13 Biological Control of Nematodes by Plant Growth Promoting Rhizobacteria: Secondary Metabolites Involved and Potential Applications

Marieta Marin-Bruzos and Susan J. Grayston

13.1 Introduction

Plant-parasitic nematodes are one of the most destructive agronomic pests. Because of their nature, nematodes are difficult to manage and detect, as the appearance of affected crops can resemble other pathogenic diseases or nutrient deficiency. Current estimates put crop losses to nematodes worldwide, of at around USD 157 billion per year (Singh et al. 2015). For several decades, the control of plant-parasitic nematodes on agricultural crops has depended on chemical pesticides. These chemicals are in general very toxic with high potential to pollute the environment. Specifically, methyl bromide, which was widely used as soil fumigant from the 1960s, was shown to contribute to the depletion of the ozone layer. As a result, its use was banned under the Montreal Protocol in 2005 (Meadows 2013). Since then, research into alternate products has become a priority. In this context, the biological control agents have arisen as an environmentally friendly alternative (Beneduzi et al. 2012).

Rhizobacteria and nematode populations cohabit in plant root systems. These organisms affect each other's functioning along with the health of the plants whose rhizosphere they colonize (Singh et al. 2016, 2017). Several rhizobacterial strains are able to control nematode populations using different mechanisms of action, improving plant health and yield. For example, *Pasteuria penetrans* is a nematode parasite that can control *Meloidogyne incognita* on tomato and cucumber and *M. arenaria* on Snapdragon (Kokalis-Burelle 2015); *Bacillus nematocida* can control nematodes by producing extracellular proteases that can destroy their cuticles (Niu et al. 2006), and *B. thuringiensis* produce

M. Marin-Bruzos (✉) · S. J. Grayston
Belowground Ecosystems Group, Department of Forest and Conservation Sciences, University of British Columbia, Vancouver, BC, Canada
e-mail: mmarinb@mail.ubc.ca

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Cry proteins that are toxic to these phytopathogens (Bravo et al. 2007). In all cases, the production of virulence factors is vital for the performance of bacterial biological control activity. These factors are secondary metabolites.

Bacteria produce a wide range of secondary metabolites that have several important ecological functions, for example, stimulating competition against other bacteria or eukaryotic organisms, operating as metal transporting agents or as facilitators of symbiotic relations with other organisms (Demain and Fang 2000). The aim of this chapter is to review the secondary metabolites produced by rhizospheric bacteria that have been identified as being involved in the control plant-parasitic nematodes. In general, secondary metabolites can act directly or indirectly on nematode populations. Direct mechanisms affect nematode integrity through the production of lytic enzymes, toxins, gases, volatile organic compounds, and other metabolites or through indirect mechanisms inducing other rhizospheric factors that can reduce the nematode population helping the plant overcome the infestation.

13.2 Secondary Metabolites with Direct Nematocidal Activity

13.2.1 Lytic Enzymes: Chitinases, Proteases, and Glucanases

Among the secondary metabolites produced by rhizobacteria, lytic enzymes have attracted the attention of scientists since the initiation of research into the biological control of nematodes (Miller and Sands 1977; Galper et al. 1990). Lytic enzymes are an attractive proposition because nematodes have a very simple structure with an outer cuticle of keratin and collagen-like proteins that function not only as a skin but also as an exoskeleton maintaining and defining the shape of the organism (Johnstone 1994). In the same way, nematode egg shells are composed mainly of chitin fibrils inserted in a protein matrix, with the chitin complex as the major barrier against fungal infections (Wharton 1980). Extracellular enzymes that digest the main chemical components of the nematode cuticle and eggshell have been studied in potential nematode control bacteria (Tian et al. 2007; Yoon et al. 2012; Yang et al. 2013). Table 13.1 summarizes some examples of the reported rhizobacterial lytic enzymes with nematicidal activity.

Chitinases produced by *Lysobacter capsici* have been found to degrade the eggshell of *Meloidogyne* spp. causing a decrease in hatching (Jung et al. 2014). In a pot trial, *Streptomyces cacaoi* GY525 producing chitinase and β-1,3-glucanase inhibited hatching and caused mortality of *Meloidogyne incognita* J2 stages, reducing the population of J2 in soil and the number of nematode egg masses in tomato plant roots (Yoon et al. 2012). Similarly, El-Hadad et al. (2010) reported *Bacillus megaterium* strain PSB2-inhibited root colonization by *M. incognita* and caused 100% mortality of J2 stages. The authors detected high production of lytic enzymes like proteases, chitinases, and gelatinases by the isolate that could be considered virulence attributes.

Table 13.1 Rhizobacterial lytic enzymes with nematicidal activity

Rhizobacteria	Enzymes	Nematode	Reference
Serratia marcescens Streptomyces griseus	Chitinases	*Meloidogyne hapla*	Mercer et al. (1992)
Paenibacillus illinoisensis KJA-424	Chitinases	*Meloidogyne incognita*	Woo Jin et al. (2002)
Pseudomonas fluorescens CHA0	AprA extracellular protease	*M. incognita*	Siddiqui et al. (2005)
Brevibacillus laterosporus	Alkaline serine protease BGL4	*Panagrellus redivivus*	Huang et al. (2005)
Bacillus sp. RH219	Alkaline serine protease Apr219, neutral protease Npr219	*Panagrellus redivivus*	Lian et al. (2007)
Bacillus nematocida B16	Alkaline serine protease Bace16, neutral protease Bae16	*Caenorhabditis elegans*	Niu et al. (2010)
Streptomyces cacaoi GY525	Chitinases, glucanases	*M. incognita*	Yoon et al. (2012)
Bacillus thuringiensis	Metalloproteinase Bmp1	*C. elegans*	Luo et al. (2013a, b)
Lysobacter capsici YS1215	Chitinases, proteases	*M. incognita*	Lee et al. (2014)
Bacillus firmus DS-1	Sep 1 serine protease	*M. incognita*, *C. elegans*, soybean cyst nematode	Geng et al. (2016)
Alcaligenes faecalis ZD02	Extracellular serine protease	*M. incognita*, *C. elegans*	Ju et al. (2016)
P. fluorescens FP805PU	Collagenase, chitinases, lipases	*Xiphinema index* and *M. ethiopica*	Aballay et al. (2017)
Brevibacterium frigoritolerans FB37BR	Collagenase, proteases, chitinases, lipases		

Proteases have also been widely studied in nematode antagonistic bacteria, especially serine and cysteine proteases. The extracellular alkaline serine protease BLG4 from *Brevibacillus laterosporus* has been very well characterized as virulence factor; BGL4-deficient mutants were 57% less effective than the wild strain at controlling nematodes (Tian et al. 2006). Serine proteases with the ability to degrade nematode cuticles from other rhizobacteria and nematophagous fungi have shown a high percent similarity (97–99% sequence match) to those of *Brevibacillus* (Tian et al. 2006). This fact suggests that these proteases are highly conserved across microbial species. The role of proteases in the biological control of nematodes was also demonstrated by Siddiqui et al. (2005) using mutants of *Pseudomonas fluorescens* CHA0 for the gene *apr A* which encodes an extracellular protease with nematicidal activity. Mutants had no nematocidal activity.

Other virulent proteases like extracellular alkaline serine protease Bace16 and neutral protease Bae16 have been described in different *Bacillus* species with a Trojan horse-like mechanism. Through this mechanism, once the rhizobacteria

reach the intestine of the worm, they secrete Bace16 and Bae16, both of which target vital intestinal proteins, killing the nematode (Lian et al. 2007; Niu et al. 2010). Combinations of diverse kinds of proteases may occur in the nematicidal spore-forming Bacilli group (Zheng et al. 2016) and in other rhizobacterial groups.

Even when phytoparasitic nematodes have a higher lipid content, few studies have focused on lipases as potential virulence factors. Castañeda-Alvarez et al. (2016) performed an in vitro study and reported strains belonging to *B. thuringiensis*, *B. megaterium*, and *B. amyloliquefaciens* with strong lipase activity that caused mortality of the nematode *Xiphinema index*; they also found that *B. megaterium* FB133M with no lipase activity displayed the lowest nematicidal effect. Other lytic enzymes like glucanases, cellulases, and pectinases from *Pseudomonas* spp. have been reported to be involved in the control of *M. incognita* (Krechel et al. 2002). However, their specific role has not been addressed as they are secreted together with proteases and other secondary compounds that can overlap in activity. In general, lytic enzymes play a crucial role in the rhizobacterial activity against nematodes due to their different mechanisms of action and the relatively simple physiology and structure of nematodes.

13.2.2 Cry Toxins from *Bacillus thuringiensis*

During sporulation, *Bacillus thuringiensis* strains produce endotoxins called Cry proteins which are toxic to a large number of insect species (Maagd et al. 2001). It has been found that some Cry proteins are toxic to plant-parasitic nematodes (Bravo et al. 2007; Guo et al. 2008). Fifty-four families of Cry toxins have been identified; among them Cry5, Cry6, Cry12, Cry13, Cry14, Cry21, and Cry55 have been described with nematicidal activity (Bravo et al. 1998; Marroquin et al. 2000; Frankenhuyzen 2009).

The mechanism of action reported for Cry proteins affecting nematodes is similar to the one described in insects. The toxin attaches to the epithelial cells of the nematode intestine inducing the formation of pores and vacuoles and ending with the degradation of the intestine (Marroquin et al. 2000). Iatsenko et al. (2014) reported two novel plasmid-encoded protoxins (Cry21Fa1 and Cry21Ha1) from *B. thuringiensis* DB27 that also display nematicidal activity.

13.2.3 Other Secondary Metabolites Produced by *Bacillus*

Among the wide range of bacteria described as active against nematodes, members of the *Bacillus* genus are the most thoroughly studied. Other secondary compounds from *Bacillus* strains (different than lytic enzymes and Cry proteins) have been reported with nematode control activity. Mendoza et al. (2008) reported that *B. firmus* produced unidentified metabolites during culture that significantly reduced egg hatch of *M. incognita* and controlled *Radopholus similis*. Similarly, dichloromethane-soluble metabolites produced by *B. cereus* and *B. subtilis* showed in vitro activity

against *M. exigua* J2; these compounds were identified by HPLC and mass spectrometry as uracil, 9H-purine, and dihydrouracil, the latter being the most effective (Oliveira et al. 2014).

The peptide plantazolicin, product of the gene RBAM_007470, was identified as the nematicidal factor from *B. amyloliquefaciens* strain FZB42 (Liu et al. 2013). Other nematode control-related metabolites produced by *B. cereus* strain S2 were identified by LC-MS as C16 sphingosine and phytosphingosine. Sphingosine induced reactive oxygen species in the intestinal tract of *C. elegans* and destroyed the genital area of the nematode with the consequent inhibition of reproduction (Gao et al. 2016).

In *B. thuringiensis*, Liu et al. (2010) reported a mechanism of action different from that of Cry toxins. The bacterium produces an adenine nucleoside derivative called thuringiensin (β-exotoxin) with insecticidal and nematicidal abilities that inhibits RNA polymerases by competing with the ATP molecule for binding sites. *B. thuringiensis* strains expressing thuringiensin can kill nematodes with a higher mortality rate than those not expressing the molecule (Zheng et al. 2016).

13.2.3.1 2,4-Diacetylphloroglucinol (DAPG)

The polyketide antibiotic 2,4-diacetylphloroglucinol (DAPG) is produced by some strains of the plant growth-promoting rhizobacteria *P. fluorescens*. A DAPG-overproducing strain inhibited *M. incognita* gall formation on the root systems of mungbean, soybean, and tomato plants, whereas a mutant strain, DAPG-deficient, did not show such activity (Siddiqui and Shaukat 2003). It has been shown that DAPG does not affect all nematodes in the same way. A study by Meyer et al. (2009) found that DAPG exposure decreased the hatch of *M. incognita* eggs but had no effect on its J2 stage; it stimulated hatching of *C. elegans* eggs and was toxic to adults of *Xiphinema americanum*. However, other nematodes tested (*Heterodera glycines* eggs and J2, *Pristionchus scribneri* juveniles and adults, *Pratylenchus pacificus* eggs and adults, and *Rhabditis rainai* eggs and adults) were not affected by the metabolite.

Different authors have suggested that the biocontrol activity of phytoparasitic nematodes exerted by DAPG is due to synergistic action with other metabolites produced by the rhizobacteria, like HCN and pyoluteorin or inducing agents of systemic resistance in plant roots (Siddiqui and Shaukat 2003). DAPG alters the plasma membrane and vacuolization and causes cell content disintegration in fungi (de Souza et al. 2003), but its activity on nematodes is unknown.

13.2.3.2 Gaseous Compounds: H_2S, NH_3, and HCN

Some gaseous compounds released by rhizobacteria mainly as a result of amino acid metabolism have been reported to be effective in the control of nematodes (McSorley 2011).

H_2S can be produced in large amounts by some bacteria as the result of the metabolism of peptides rich in cysteine or other sulphurated amino acids or by the activity of sulfate-reducing bacteria (Carbonero et al. 2012). Early work of Rodriguez-Kabana et al. (1965) described a decrease in nematode populations due

to H_2S formation in flooded soils resulting from the growth of sulfate-reducing bacteria on organic substrates. More recently, Marin et al. (2010) reported the PGPR strain *Tsukamurella paurometabola* C-924 had the potential to control plant parasitic nematodes through the release of H_2S and chitinases.

Ammonia released by ammonifying bacteria during the breakdown of soil organic matter can result in reduced phytoparasitic nematode populations (Rodriguez-Kabana 1986). In this sense, the practice of amending soil with organic matter high in ammonia content like urea could increase the release of ammonia by rhizospheric bacteria, with consequent decrease in nematodes (McSorley 2011). The production of ammonia by rhizobacteria has been included among the strategies to select strains with biological control abilities as this compound can not only control nematodes, it could also serve as a nitrogen source for plants improving plant nutrition, enhancing yields, and triggering crop tolerance to phytoparasites (Mota et al. 2017).

Another gas that has been described by Siddiqui et al. (2006) as "an antagonistic factor that contributes to biocontrol of *Meloidogyne javanica*" is cyanide. Siddiqui et al. (2006) demonstrated a mutant of *P. fluorescens* CHA77, unable to produce cyanide, did not exert the nematicide activity that the wild strain exhibited. In the same way, *P. aeruginosa* PA01 caused irreversible paralysis of nematodes by releasing hydrogen cyanide (Gallagher and Manoil 2001). More recently, Nandi et al. (2015) performed a binary choice assay, where *C. elegans* were allowed to choose for grazing among colonies of *Pseudomonas chlororaphis* PA23 wild strain producing cyanide or the HCN nonproducer mutant. It was found that hydrogen cyanide, produced by *Pseudomonas chlororaphis* PA23, repelled *C. elegans* as the *hcn* mutant was preferred over the wild type.

13.2.3.3 Volatile Organic Compounds (VOCs)

Volatile organic metabolites are usually lipophilic liquids with high vapor pressures. Due to their nature, they freely cross membranes and are released into the soil environment with little restrictions. Similarly, they can move with relative facility through the soil pores extending their area of action and reaching potential targets (Pichersky et al. 2006). Rhizobacteria can also produce volatile compounds that potentially are able to control nematodes; however, their nematicidal activity has only been studied in vitro or in pots probably due to the difficulties of managing these substances in the open field.

An assay performed using compartmented Petri dishes and a pot experiment showed that the VOCs producer *Bacillus megaterium* strain YMF3.25 significantly decreased egg hatching and reduce infection by *M. incognita*. Gas chromatograph/mass spectrometer analysis revealed at least six compounds that could be involved in the nematode control activity (Huang et al. 2010). In the same way *Lysinibacillus mangiferahumi*, isolated from mango rhizosphere soil, also exhibited nematicidal activity versus *M. incognita* through the production of VOCs (Yang et al. 2012).

More recently, Xu et al. (2015) reported five different bacterial strains that, when incubated independently in sealed Petri dishes with *C. elegans* or *M. incognita*, progressively reduced nematode movement until they stopped completely and

irreversibly at 24 h. The active compounds were identified as acetophenone, S-methyl thiobutyrate, dimethyl disulfide, ethyl 3,3-dimethylacrylate, nonan-2-one, 1-methoxy-4-methylbenzene, and butyl isovalerate.

13.2.3.4 Lactic Acid and Amino Acids

In the search for active compounds for biological control, some other rhizobacterial secondary metabolites have been found with a direct nematicidal effect. *L. capsici* YS1215, isolated from soil by Lee et al. (2014), produced lactic acid (2-hydroxypropanoic acid) in culture medium that inhibited the egg hatching of *M. incognita*. In the same way, amino acids present in the culture media of *P. macerans* induced mortality of J2 stages of *Meloidogyne exigua* and reduced the nematode population in coffee plants to levels comparable to the chemical pesticide aldicarb (Oliveira et al. 2009).

13.3 Secondary Metabolites with Indirect Nematocidal Activity

13.3.1 Metabolites Inducing Nematode-Trapping Fungi

There are around 200 species of nematode-trapping fungi. They can develop specific structures like adhesive nets, branches, and mechanical trap rings like to capture, kill, and digest soil nematodes (Liu et al. 2009). Rucker and Zachariah (1986) found that different bacterial species can influence trap production by the fungi *Dactylaria brochopaga* and *Arthrobotrys conoides*.

Li et al. (2011) performed a bioassay to screen soil samples for trap-inducing bacteria using the fungus *Arthrobotrys oligospora*. They found 18 isolates able to induce fungal traps and identified induction activity was due to bacterial cells and their metabolites. Recently, Su et al. (2016) found that volatile organic compounds and ammonia released by bacteria can induce trapping structures on fungi. Similarly, Wang et al. (2014) reported urea as the metabolite produced by bacteria that can trigger the shift in *A. oligospora* from saprophytic to nematode-trapping form and ammonia as the signal molecule that initiates the lifestyle modification in the fungus.

13.3.2 Secondary Metabolites Involved in the Development of Induced Systemic Resistance (ISR) in Plants Against Nematodes

Rhizobacteria can suppress a disease, like a nematode infestation, by inducing a resistance mechanism in plants (van Loon et al. 1998). Induced systemic resistance (ISR) involves expression of defense-related genes and other compounds that help plants overcome pathogen attack. To trigger ISR, one or more bacterial metabolites need to be recognized by root cell receptors (Beneduzi et al. 2012). Several

ISR-inducing compounds have been identified: lipopolysaccharides, siderophores (Van Loon et al. 1998), flagella, N-acyl-homoserine lactones, antibiotics, and exopolysaccharides (Vleesschauwer and Höfte 2009).

The induction of systemic resistance against nematodes is one of the approaches that has been studied in the search for environmentally friendly alternatives for their control. *Bacillus subtilis* triggered ISR in eggplants inhibiting *M. javanica* infection while increasing ascorbate peroxidase, superoxide dismutase, and phenylalanine ammonia lyase activities (Abbasi et al. 2014). *P. fluorescens* CHA0 and salicylic acid induced resistance on tomato plants against the root-knot nematode *M. javanica* (Nikoo et al. 2014). Similarly, Kempster et al. (2001) reported induction of resistance to the clover cyst nematode, *Heterodera trifolii*, on white clover (*Trifolium repens*), when inoculated the pectinolytic *P. fluorescens* P29 or *B. cereus* B1.

Finally, the bacterial enzyme called 1-aminocyclopropane-1-carboxylate (ACC) deaminase, involved in the ethylene pathway, is known to help crops stand abiotic and biotic stresses like pathogenic nematodes. This enzyme degrades ACC, the precursor of ethylene, lowering the hormone levels in plant tissues (Glick 2014). Nascimento et al. (2013) reported bacterial ACC deaminase as a crucial attribute in decreasing populations of *Bursaphelenchus xylophilus*, which is the causal agent of pine wilt disease. Therefore, plant inoculation with rhizobacteria producing ACC deaminase may enhance plant resistance to nematode infestation (Gamalero and Glick 2015).

13.4 Biocontrol Potential of Secondary Metabolites

A review published by Siddiqui and Mahmood almost 20 years ago (1999) stated that the lack of commercial interest in bacterial inoculants to use as biocontrol agents for plant-parasitic nematodes was a major problem to research advancement in this area. Nowadays, with the ban on use of many nematicide fumigants, like methyl bromide, due to human and environmental toxicity, the need to find alternatives for controlling nematodes has become a priority (Zasada et al. 2010). Biological control agents and their related metabolites have been the focus of the search for environmentally friendly alternatives. Among the biological control agents on the market or in an advanced research/development stage, rhizospheric bacteria have gained a preeminent place. In this sense, the secondary metabolites produced by rhizobacteria are a potential source of a new generation of pesticides.

To achieve the introduction into the market of secondary metabolites as pesticides for the control of nematodes, some challenges need to be overcome. The most important are costs. It is more expensive and time-consuming to produce and commercialize a molecule (USD 256 million) than to develop and market a biological agent (USD 20–50 million) (Olson 2015). Other difficulties needing to be addressed are the infield stability of the metabolites, the spectrum of target pathogens, the interaction with plants and other organisms, and its effect on the environment. However, the use of these compounds could help to overcome problems related to survival of biocontrol agents, as they frequently fail when introduced into a new ecosystem because of the competition with autochthonous populations. In the same

way, the study of the metabolic pathways that lead to the production of these compounds can help to discern the conditions needed to naturally trigger their production and consequent activity in the rhizosphere.

Finally, some of these metabolites have been the starting point in developing transgenic plants with inbuilt resistance to nematodes. For example, *B. thuringiensis* Cry5B toxins expressed on tomato roots can make the plant resistant to attack by *M. incognita* (Li et al. 2008). The application of molecular and metabolomic techniques, as well as bioinformatics, is improving our understanding of rhizosphere processes, but the function of many metabolites with biocontrol potential still remains unknown.

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