatile metabolites and produced hydrogen cyanide in vitro. In green house assay, one of three *Bacillus sp.* isolates increased cotton root length in soil infested with the fungus (Tehrani *et al*., 2001).

Bacillus thuringiensis, A BIOSTIMULATOR PLANT GROWTH PROMOTING BACTERIUM (PGPB)

Indole-3-acetic acid (IAA) or auxins

Phytohormones play an important role as signals and regulators of growth and development in plants. Auxins, among them in particular indole-3-acetic acid (IAA), are the most studied plant growth regulators, and this includes physiological, biochemical and genetic aspects (del Pozo *et al*., 2005). The ability to produce the phytohormones is often considered as a trait of the plant kingdom. However, production of phytohormones is also widespread among soil and plant-associated prokaryotes (Costacurta and Vanderleyden, 1995). Phytohormones produced by plant-associated bacteria are implicated as key determinants in stimulation of plant growth (Patten and Glick, 2002), in plant pathogenesis (Glickmann *et al*., 1998) and in plant-microbe symbiotic interactions (Sergeeva *et al*., 2002). Known plant growth-promoting bacteria include species within genera such as *Herbaspirillum, Rhizobium* and *Azospirillum*, interacting with plant roots. On the other hand, pathovars of *Pseudomonas savastanoi*, *Pseudomonas syringae*, *Erwinia* and *Agrobacterium* elicit galls or tumours on plants. Genetic mechanisms underlying IAA biosynthesis and its regulation have been studied in these genera and multiple pathways for IAA synthesis have been identified, including both tryptophan-dependent and independent pathways (Glick *et al*., 1999). The synthesis of IAA from Tryptophan (Trp) could occur via the indole-3-acetamide and the indole-3-pyruvic acid (IPyA) pathways. In phytopathogenic bacteria, IAA is produced from Trp, preferentially via the intermediate indoleacetamide and has been implicated in the induction of plant tumors (Liu *et al*., 1982; White *et al*., 1991). Beneficial bacteria synthesize IAA predominantly by an alternate Trp-dependant pathway, through indole pyruvic acid (Costacurta *et al*., 1994; Patten and Glick, 2002; Schutz *et al*., 2003). However, the presence of more than one pathway for IAA biosynthesis has been reported for *Azospirillum spp.* (Prinsen *et al*., 1993, Broek *et al*., 1999; Yagi *et al*., 2001 and references therein).

Up to now, there has been no identification of phytohormone production in *B. thuringiensis*. Thus, in a study which aims to examine the potential in *B. thuringiensis* to produce the phytohormone IAA, we demonstrate that 16 *B. thuringiensis* isolates were capable of releasing IAA in the range of beneficial concentrations for the plant. This was done by screening of IAA release and PCR amplification of *ipdC* gene encoding an indolepyruvate decarboxylase, a key enzyme implicated in the biosynthesis of IAA from Trp via the indole-3-pyruvic acid pathway. We suggest that IAA accumulation is stimulated by exogenous tryptophan and may proceed via the indole-3-pyruvic acid and the indole-3-acetamide pathways since some strains produced IAA although they did not give an amplicon for the *ipdC* gene (Raddadi *et al*., unpublished data).

ACC deaminase

1-Aminocyclopropane-1-carboxylic acid (ACC) is a naturally occurring amino acid that has been shown to be the precursor of ethylene, an essential phytohormone important for normal development in plants as well as for their response to stress. It regulates seed germination, senescence, fruit ripening, wound healing, and many additional plant growth processes (Abeles *et al*., 1992; Deikman, 1997). Several microorganisms have been found to contain ACC deaminase (ACCD), an enzyme that converts ACC to α-ketobutyrate and ammonium (Hontzeas *et al*., 2004). ACCD has been found in various plant growth-promoting bacteria (Wenbo *et al*., 2003; Ghosh *et al*., 2003, Glick, 2005 and references therein) as well as some yeasts (Minami *et al*., 1998) and fungi (Jia *et al*., 2000). This enzyme enables these microorganisms to utilise ACC as a sole N source or both N and C sources (Belimov *et al*. 2005). In addition to facilitating the growth of plant roots by lowering the level of ethylene (Glick, 1995; Glick *et al*., 1998), plant growth-promoting bacteria expressing ACCD were shown to protect plants from the deleterious effects of some environmental stresses including heavy metals (Burd *et al*., 2000; Belimov *et al*., 2005), flooding (Grichko and Glick, 2001), salt (Mayak *et al*., 2004a), drought (Mayak *et al*., 2004b) and phytopathogens (Wang *et al*., 2000).

With regard to the investigation of ACCD activity in the genus *Bacillus*, few data are available. Recently, different *Bacillus* species were shown to have ACCD activity and to stimulate root elongation in canola seedlings under gnotobiotic conditions. Soil inoculations with these bacterial strains increased the root and shoot lengths and fresh and dry weights of potted canola plants (Ghosh *et al*., 2003). Many strains in the *B. cereus* group were shown to have putative *accd* genes based on sequence similarity. These include *B. cereus* E33L (Brettin *et al*., unpublished), *B. cereus* ATCC 10987 (Rasko *et al*., 2004), *B. cereus* ATCC 14579T (Ivanova *et al*., 2003), *B. cereus* G9241 (Hoffmaster *et al*., 2004), *B. anthracis* strain A2012 (Read *et al*., 2002), *B. anthracis* strain Ames (Read *et al*., 2003), *B. anthracis* strain 'Ames Ancestor' (Ravel *et al*., unpublished), *B. anthracis* strain Sterne (Brettin *et al*., unpublished) and *B. thuringiensis* serovar *konkukian* strain 97-27 (Brettin *et al*., unpublished). Also, 16 *B. thuringiensis* isolates were PCR positive for the presence of *accd* gene. Partial sequencing of the corresponding amplificates showed 97-99% homology to *B. cereus* ATCC 14579^T *accd* gene, and seven out of the 16 *B. thuringiensis* isolates tested were able to grow on mineral medium containing ACC as the unique nitrogen source (Raddadi *et al*., unpublished data).

Bacillus thuringiensis, A BIOFERTILISER PGPB

A biofertiliser could be defined as a substance which contains living microorganisms which, when applied to seed, plant surfaces, or soil, colonizes the rhizosphere or the interior of the plant and promotes growth by increasing the availability and uptake of mineral nutrients for plants (Vessey, 2003). Biofertilisers can contain rhizospheric fungi such as arbuscular mycorrhizae (Douds *et al*., 2005) and *Penicillium bilaii*, *Penicillium radicum* (Grant *et al*., 2002; Wakelin *et al*., 2004), and/or plant growth promoting rhizobacteria (PGPR) (Mukherjee and Rai, 2000; Wu *et al*., 2005). Among the means by which PGPR enhance the nutrient status of host plants, will be discussed the increasing of the availability of nutrients in the rhizosphere mediating soil P solubilization and siderophore production.

Phosphate solubilization

Although phosphorus (P) is quite abundant in many soils, it is one of the major nutrients limiting plant growth. The low availability of P to plants is because the vast majority of soil P is found in insoluble forms, and plants can only absorb P

in two soluble forms, the monobasic ($H_2PO4^?$) and the dibasic ($HPO_4^{2?}$) ions (Glass, 1989). Soil P is generally found in two forms: Mineral phosphates represented by calcium phosphates, hydroxyapatite (HAP) and rock phosphate; and organic P represented essentially by phytates or inositol phosphates, in addition to phosphoesters. To become available for plants, both mineral and organic phosphates should be solubilized. Phosphate solubilizing bacteria (PSB) are commonly found in most soils and are known to mobilize insoluble phosphate to soluble forms through enzymatic actions (Goldstein, 1986; Pal, 1998; Rodriguez and Fraga, 1999; Nautiyal *et al*., 2000). The main mechanism for mineral phosphate solubilization is the production of organic acids which results in acidification of the microbial cell and its surroundings leading to the release of ionic phosphate by proton substitution for Ca^{2+}. The mineralization of organic phosphorous in soil is carried out by acid phosphatases and phytases play a major role in these dephosphorylating reactions (Rodriguez and Fraga, 1999 and references there in).

The solubilization of P in the rhizosphere is the most common mode of action implicated in PGPR that increase nutrient availability to host plants (Richardson, 2001). Among recently studied associations can be sited *Azotobacter chroococcum* and wheat, *Enterobacter agglomerans* and tomato, *Pseudomonas chlororaphis* and *Pseudomonas putida* and soybean, *Rhizobium* sp. and *Bradyrhizobium japonicum* and radish, and *Rhizobium leguminosarum* bv. *phaseoli* and maize (Vessey, 2003 and references therein). In the genus *Bacillus*, studies include *Bacillus* sp. and five crop species (Pal, 1998), *Bacillus circulans* and *Cladosporium herbarum* and wheat (Singh and Kapoor, 1999), *Bacillus megaterium* and sugar beet and barley (Çakmakçi *et al*., 1999). However, there are no reports on a possible phosphate solubilization activity of strains in the *Bacillus cereus* group and especially on *B. thuringiensis*. Based on sequence similarity, different acid phosphatase genes were described in the sequenced genomes of *B. cereus* group species, and our screening on 16 *B. thuringiensis* strains showed that they were PCR-positive for this gene which partial sequencing showed a homology of 99% to *B. cereus* ATCC 14579^T acid phosphatase gene. Also some of the strains gave a positive amplification using degenerate primers for the phytase gene amplification and showed a high phosphate solubilizing capacity in vitro (Raddadi *et al*., unpublished data).

Siderophore production

Plant growth and reproduction can be severely affected by various biotic and abiotic stresses. Among the abiotic stresses, iron (Fe) deficiency constitutes a major factor leading to a reduction in crop yield, especially in calcareous soils in which the solubility of Fe is extremely low (Kobayashi *et al*., 2005). Plants commonly excrete soluble organic compounds (chelators and phytosiderophores) which bind Fe^{3+} and help to maintain it in solution. Chelators 'deliver' the Fe^{3+} to the root surface where it is reduced to Fe^{2+} and immediately absorbed (i.e., 'Strategy I' plants). Phytosiderophores, excreted by grasses (i.e., 'Strategy II' plants), are absorbed with the Fe^{3+} across the plasmalemma (von Wiren *et al*., 2000). Some rhizospheric bacteria also produce siderophores via non ribosomal peptide synthetic pathways (Crosa and Walsh, 2002). A number of plants possess heterologous iron uptake mechanism for acquisition of iron through iron-bacterial siderophore complex (Yehuda *et al*., 1996; Sharma *et al*., 2003). It has been reported that under non-sterile soil system, plants show no iron-deficiency symptoms and have fairly high iron level in roots in contrast to plants grown in sterile system (Masalha *et al*., 2000), which suggests the role of soil microbial activity in iron acquisition and plant growth. Siderophore production is a common character of the *B. cereus* group as was shown for *B. cereus* (Park *et al*., 2005b) and *B. anthracis* (Cendrowski *et al*., 2004) and recently for *B. thuringiensis* (Wilson *et al*., 2006; Raddadi *et al*., unpublished). In the case of *B. thuringiensis* this character could be relevant for biocontrol of phytopathogenic fungi due to competition effects for iron, but also for providing the plant with iron.

SAFETY CONSIDERATIONS

Bacillus thuringiensis, B. cereus and *B. anthracis* are often considered to be members of the same species on the light of the genomic data (Carlson *et al*., 1994; Helgason *et al*., 2000), and distinguishing these species is rather difficult even with modern molecular tools (Daffonchio *et al*., 2000, Cherif *et al*., 2003a; Rasko *et al*., 2005 and references therein). *Bacillus thuringiensis* could be distinguished from *B. cereus* by the production of insecticidal crystal proteins (ICPs). *Bacillus cereus* is an opportunistic human pathogen that causes food poisoning and other infections (Beecher *et al*., 2004; Fricker *et al.*, 2007). Two principal types of food poisoning caused by *B. cereus*, emetic and diarrhoeal, have been described. The emetic type is effected by cereulide while diarrhoeal types are attributed to enterotoxins (Hansen and Hendriksen, 2001 and references therein). The three most well characterised enterotoxins are haemolysin BL (HBL), the non-haemolytic enterotoxin (NHE) and the single-component cytotoxin K (CytK) (Lund and Granum, 1997; Lund *et al*., 2000; Lindback *et al*., 2004). Recent research has identified a new variant of *cytK*, designated as *cytK-2*, with the original *cytK* being *cytK-1*. CytK2 has only 89% identity at amino acid sequence level to the original CytK, and was shown to have a lower toxicity than CytK-1 against mammalian cell lines (Fagerlund *et al*., 2004). In addition to these main toxins, *B. cereus* was shown to produce several other virulence factors. These include bc-D-ENT or enterotoxin T which have cytolytic activity (Agata *et al*., 1995), haemolysin II (Budarina *et al*., 2004), haemolysin III (Baida and Kuzmin, 1995), enteroxin FM (Ghelardi *et al*., 2002) and cereolysins (Gilmore *et al*., 1989). However, to date their roles in specific infections have not been established (Schoeni and Wong, 2005).

After the commercialisation of *B. thuringiensis*-based insecticides, studies have shown that *B. thuringiensis* (including commercial strains used for insect control) possesses genes known to be involved in *B. cereus* pathogenesis and shows enterotoxin profiles and toxin levels similar to those of the *B. cereus* diarrhoeal-type strain (Damgaard, 1995; Rivera *et al*., 2000; Hansen and Handriksen, 2001; Yang *et al*., 2003). Also our PCR screening of 16 *B. thuringiensis* strains for a set of *B. cereus* toxins revealed that these toxins are widespread in all the strains which in some cases show a cytotoxicity toward vero cells higher than the diarrhoeal *B. cereus* reference strain (Raddadi *et*

al., unpublished data); and confirm the results of previous studies which showed that it is difficult (< 0.05%) to find a non-enterotoxigenic bioinsecticide producing *B. thuringiensis* strain from the environment (Damgaard, 1995). Thus, it is important for the bioinsecticide industry to consider that although *B. thuringiensis* insecticide has been used for many years, introduction of *B. thuringiensis* spores into the human food chain through the application of this bacterial species to crops, followed by spore regermination may cause a risk of food-borne poisoning cases. Accordingly, to reduce such a food-poisoning risk, it could be very interesting to isolate non enterotoxigenic *B. thuringiensis* strains for bioinsecticide production. However, it is difficult to find such isolates in nature. Hence, selection of *B. thuringiensis* isolates expressing as less as possible enterotoxin genes could be of great interest for biopesticide elaboration. Also, the discovery of a *B. thuringiensis* strain without enterotoxigenicity, cytotoxicity and psychrotrophic characteristics for the production of Cry toxin is important from the view point of food or crop safety, because foods may be contaminated by the spores of *B. thuringiensis* (van Netten *et al*., 1990; Rosenquist *et al*., 2005). However, the production of enterotoxins by *B. thuringiensis* may be affected by the culture medium, time, and fermentation conditions, and boiling for 12 min could reduce the diarrhoeal enterotoxigenicity (Damgaard, 1995, Glare and O'Callaghan, 2000). Also, *B. thuringiensis* has, only in one case been described to be implicated in foodborne disease (Jackson *et al*., 1995), and despite of the detection of *B. thuringiensis* in faecal samples of 8/20 exposed greenhouse workers, no gastrointestinal symptoms correlated with the presence of *B. thuringiensis* were found (Jensen *et al*., 2002). In addition, it is important that cooked foods for use in salads or other dishes be stored in such a way to prevent spore germination or bacterial growth.

Another point to be considered regarding the safety of *B. thuringiensis* is its closely relatedness to the etiological agent of carbon disease, *B. anthracis* (Turnbule *et al*., 1992). In fact, while it is true that *B. anthracis* can be readily differentiated from *B. cereus* and *B. thuringiensis* based on biochemical tests, a problem still exists for borderline isolates such as the pathogenic *B. cereus* G9241, where these tests fail to recognize the pathogenic potential of this isolate (Hoffmaster *et al*., 2004). Also, in a study aiming to determine a strategy for the identification of the *B. anthracis* borderline isolates in the *B. cereus* group, two *B. cereus* reference strains and one *B. thuringiensis* isolate were found to be potential near neighbours of *B. anthracis* based on RSI-PCR patterns, rep-PCR profiles and MLST analysis. These strains closely related to *B. anthracis* were tested for the presence of *B. anthracis* virulence genes *cap*, *pag*, *lef*, and *cya* by PCR using the specific primers as in Ramisse *et al*. (1996), but none of them resulted positive for any of the four genes (Daffonchio *et al*., 2005). In addition, two other pathogenic isolates, *B. cereus* Zebra Killer (ZK) and *B. thuringiensis* 97-27 (subsp. *konkukian* (serotype H34)) (Hernandez *et al*., 1998, 1999, 2000) were shown, together with *B. cereus* G9241, to be closely related to *B. anthracis* based on phylogenetic analysis using AFLP and MLST (Hill *et al*., 2004). The proteome of all three isolates show a higher similarity to that of *B. anthracis* than to that of the non-pathogenic *B. cereus* ATCC 14579 (Rasko *et al*., 2005 and references therein). Thus, considering the potential virulence shown by strains genetically near neighbour of *B. anthracis*, approaches that might allow to rapidly identify strains appear of great interest for the study of *B. anthracis* virulence mechanisms as well as to prevent the use of such strains for *B. anthracis*-based bioweapon development.

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