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Plant-Nematode Interactions Assisted by Microbes in the Rhizosphere

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Abstract
Plant health is strongly influenced by the interactions between parasites/pathogens and beneficial microorganisms. In this chapter we will summarize the up-to date knowledge on soil suppressiveness as a biological tool against phytonematodes and explore the nature of monoculture versus crop rotation in this regard. Since nematodes are successfully antagonized by different microbiological agents, we highlighted this phenomenon with respect to the most important antagonists, and a nature of these interactions. The focus is on the hyperparasitic microbes of phytonematodes such as *Pasteuria* sp. and egg parasites. Furthermore, we comprised the studies on the defence system expressions in plants triggered by nematode-associated microbes. The attachment of bacteria and fungi to phytonematodes and putative effects of the attachment on the induced systemic resistance in plants are discussed. Finally, our chapter is rounded up with the importance of incorporating the knowledge on plant-nematode-microbe interactions in the integrated pest management.

Introduction
Considering that every living macroorganism can be regarded as a holobiont as it is inevitably interconnected with its corresponding microbial cohabitants (Bordenstein and Theis, 2015; Vandenkoornhuyse et al., 2015), and transferring this phenomenon on the tripartite plant-nematode-microbiome system, we can assume that the destiny of plants attacked by plant-parasitic nematodes (PPN) much depends on which microbes are enriched endophytically and in the rhizosphere before and during parasitism events. PPN are considered one of the major pests of agricultural plants and it has been estimated that they cause yield losses up to $80 billion (Handoo, 1998). The majority of PPN belongs to the order Tylenchida, with the endoparasitic root-knot nematodes (RKN), *Meloidogyne* spp., cyst nematodes (CN), *Heterodera* spp. and *Globodera* spp., and root-lesion nematodes (RLN), *Pratylenchus* spp., being the most devastating phytonematodes (Nicol et al., 2011). The RKN and CN are sedentary endoparasites with infective second-stage juveniles (J2) which move through soil and infect roots of host plants. After reaching suitable root cells, they become sedentary, and start producing feeding sites, syncytia (CN) or giant cells (RKN). This results in nematode development into females that protrude egg masses inside or outside the root galls (RKN), or the eggs are encumbered in encysted female bodies (CN). The genus *Pratylenchus* includes migratory endoparasitic nematodes with all life stages (females, males, juveniles) being motile and infective.

Infective stages of PPN encounter a vast number of soil microbiota before entering plants. This allows the attachment of diverse microbes to their cuticle and surface coat. What nematodes are probably not aware of is that when allowing the attachment and agree on carrying the microbes to the plants, they may cause self-deleterious effects, i.e. they can be antagonized by transmitted microbiota. In the following lines, we will review the up-to-date knowledge on the importance and ability of specifically attached soilborne microbes to suppress invasion and reproduction of PPN in plants. Our intention is to confront the attainments, merits and demerits of a plant mediated versus direct antagonism of PPN, with respect to different nematode life strategies and antagonists involved. The molecular aspects of a cross-communication between the plant, nematodes and nematode-attached microbes will be discussed, and the

benefits of nematode-attached microbes to the plant health will be summarized.

Nematode-suppressive soils

Two types of soil suppressiveness have been described in the literature. One is general (non-specific) soil suppressiveness which characterizes the ability of any soil to suppress many pathogens to a certain extent and is related to microbial activity (Davies and Spiegel, 2011). Specific soil suppressiveness is directed towards a particular pathogen. It is exerted by a complete absence of pathogen establishment or, in the worst-case scenario it can cause a severe disease and then draw back with a continued growing of the host plant (Baker and Cook, 1974). Both types of soil suppressiveness are removed by sterilization, indicating the biological nature of soil suppressiveness, but the mechanisms and which microbial species are involved is not sufficiently explored. The previous research was focused on direct antagonism of soil microbes towards soilborne phytopathogens, while plant-mediated mechanisms and plant-associated microbes have not been considered sufficient to explain and manage soil suppressiveness. The follow-up examples support the evidence that suppressive soils can be used as a powerful biocontrol measure against PPN. In an early study by Crump and Kerry (1987) a population of *Heterodera schachtii* failed to increase in suppressive soil of a 2-year monoculture of sugar beet and increased only in the third year. Treatment of this soil with the fungicide Captafol resulted in a greater nematode multiplication and a low fungal parasitism of females, suggesting that fungi played a role in this soil suppressiveness. The soil was enriched with the nematophagous fungi *Pochonia chlamydosporia*, *Fusarium* spp., and *Cylindrocarpon destructans*, which was isolated from infected females. These fungal species are well known parasites of CN (Jorgenson, 1970; Kerry, 1988). When Westphal and Becker (1999) had followed reproduction of *H. schachtii* on Swiss chard (*Beta vulgaris* L.) in a monoculture California field amended with *H. schachtii*-infested soil, the nematode population started declining after several years and remained very low in the following period. The soil suppressiveness was removed by biofumigation or a biocide-treatment. Similarly, a biological soil suppressiveness was responsible for a decreased reproduction of *H. schachtii* on Swiss chard (Westphal et al., 2011). The soil fumigation with iodide resulted in a higher nematode multiplication. In a rare example of soil suppressiveness against an ectoparasitic PPN the population density of *Criconemella xenoplax* dropped significantly in a suppressive soil between 1988-1991 (Kluepfel et al., 1993). Although edaphic factors were nearly identical for both suppressive and non-suppressive sites, it was unclear whether these two sites were indeed comparable, and nematode population densities were not reduced below the damage threshold in the fields. Taking into an account the feeding strategy of ectoparasitic nematodes, which do not enter the roots but feed only by piercing the epidermal root cells with their stylets, it should be noted that the soil microbes attached to the cuticle of these nematodes do not get into a direct contact with plants. This means that soil suppressiveness against ectoparasitic PPN might be inefficient because they are less prone to plant-mediated mechanisms of suppression.

On many occasions, it was proposed that the general indicators of the abundance and activity of soil microbiota could give an indication whether microbial factors are responsible for soil suppressiveness. For instance, a role of the blanket of sugarcane residues and mill mud amendments covering the surface of a sugarcane field was tested against the endoparasitic nematode *Pratylenchus zeae* (Stirling et al., 2011). Although more than 90% of the sugarcane root biomass occupied the depth just beneath the trash blanket, the nematode density at this depth was very low. One would expect that a high total carbon and the readily oxidisable carbon fraction measured within the upper soil profile when the soil surface mulched could have positively influenced soil microbial activity and reduced nematode population density at this depth (Stone et al., 2004; Stirling et al., 2005; Stirling et al., 2011). A similar observation was noticed after the density of *Pratylenchus thornei* had been depressed in upper soil layers of the wheat fields (Stirling, 2011).

The most common way to prove the biological nature of soil suppressiveness includes the comparison of nematode performance in sterilized and non-sterilized soil. In assessing the effects of gamma irradiation on soil properties, decreased levels of $NO3^-$ and an increase of $NH4^+$ were recorded due to elimination of denitrifying bacteria (Buchan et al., 2012). The absence of a microbial community also resulted in a high abundance of labile carbon content due to its insufficient utilization. This leads to the conclusion that the soil microbiota has a profound effect on plants by manipulating soil mineral components, and soil sterilization acts both against deleterious and

beneficial microflora. For instance, a negative correlation was found between a shoot growth of white clover and soil gamma irradiation when studying soil suppressiveness against *Meloidogyne hapla* (Bell et al., 2016). Thus, in parallel with its increased attractiveness, soil suppressiveness still needs to be considered a sensitive topic. Further studies on the cooperation between different soil factors would arm us with a better knowledge on the successful manipulation of specific soil suppressiveness against PPN.

The key mechanisms underlying biological soil suppressiveness involve a direct antagonism of PPN by soil microbiota, and induced systemic resistance in plants (Sikora et al., 2007). To better understand how plants can benefit from the antagonistic interactions between microorganisms and PPN, following lines will review some bacterial and fungal groups that are found to suppress PPN, and the processes taking place beneath these interactions.

Egg parasites of phytonematodes

An extensive literature can be accessed regarding different bacterial and fungal facultative and obligate parasites of PPN (Stirling and Mankau, 1978; Nigh et al., 1980; Kerry, 1988; Meyer et al., 1990; Jaffee et al., 1992; Dijksterhius et al., 1994; Meyer and Wergin, 1998; Hidalgo-Diaz et al., 2000; Lopez-Llorca et al., 2002; Verdejo-Lucas et al., 2002; Olatinwo et al., 2006; Singh et al., 2007; Liu et al., 2009; Castillo et al., 2010; Davies and Spiegel, 2011; Kiewnick et al., 2011; Moosavi and Zare, 2012; Manzanilla-Lopez et al., 2013; Stirling, 2014; Hussain et al., 2017). As for molecular and biochemical aspects of nematode-parasite interaction, the most extensively studied obligate biotroph of PPN is the gram-positive bacterium *Pasteuria* sp. It forms endospores that attach to the nematode's cuticle while it is moving through soil. When the nematodes enter the plant, endospores penetrate the nematode body wall and reach the pseudocelom where they start to germinate and complete their life cycle. Three different species of *Pasteuria* have been recognized to antagonize PPN, *Pasteuria penetrans* on *Meloidogyne* spp., *Pasteuria thornei* on *Pratylenchus* spp. and *Pasteuria nishizawe* on *Heterodera* spp. and *Globodera* spp. (Chen and Dickson, 1998). The mechanism by which nematodes are colonized by this bacterium has been well studied (Chen and Dickson, 1998; Davies and Curtis, 2011; Stirling, 2014). The bacterial spores probably attach to glycoproteins of the surface coat of PPN which contain carbohydrate residues that specifically bind lectins of the bacterial surface (Spiegel et al., 1995). The recognition between epitopes present on the bacterial surface and on the surface coat of nematodes is an initial and essential step in the endospore attachment (Davies and Curtis, 2011), and the specificity of the *Pasteuria*-nematode association is very high and varies even between different individuals of the same species (Davies et al., 1994; Davies and Williamson, 2006; Davies et al., 2008). Although evidence is gathering on a successful control of PPN by high densities of *Pasteuria* spp. (Bird and Brisbane, 1988; Schmidt et al., 2010; Stirling, 2014), the variation in specificity of the attachment in combination with costly mass production of this obligate biotrophic microorganism *in vitro* imposes limitations for use of this hyperparasite as a broad-spectrum biocontrol agent against nematodes. Furthermore, the density of *Pasteuria* endospores is ironically dependent on the density of nematodes (prey) (Stirling, 2014). If the nematode population in soil is low, not many of them will encounter bacterial spores and further endospore propagation will be negligible. Conversely, when the majority of nematodes is being infected with bacteria, they will not only be subjected to its own decline, but will no longer represent the source of an increased endospore inoculum. A pronounced host specificity of this hyperparasitic bacterial group could also appear problematic in cases where mixed nematode populations cause disease in a certain plant crop, resulting in a selective advantage of populations being not a host for *Pasteuria*. So, although *Pasteuria* spores were responsible for the decline of a *Meloidogyne arenaria* race 1 population in a peanut crop, the yield losses were still apparent due to the presence of *Meloidogyne javanica* that could not host the same *Pasteuria* strain and resisted hyperparasitism (Cetintas and Dickson, 2004). Therefore, one needs to consider adjusting many factors before expecting a decline of PPN populations by *Pasteuria* sp. in different crops.

Many fungal isolates were also found to directly antagonize PPN. The roughest subdivision of nematophagous fungi involves: the nematode-trapping fungi which use specialized morphological structures, traps, to hook free-living nematodes, the endoparasitic fungi which infect nematodes by using adhesive spores, and the egg- and cyst-parasitic fungi (Barron, 1977). Several records witness PPN suppression by nematode-trapping fungi (Kerry, 1988; Kumar and Singh, 2006; Singh et al., 2007), and physiological, biochemical and molecular

background of nematode trapping by these fungi have been described (Dijksterhius et al., 1994; Davies and Spiegel, 2011). A successful example is a significant decrease of the disease incidence and nematode fecundity on rice plants when the nematophagous fungi *Arthrobotrys dactyloides* and *Dactylaria brochopaga* were applied to soil infested with J2 of *Meloidogyne graminicola* (Singh et al., 2007). However, these fungi can only trap nematode migratory stages and species in soil, and the period of trapping activity might not be synchronized with the migration of *Meloidogyne* J2 to the roots, resulting in inefficient nematode control (Kerry, 1988). With respect to this, a much better alternative involves nematode control with obligate parasites of eggs and sedentary stages (females) in plants. The fungus *Pochonia chlamydosporia* and the oomycete *Dactylella oviparasitica* have been the most successful in colonizing and cutting down RKN and CN (Stirling and Mankau, 1978; Kerry, 1988; Verdejo-Lucas et al., 2002; Olatinwo et al., 2006). The examples of reduced nematode multiplication caused by these organisms and mechanisms on nematode parasitism are reviewed in books of Davies and Spiegel (2011) and Stirling (2014).

The application of facultative saprophytic fungi, *Trichoderma* sp., has also had a positive result in reducing RKN (Sharon et al., 2001), but the mode of suppression seems to be plant-mediated (Mukherjee et al., 2012; Martínez-Medina et al., 2013; Martínez-Medina et al., 2016; de Medeiros et al., 2017). The recognition between the fungus and the nematode is also carbohydrate-lectins dependent, as mentioned in case of *Pasteuria* sp. (Sharon et al., 2009). Sharon et al. (2007) have shown that the gelatinous matrix, in which the eggs of *Meloidogyne* are embedded, plays a key role in the agglutination of *Trichoderma* (except for *T. harzianum*) conidia in Ca^{2+}-dependent manner, and eggs separated from it are hardly infected by this fungus. This is inconsistent with the study by Orion et al. (2001), where eggs separated from the gelatinous matrix were heavily infected by soil microbiota, suggesting a protective role of the gelatinous matrix. However, we should not forget that *Trichoderma* sp. is a facultative saprophyte and may feed on the gelatinous matrix rather than parasitizing nematodes. Being a facultative saprophyte, which survives in the absence of nematodes but is still able to trigger plant responses against them, may have an advantage compared to obligate parasites of phytonematodes. Although obligate parasites have shown to be successful in suppressing PPN in greenhouse experiments, their mass production *in vitro* is the major problem when applying them as biocontrol agents. Their ability to outcompete the indigenous soil bacteria when introduced to the soil and the inoculum amount for an effective control, also need to be considered before their application (Eilenberg et al., 2001; Inceoglu et al., 2012).

The role of rhizobacteria in suppression of phytonematodes

The soil type and plant genotype determine which soil microbiota will be recruited by the plant and colonize the roots (Bulgarelli et al., 2012; Haney et al., 2015). Although the correspondence between soil-type-specific and root-endophytic bacteria indicate that most endophytes originate from soil and can be found in the rhizosphere (Bulgarelli et al., 2012), in this section we will discuss those bacteria that are antagonistic against PPN and isolated from plant rhizospheres. Nematodes penetrate plant root areas with a continuous excretion of root exudates. Bais et al. (2006) have recently reviewed the role of root exudates in interactions between plant, microbes and nematodes in the rhizosphere. These interactions can be fruitful for phytonematodes, when e.g. root volatiles attract cyst nematodes to the roots (Farnier et al., 2012), or deleterious, instanced by a negative effect of lauric acid from *Chrysantemum coronarium* L. on chemotaxis and infection ability of root-knot nematodes (Dong et al., 2014). As it is postulated that plants have evolved the ability to cultivate specific beneficial microbiomes within their rhizosphere (Haney et al., 2015), the follow-up examples show the ability of rhizomicrobes to act against PPN. Kloepper et al. (1992) studied the suppression of the phytonematodes *Heterodera glycines* and *Meloidogyne incognita* by isolated rhizobacteria from soybean (*Glycine max* L.) and several non-host plants of these nematodes, including velvet bean (*Muncuna deeringiana* L.), castor bean (*Ricinus communis* L.), sword bean (*Cannavalia ensiformis* L.) and Abruzzi rye (*Secale cereale* L.). With both nematodes, bacterial isolates from antagonistic plants reduced disease incidence 4-6 times compared to those from soybean, suggesting a contribution of these rhizobacteria to the non-host status of the plants they originated from. In another study, Gram-negative rhizobacteria were responsible for the reduction of the early infection of sugar beet in the greenhouse by *H. schachtii* (Ostendorp and Sikora, 1989). However, this effect was weakly expressed in field experiments for most bacterial isolates, especially in the second year after application. This was

attributed to a high competition between the indigenous microflora and introduced isolates which could not well establish in the rhizosphere. As reported by Scher et al. (1988) the mean root colonization by different strains of *Pseudomonas putida*, *Pseudomonas fluorescens* and *Serratia* sp. was 1.0-1.5 log units lower per gram of root in a field compared to a greenhouse experiment. Furthermore, although two fluorescent pseudomonads, strains SS3 and 3K, failed to colonize maize roots in field soil, they reached population densities of >1x10^7 cfu/g root in autoclaved soil. The latter discussion requires consideration of many factors before designing experiments on nematode suppression by beneficial microbes, especially equalizing the greenhouse with real field conditions (Kloepper and Beauchamp, 1992; Eilenberg et al., 2001). Beside the ability to directly antagonize PPN, rhizomicrobiota can also enhance the systemic resistance of plants through mediation of jasmonic acid- and ethylene-pathways (van Loon et al., 1998), and some studies in this regard are gathered in the section on induced systemic resistance.

The role of plant endophytes in suppression of phytonematodes

Knowing that plant endophytes persist inside the plant itself, either through their entire life cycle or during a certain life stage, we cannot use this term to make a distinction between plant deleterious and plant mutualistic inhabitants. However, in this section we will elaborate the plant bacteria and fungi that live internally, within plant tissues (endorhiza), but for which it has been reported to suppress PPN. Sikora and Pocasangre (2006) have emphasized the importance of the so called pathozone, or the zone in soil used for initial root growth which is exposed to an early infection by nematodes. This zone can extend by 25-50 cm in soil from the plant base, while the application of pesticides mostly covers the upper 25 cm of soil. Considering that nematodes can move up to 50 cm in soil over a seven-day period, it means that newly formed roots remain unprotected from the nematode attack. Thus, a seek for effective mutualistic plant endophytes which are able to antagonize PPN would overcome the aforementioned problem (Sikora and Pocasangre, 2006).

Plant endophytic bacteria

Maybe the only advantage that plants can get from the PPN is the introduction of beneficial endophytes through the wounds that nematodes make by piercing the root cells. As mentioned in the previous section, it has been suggested that most of the endophytic bacteria cannot be marked as obligate endophytes because they also inhabit the rhizosphere and phylloplane (Kloepper and Beauchamp, 1992; Sikora et al., 2007; Bulgarelli et al., 2012). The attachment of beneficial endophytes to the cuticle of motile nematode stages in soil can presumably also lead to their transmission inside the roots. Although a knowledge gap still exists in this area, nematode interactions with plant endophytic bacteria have been observed by several authors (Hallmann et al., 1997; Hallmann et al., 1999; Hallmann et al., 2001; Siddiqui and Shaukat, 2003a; Sikora et al., 2007; Schouten, 2016). There are several known mechanisms by which endophytic bacteria can suppress plant infection caused by PPN, including competition for niche, direct antagonism by toxic compounds and induced systemic resistance (ISR) (Hallmann et al., 2001). However, a high density of bacterial antagonists (opportunistic bacteria) not always results in nematode suppression, and a direct toxicity might be compromised by a low expression of toxic compounds *in planta* (Sikora et al., 2007). This means that the induced systemic resistance might be the most important way of nematode control by endophytic bacteria (see section 6).

Plant endophytic fungi

Recently, Schouten (2016) has collected a vast literature on the involvement of endophytic fungi on PPN suppression, and covered the most important mechanisms that contribute to it. Recalling the concept of a holobiont (Bordenstein and Theis, 2015), mycorrhizal fungi represent an inextricable part of almost every plant system. Their role in suppression of PPN has been extensively studied and reviewed (Sitaramaiah and Sikora, 1982; Saleh and Sikora, 1984; Cooper and Grandison, 1987; Hol and Cook, 2005; de la Pena et al., 2006; Sikora et al., 2007; Sikora et al., 2008; Veresoglou and Rillig, 2011; Banuelos et al., 2014; Schouteden et al., 2015; Schouten, 2016). Hol and Cook (2005) have listed all recorded interactions between endoparasitic or ectoparasitic PPN and arbuscular mycorrhizal fungi (AMF), noting that the association of plants with AMF decreased the damage caused by sedentary endoparasites (RKN, CN) but increased the damage caused by ectoparasitic nematodes. They considered the possibility that ectoparasitic nematodes damage the AMF hyphae while browsing and, thus, evade the plant defense reactions. Numbers of migratory endoparasitic nematodes (*Pratylenchus, Radopholus*) were slightly increased on AMF-infected plants compared

to AMF-free plants, but the damage was low in the reviewed studies. The mode of action of mycorrhizal fungi against PPN can be exhibited through a direct effect, by competition for nutrients and space, or indirect effect, by increasing plant tolerance, mediating ISR in plants, altering rhizosphere interactions by altered root exudations, or all of these combined (Schouten, 2016). The altered root exudation of AMF plants can directly affect nematode hatching, motility, chemotaxis, and host location (see (Stirling, 2014; Schouteden et al., 2015)). The ability of AMF to act against phytonematodes by mediating plant responses is discussed in the next section.

The association between phytonematodes and grass endophytes has also been reviewed (Cook and Lewis, 2001; Schouten, 2016). The most prominent genus is *Neothypodium*. Although it was reported to suppress some PPN, including *Meloidogyne* and *Pratylenchus* (Ball et al., 1997; Elmi et al., 2000; Jia et al., 2013), it has been understood that in some other cases this was not true (Nyczepir and Meyer, 2010), possibly due to plant genotype differences and different fungal isolates (Cook and Lewis, 2001). As studied by Meyer et al. (2013) the compounds from tall fescue root exudates and extracts reduced *M. incognita* vitality and fecundity in laboratory and greenhouse tests. However, a clear mode of action of these fungi against nematodes has not been understood yet and knowledge gaps on responsible fungal isolates prevents their incorporation in commercial plant cultivars (Stirling, 2014). There are certain indications which place some antagonistic *Fusarium* sp. strains into a group of plant-mediators when reducing reproduction of *Meloidogyne* spp. (Martinuz et al., 2013; Le et al., 2016). A more elaborative discussion on mediating plant responses by endophytic bacterial and fungal antagonists against PPN is presented in the next section.

Do microbiomes associated with infective stages of PPN trigger plant defenses?

From a myriad of microorganisms present in soil, only a small subset manages to bind to the nematode's cuticle. Despite several studies which indicate how the actual microbial attachment to PPN occurs, the questions have remained unanswered on what drives this high binding specificity and determines which microbes will be attached and which not. Further research on the nematode/microbial selectivity in the attachment and the influence of plants on these interactions would better elucidate possibilities in manipulation of this binding for plant health purposes.

As summarized in previous sections, most studies on soil suppressiveness have tested an antagonistic potential of responsible microorganisms through their direct effect on PPN, including parasitism or production of toxins and enzymes (Mazzola, 2004; Westphal, 2005). However, evidence is mounting that plant-mediated mechanisms play a pivotal role in nematode suppression by soil microbiota (Adam et al., 2014). When defining the ISR, authors are very concerned not to mix this term with systemic acquired resistance, or priming (Martinez-Medina et al., 2016a). Pieterse et al. (2014) named it ISR when the induced resistance is triggered by a beneficial microbe and demonstrated to be SA-independent, and did not distinguish ISR and priming. Others (Van Wees et al., 2008; Martinez-Medina et al., 2016b) more specifically define defense priming being also systemic as ISR but can be induced by beneficial microbes, chemicals, pathogens, or other stress agents. In addition, priming always means that after its induction the enhanced defense response is independent from the presence of the inducer, i.e. it remains memorized *in planta*. This is not strictly required for ISR, so in this sense priming may be viewed as a special case of ISR.

There are two lines of plant defense. Pattern recognition receptors (PRRs) of plants first recognize microbial compounds, called microbe- or pathogen- or damage-associated molecular patterns (MAMPs, PAMPs or DAMPs) which induce a first line of defense, PAMP-triggered immunity or PTI (Boller and Felix, 2009). The second line of defense applies to successful pathogens which are able to combat effector-triggered immunity or ETI (Dodds and Rathjen, 2010). Over the years, several factors have been found to behave like MAMPs, including bacterial flagellin (Gómez-Gómez and Boller, 2000), lipopolysaccharides (LPS) (van Peer et al., 1991; Reitz et al., 2000), siderophores (Crowley, 2006; Beneduzi et al., 2012), antibiotics (Siddiqui and Shaukat, 2003b), biosurfactants (Ongena et al., 2007; Tran et al., 2007), or bacterial volatiles (Ryu et al., 2004; Naznin et al., 2014). Nevertheless, only few studies covered the involvement of MAMPs in nematode suppression in plants. When studying the suppression of the potato cyst nematode *Globodera pallida*, Reitz et al. (2000) showed in a split-root experiment that live cells or extracted LPS of *Rhizobium etli* strain G12 reduced reproduction of *G. pallida* by mediating ISR in potato plants.

Similarly, LPS of *P. fluorescens* strain WCS417 induced ISR in carnation and triggered an enhanced defense response after challenge inoculation with *Fusarium oxysporum* f. sp. *dianthi* (van Peer et al., 1991). In a recent study, Martinez-Medina et al. (2016) have tested local and systemic effects of the fungus *Trichoderma harzianum* T-78 on reproduction of *M. incognita*. They found a significant reduction of galls, shoot biomass and nematode fecundity both locally and systemically when plants were pre-inoculated with the fungus. More than that, this study showed the synergystic action of both salicylic acid (SA)- and jasmonic acid (JA)-mediated pathways. When plants were pre-treated with the fungus, a higher expression of SA-responsive marker genes, pathogenesis-related protein 1a (PR1) and Pathogenesis-related protein P6 (PR-P6) was observed in response to the RKN. Additionally, it was reported that JA-responsive marker genes Proteinase inhibitor II (PI II) and Multicystatin (MC) were down-regulated when nematodes were inoculated alone, but this down-regulation was suppressed when plants were pre-treated with the fungus. This effect was much stronger in systemic tissues suggesting that this JA-mediated pathway is not strongly expressed locally in the roots. Selim et al. (2014) have also found the involvement of both JA and SA in suppression of *M. javanica* by *T. harzianum T10*. The nematode fecundity was the lowest when the fungus was applied together with SA on the inducer side and it was preceded by an increase in the relative water content of the plant. The authors proposed that the plant resistance to nematodes appeared as a consequence of increased activity of peroxidase and phenoloxidase in plant tissues.

A split-root experiment was used to study the ability of bacterial antibiotics to mediate a plant response by ISR to RKN (Siddiqui and Shaukat, 2003b). More specifically, the effect of 2,4-diacetylphloroglucinol (DAPG) produced by *P. fluorescens* strain CHA0 against *M. javanica* was tested. It caused a reduction in the egg hatch and invasion of J2 in the roots, and increased J2 mortality. Similarly, Adam et al. (2014) have proved the ability of bacterial antagonists of fungal pathogens, *Bacillus subtilis* isolates Sb4-23, Mc5-Re2, and Mc2-Re2, to mediate ISR in tomato plants upon challenge inoculation with *M. incognita* and noted a significant reduction of plant infection by this nematode. The ISR was also responsible for a significant reduction of tomato root infection by *M. incognita* and *Pratylenchus penetrans*, upon challenging with the AMF *Funneliformis mosseae* (Vos et al., 2012). As an early MTI-response involving the jasmonate-linked 9-LOX-pathway has been unraveled in tomato plants inoculated with *F. mosseae* (Lopez-Raez et al., 2010)(Lopez-Raez et al. 2012), Schouteden et al. (2015) suggested that this response might be triggered during an early infection by root-knot nematodes as well. Recently, the class III chitinase gene VCH3 was found to be activated in *Glomus versiforme* colonized grape roots upon infection by *M. incognita* (Li et al., 2005). Hao et al. (2011) reported that *Glomus intraradices* colonization of grape (*Vitis* sp.) triggered activation of several genes after infection by the ectoparasitic nematode *Xiphinema index*.

Plants benefit from ISR by saving costs from activating the machinery of other defense-related genes that would otherwise affect plant growth and reproduction (Van Wees et al., 2008). Conversely, although most plants are in the state of ISR due to a vast number of rhizomicrobiota, sometimes the density of certain rhizomicrobes is not high enough to trigger ISR responses (Bakker et al., 2013). Nevertheless, if ignoring the latter and if considering the disadvantages of a direct antagonism of soil microbiota against PPN that are presented in previous sections, it can consequently be concluded that plant ISR responses represent an eminent and, yet, insufficiently explored weapon in the battle against phytonematodes.

Concluding remarks

It is irrefutable that PPN represent important members of plant devastators. Different strategies have been employed in the past decades to control yield losses that they cause, and yet, not many of them resulted in success. A microbial attachment to PPN represents a hot topic nowadays as an increasing number of examples has justified its contribution to a specific soil suppressiveness against PPN. Despite obligate parasitism is an important mode of action of many nematode-associated microbes to suppress PPN, we could see that there are many limitations for relying only on this mode of action. Many biocontrol agents that were found to successfully control phytonematodes *in vitro* or in the greenhouse could not show the same effect in the field. Some reasons for that are a weak competitive ability of such antagonists and failure to establish a high density that can significantly reduce PPN populations. On contrary, the intensification of studies on ISR-mediated suppression has shown its success in cases where a direct microbial antagonism failed. In the number of supporting examples, it has been understood that

the core mechanism by which soilborne microbes counteract PPN relies on basal plant responses. However, many authors have not expanded their research beyond the split-root assays in this regard, assuming the involvement of the plant ISR without a molecular proof. Further studies are needed to unravel which genes and hormonal pathways are employed during plant basal defences against PPN that are triggered by nematode-associated microbiota. If the nematode population and species differences in microbial attachment are so pronounced, it would be intriguing to see how it affects and depends on plant ISR responses. A pursuit for specifically attached microbes that are more commonly associated with different nematode species and populations would aid their incorporation in biocontrol strategies against a broad spectrum of PPN to promote plant health.

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