Bacterial and Fungal Biocontrol Agents against Plant-Parasitic Nematodes

Subjects: Agriculture, Dairy & Animal Science

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Nematodes are non-segmented invertebrates and are by far the most abundant animals on Earth, accounting for an estimated four-fifths of all animals of the terrestrial biosphere. Among soil-dwelling nematodes, some have crucial ecological niches in the soil food web, regulating carbon and recycling nutrients (such as nitrogen, increasing its availability to plants), while others are considered a phytosanitary risk. Plant-parasitic nematodes (PPNs) pose a big threat to food security and plant health. The Commission Implementing Regulation (EU) 2019/2072 lists 15 nematode species, 10 of which do not occur in the Schengen territory and 5 do. The European and Mediterranean Plant Protection Organization (EPPO) recommends EU member states to regulate the following nematodes as quarantine pests: *Aphelenchoides besseyi*, *Bursaphelenchus xylophilus*, *Ditylenchus dipsaci*, *Globodera pallida*, *G. rostochiensis*, *Heterodera glycines*, *Meloidogyne chitwoodi*, *M. enterolobii*, *M. fallax*, *M. mali*, *Radopholus similis*, and *Xiphinema rivesi*.

bacteria | biological control | bionematicides | cyst nematodes | nematophagous fungi | pinewood nematode | root-knot nematodes | root-lesion nematodes

1. Root-Knot Nematodes (RKNs), Root-Knot Nematodes

Root-knot nematodes (RKNs) are obligate parasites, with a widespread distribution across the globe, capable of feeding on almost every species of vascular plant. Their polyphagous lifestyle usually grants *Meloidogyne* spp. the title of the most damaging plant-parasitic nematode (PPN). This genus consists of about 100 species as of 2021 [1], but the most important species, commonly referred to as the big four, are the tropical *M. arenaria*, *M. incognita*, and *M. javanica*, and the temperate *M. hapla*.

In the last 5 years, research on the management of RKNs has mostly focused on two species of the big four, namely *M. incognita* and *M. javanica*. Nevertheless, the emerging *M. enterolobii* and *M. graminicola* have also gained special attention. The current literature is especially dedicated to increasing knowledge on reducing or avoiding PPN infection in tomato, but other crops are also considered.

Among the main bacterial agents described for root-knot nematodes (*Meloidogyne* spp.), the genera *Bacillus*, *Pasteuria*, and *Pseudomonas*, followed by *Streptomyces* and some family Enterobacteriaceae members, have been the most analyzed. Liu et al. explored the drivers of the specificity change of *P. penetrans* on *M. arenaria* in peanut plots and crop rotations with peanut and soybean. Their results show a rapid change in the host specificity of *P. penetrans* against *M. arenaria*, both in space and time, and they observed an overall reduction in the attachment rate with samples from rotation plots relative to samples from peanut plots, which may reflect the lower abundance of the bacterial antagonist under crop rotation, potentially due to suppressed density of host nematodes [2]. Ghahremani et al. [3] studied the effects of *B. firmus* I-1582 on *M. incognita* and the root colonization of tomato and cucumber and noted that the bacterium degraded eggshells and colonized tomato roots more extensively than cucumber roots. The authors also observed that, although its optimal growth temperature is 35 °C, the bacterium was able to grow and form biofilms from 15 to 45 °C, while inducing systemic resistance in tomato but not in cucumber [3]. Indeed, salicylic acid (SA)- and jasmonic acid (JA)-related genes were primed at different times after nematode inoculation in tomato, but only the SA-related gene was upregulated at 7 days after nematode inoculation in cucumber [3]. Tian et al. [4] assessed the nematicidal activity of *B. velezensis* Bv-25 against *M. incognita* and its overall effects on cucumber and found that this strain inhibited egg hatching and produced a 100% mortality rate of J2s within 12 h of exposure to Bv-25 fermentation broth in vitro. Furthermore, Bv-25 colonized cucumber roots, effectively reducing the infection rate of J2s by 98.6% [4]. Pot trials showed that Bv-25 reduced cucumber root knots by 73.8%, and a field experiment demonstrated that the disease index was reduced by 61.6%, the cucumber height increased by 14.4%, and the yield increased by 36.5% in Bv-25-treated plants compared to the control [4]. Mazzuchelli et al. [5] examined two application methods of *B. subtilis* for the biological control of RKNs and root-lesion nematodes (RLNs) in sugarcane. Bacterial application at planting proved to be more effective in controlling both genera than applying *B. subtilis* post-emergence, and the effect was higher than that of carbofuran [5]. Engelbrecht et al. [6] reported that a filtrate mixture of *B. cereus*, *B. megaterium*, *B. subtilis*, and *B. thuringiensis* caused approximately 85–90% immobility of *M. enterolobii*, *M. incognita*, and *M. javanica* J2s after 96 h, theorizing that bioformulations with *Bacillus* spp. mixtures might be more effective than products from a single species in limiting juvenile motility. Bui et al. [7] found that bacterial volatiles emitted by *Bacillus* sp. and *Xanthomonas* sp. have the potential to control *M. graminicola*, albeit high volatile concentrations may hamper plant growth. Choi et al. [8] noted that the number of egg masses and root gall index produced by *M. incognita* were significantly curbed in the treatment group with two *Bacillus* strains, *B. thuringiensis* and *B. velezensis*, both in vitro and in planta, even when compared to the nematicide treatment. Interestingly, some strains showed host-specificity in their effects as biocontrol agents for RKNs [8]. Nasiou et al. [9] investigated the compatibility of fluazaindolizine and oxamyl with *P. penetrans* in populations of *M. incognita* and *M. javanica* and found that neither fluazaindolizine nor oxamyl had any negative effect on the rate of spore attachment. The spore-encumbered J2s were used to infect tomatoes, and RKN females without egg masses were extracted from the roots 50 days after inoculation and checked for eggs in the ovaries and mature spores of *P. penetrans* [9]. Although no mature endospores were present in the females, there was evidence of a low percentage of infection in a few treatments, which might be explained by a loss of the pathogenicity of the bacterium, as it kept in the form of dried roots for a long period [9]. *Pseudomonas fluorescens* CHA0 is capable of significantly reducing disease severity in tomato cultivars to a higher extent than in cucumber [10]. Other strains of *Bacillus* sp. CBSAL02 and *Pseudomonas* sp. CBSAL05 displayed broader activities, significantly reducing the hatching of *M. javanica* eggs by 74% and 54%, respectively [11]. Bhuiyan et al. [12] set up two experiments to determine the suppressive effects of *P. penetrans* endospores against *M. javanica* in sugarcane. In the first one, eggs of the RKN were inoculated into *Pasteuria*-free and naturally infested soils, and the results revealed that the RKN population was 96 and 99% lower in the naturally infested soil 19 and 37 weeks after inoculation, respectively [12]. The second experiment consisted of determining the effect of endospore concentration on the multiplication of *M. javanica*, and the results showed that regardless of harvest time, the severity of root galling and the number of nematode eggs produced per plant were inversely proportional to the endospore concentration [12]. Walia et al. [13] reported that olive plantation soils with a naturally high incidence of *P. penetrans* (50–90%) had suppressive levels and kept *M. javanica* populations below damaging thresholds.

2. Cyst Nematodes (CNs), Globodera, and Cyst Nematodes

Globodera spp. are highly specialized, obligate endoparasitic nematodes and major quarantine pests, native to South America, having spread to nearly all potato-producing regions of the globe [14]. The major CN species are *G. pallida* and *G. rostochiensis* (potato cyst nematodes, PCNs), *Heterodera glycines* (soybean cyst nematode, SCN), *H. avenae*, *H. filipjevi* (cereal cyst nematodes, CCNs), and *H. schachtii* (beet cyst nematode, BCN), and CNs are known for their capacity to survive for prolonged periods in the soil in the absence of a suitable host [15][16], making cultural control through crop rotation or trap crops difficult and eradication, once established, nearly impossible. Although the economic impact of these PPNs is difficult to ascertain, *G. pallida* and *G. rostochiensis* might be responsible for worldwide potato crop losses of approximately 9% [17]. The SCN is the most devastating pest in soybean-producing areas throughout the United States and Canada [18], being responsible for economic losses ascending to USD 1.5 billion per year in the U.S. alone [19]. Crop losses caused by CCNs are heavily dependent on environmental conditions but can exceed 90% in some fields [20].

From 2018 to 2022, the most commonly studied bacterial agents against cyst nematodes belong to the *Bacillus* genus. Huang et al. [21] explored the effects of *B. firmus* I-1582 on the plant–nematode interaction between *A. thaliana* and *H. schachtii* and found that the root colonization by the rhizobacterium significantly protected *A. thaliana* from infestation by the BCN, negatively affecting nematode reproduction as well as pathogenicity and development over two generations in vitro [21]. Widianto et al. [22] evaluated the pathogenicity of *B. cereus*, *B. flexus*, *B. megaterium*, *B. pumilus*, and *B. subtilis* on *G. rostochiensis*, and noticed significantly contrasting protease and chitinase activities in these strains compared to the control. Ahmed et al. [23] investigated the effects of twenty *Bacillus* isolates on J2s of *H. avenae* in vitro, and significant mortality rates were observed for *B. cereus* XZ-33-3, followed by *B. cereus* XZ 24-2-1 and *B. weihenstephansis* MH-58-60-01. Out of all the tested *Bacillus* strains, *B. cereus* XZ 24-2-1, *B. cereus* XZ-33-3, *B. weihenstephansis* MH-58-60-01, and *B. thuringiensis* MH 032-003 fared the best in controlling *H. avenae* cyst development in greenhouse conditions [23]. In a subsequent study, Ahmed et al. [24] assessed the biocontrol potential of bacteria isolated from cysts against *H. avenae* in vitro. Morphological, physiological, and biochemical analyses showed that the most promising belonged to the *B. cereus* group, which was subjected to further testing under greenhouse conditions [24]. *Bacillus cereus* B48 was responsible for a 78% reduction in cyst development in roots, just below the avermectin control (84%) [24]. Zhao et al. [25] explored the biocontrol potential of bacterial strain *B. aryabhattai* Sneb517 against *H. glycines* and observed a 70% reduction in juveniles inside the roots and more than 60% in the number of cysts during field experiments.

Lund et al. [26] assessed the efficacy of a bioformulation containing *P. nishizawae* against the SCN, under different management practices, and observed that the bacterium reduced the reproduction factor of *H. glycines* when the seeds were treated with the formulation.

In terms of fungal biocontrol, Vieira dos Santos et al. [27] performed in vitro bioassays to assess the parasitism of 10 isolates of *P. chlamydosporia* on *G. pallida* eggs, reporting pathogenicity varying between 34 and 49%. These low parasitism levels might be explained by the spontaneous hatching observed when *P. chlamydosporia* isolates seem to parasitize immature eggs more actively than eggs containing second-stage juveniles [27][28]. Zhang et al. [29] explored the effectiveness of *Beauveria bassiana* 08F04 and *Agrobacterium tumefaciens*-mediated transformants on *H. filipjevi* in vitro and observed significant changes in the growth rate and biocontrol potential among some of the transformants, particularly G10. They also noted that the application of wild-type *B. bassiana* 08F04 and transformant G10 significantly reduced the population of the CCN females in roots [29]. Benedetti et al. [30] tested the effect of the AMF *G. etunicatum* on *H. glycines* under greenhouse conditions and reported a 28% decrease in nematode females in the root system of mycorrhizal plants compared to untreated roots. These results suggest that *G. etunicatum* promotes tolerance of the host plant to the presence of the SCN [30].

3. Root-Lesion Nematodes (RLNs), Root-Lesion Nematodes

RLNs are obligate biotrophic, soil-inhabiting parasites recognized worldwide as major constraints to important agricultural crops, such as cash crops (cotton and coffee), food crops (cereals, fruits, and vegetables), fed crops (alfalfa), industrial crops (sugarcane), oil crops (soybean), and ornamental crops [31][32]. The motile stages of RLNs are able to enter and leave their host plant, feeding on root cells (epidermis, cortex, and vascular cylinder) and causing extensive necrotic lesions, eventually leading to cell death [32]. As a result, infected plant hosts often exhibit a decrease in root system development (distortion or stunting) and poor growth and yield. This situation is worsened by the fact that RLNs are also known to form disease complexes with other root pathogens, one such example being *P. penetrans* and *Verticillum dahlia* [33].

Controlling RLNs is a major challenge for crop producers. Thus far, a total of 103 *Pratylenchus* species have been described [34][35], which can be underestimated due to the low number of morphological features and high intraspecific variability that characterize them [31]. Hence, in the past five years, the study of biological control has been limited to a few RLN species (*P. brachyurus*, *P. coffee*, *P. penetrans*, *P. vulnus*, and *P. zeae*), with only four studies focusing on bacteria and seven on fungi. Bacterial species from *Bacillus*, *Pseudomonas*, and *Streptomyces* were the most analyzed against *Pratylenchus* spp., while the most common fungal biocontrol agents were AMF (specifically from the *Glomus* genus) and *Trichoderma* spp. Promising results were obtained for *P. brachyurus* using different fungal species in corn and soybean [36][37][38][39]. Dias-Arieira et al. [38] compared the single application with the combined activity of *P. lilacinum* and *T. harzianum* in soybean crops, denoting that both fungi were more effective when applied independently. In a later study, different combinations of *B. subtilis*, *P. lilacinum*, and *T. asperellum* were tested against *P. brachyurus* infecting soybean. All combinations were efficient in controlling this RLN, outperforming the chemical nematicide abamectin, 120 days after sowing. The reproduction factor (Rf) of *P. brachyurus* was lower (Rf = 0.4) in the treatment combining *B. subtilis* and *P. lilacinum* in the crop season, while in the fallow season, the treatment with *P. lilacinum* alone resulted in the most significant reduction (Rf = 0.6) [39]. Pacheco et al. [37] showed that *P. chlamydosporia* Pc-3, Pc-10, Pc-35, and *Trichoderma* sp. T-10 were the most effective for the control of *P. brachyurus* in soybean and corn. Using an in vitro approach, Oliveira et al. [36] tested *Trichoderma* spp. extracts (non-volatile metabolites) against J2s of *P. brachryurus* and recorded 41–46% mortality rates with *T. asperellum* T00, and 64–65% with *T. harzianum* ALL42. Afterwards, these *Trichoderma* species were applied to two soybean cultivars commonly grown in Brazil (BRSGO Caiapônia and BRS 8560RR), under greenhouse conditions, reducing the nematode populations by 51 and 89% using T00 and ALL42, respectively [36].

As for *P. coffeae*, Asyiah et al. [40] used a bacterial consortium composed of endophytic *Bacillus* sp. and *Pseudomonas* sp. directly applied onto Robusta coffee (*Coffea canephora* A.) pots, which successfully suppressed nematode population in soil and roots by nearly 60–70%. Additionally, Duong et al. [41] tested direct in vitro nematicidal activity of different isolates of *Arthrobacter*, *Bacillus*, *Enterobacter*, *Herbaspirillum*, and *Pseudomonas*, among which *B. mycoides* CCBLR14 and other non-described isolates from the *B. cereus sensu lato* group, CCBLR15, CCBLR13, and CCBMTR4, were the most antagonistic to *P. coffeae*.

4. Pinewood Nematode (PWN), *Bursaphelenchus xylophilus*

The PWN is believed to be native to North America [42]. It is a devastating migratory endoparasite of conifers, mostly *Pinus* spp., especially in Asia and Europe, where it causes pine wilt disease (PWD) to autochthonous trees [43][44]. Four elements come into play during PWD: the PWN, its insect vector (*Monochamus* spp.), a susceptible pine host, and Ophiostomatales fungi, which the nematode feeds upon during its mycophagous phase [45]. While the prevention and regular monitoring of the PWN and its insect vector are the most common strategies to manage PWD, dissemination can eventually occur. In Europe, the nematode was first reported in mainland Portugal, in 1999 [46], and despite the country’s herculean efforts to halt its spread, the PWN has found its way to Madeira Island and a Northwestern province of Spain [47][48].

Biocontrol options are very limited, especially when it comes to bacterial agents. Liu et al. [49] reported that two isolates of *E. coli*, M131 and M132, and one of *S. marcescens*, M44, showed significant nematicidal activity against the PWN in vitro after 12 h. The most promising fungal BCAs comprise two species of the *Esteya* genus: *E. vermicola* [50] and *E. floridanum* [51]. Currently, nine isolates of *Esteya* spp. are described and they are frequently associated with insects [52][53]. Two *Esteya* spp. isolates have been successfully used to suppress the PWN in Asian pines, like *P. densiflora*, but the efficiency of their application in other pine species remains unknown. The infective cycle of *E. vermicola* begins when the fungus attracts the nematodes towards the hyphae, where the spores adhere to the PWN cuticle. These conidia usually germinate within 18–24 h, causing death after the nematode’s organs and tissues are completely destroyed by a mass of hyphae, growing outward and producing more lunate conidia to begin the cycle anew [54]. *Esteya floridanum* was recently discovered, so its efficiency and infection mechanism are only just beginning to be unveiled [51]. The benefits of *Esteya* spp. have also been demonstrated in vivo, where the survival rate of *P. densiflora* infected by the PWN can range from 30–50%, over a time period of 3–6 years, when these fungi were used as a remedial effect and depending on the culture substrate employed [55]. Furthermore, when *P. thunbergii* trees were inoculated with spores of *Esteya* spp. prior to nematode infection, their survival rate was significantly higher [56]. *Esteya floridanum* was also shown to have a positive effect in controlling the PWN on *P. koraiensis* seedlings, although the fungus was only able to defer the death of the treated plants for 2–6 weeks [51]. Nevertheless, seedlings are usually more susceptible to pathogens and pests [57], which might explain the results obtained by Li et al. [51].

5. Reniform Nematode (RN), Rotylenchulus reniformis

Among the few described species of reniform nematodes, *R. reniformis* gained notoriety as the most economically significant, most likely due to its widespread distribution [58]. *Rotylenchulus reniformis* is a semi-endoparasitic nematode, occurring most notably in tropical and subtropical regions, where it parasitizes a wide variety of crops, including cotton, vegetable crops, and several tropical fruit species [59][60][61][62][63].

In terms of biocontrol, Xiang et al. [64] showed that rhizobacteria strains, *B. mojavensis* Bmo3 and *B. velezensis* Bve2, significantly reduced the total numbers of *R. reniformis* eggs at 45 days after planting on soybean under controlled conditions, while Bmo3 also significantly increased plant biomass during the same timeframe. In soybean field trials, the strain Bmo3 significantly reduced *R. reniformis* eggs/g root at 45 days after planting and was statistically equivalent to the chemical nematicide abamectin [64]. Lira et al. [65] investigated the biocontrol potential of filtrates from *Fusarium inflexum*, *Thielavia terricola*, *T. longibrachiatum*, *T. brevicompactum*, *T. harzianum*, *Penicillium citrinum*, and two new *Penicillium* species, and reported promising nematicidal and hatch-inhibitory activities. These fungi caused nematode mortalities that ranged from 58 to 100% and only 5 to 20% of juveniles hatched in the in vitro tests. The same authors performed in vivo tests with coriander and cowpea and concluded that filtrates from the aforementioned fungi significantly reduced the number of egg masses and the reproduction factor of *R. reniformis* [65].

6. Fanleaf Virus Nematode (FVN), Xiphinema index

Xiphinema spp., also known as dagger nematodes, are considerably larger than most PPNs and are exclusively ectoparasites. Some species of *Xiphinema* are virus vectors and can transfer them to the plant host upon feeding [66][67]. For instance, *Xiphinema* spp. can cause the death of important crops by spreading viral mosaic and wilting diseases, thereby leading to significant economic losses [68]. *Xiphinema index* has gained particular attention because it vectors the *Grapevine fanleaf virus*, one of the most serious viruses of grapevine [69], but also due to its widespread distribution across the globe [67][70][71][72]. Although *X. index*'s most important hosts are grapevine and fig, it is known to parasitize other plants [73]. The nematode's feeding activity causes poor root extension, resulting in swelling and gall formation, and leading to the reduced growth of infected plants.

Aballay et al. [74] explored the potential for the biocontrol of bioformulations containing different combinations of rhizobacterial agents on *X. index* on grapevine under greenhouse conditions. They showed that the powder formulation with *Brevibacterium frigoritolerans*, *B. megaterium*, *B. thuringiensis*, and *B. weihenstephanensis* was the most effective, which was comparable to the effect of the chemical nematicide Rugby® 200 CS (cadusafos) in suppressing the nematode [74]. On the other hand, Aballay et al. [74] noted that all the tested microbial agents and formulations, regardless of combination and type, decreased the severity of damage produced by *X. index*.

7. Other Economically Important Plant-Parasitic Nematodes

Between 2018 and 2022, biocontrol research on *R. similis*, *D. dipsaci*, *N. aberrans* and *A. besseyi* has been very limited, despite their economic relevance.

The burrowing nematode (BN), *R. similis*, is a polyphagous, migratory endoparasite, globally widespread but occurring mostly in tropical and subtropical regions, especially where bananas are grown. The BN can also be very destructive in citrus orchards and black pepper, among other horticultural crops [75]. The juvenile stages and adult females of *R. similis* are infective; contrastingly, males have an atrophied stylet and are non-parasitic to plants. Thammaiah et al. [76] combined two bacteria species, *B. subtilis* and *P. fluorescens*, with *P. lilacinus* to manage *R. similis* on banana. Both treatments were effective in nematode reduction, yet the best results were obtained when applying the chemical nematicide carbofuran [76].

Within the Anguinidae family, the stem and bulb nematode (SBN), *D. dipsaci*, is characterized by attacking a wide range of field crops, like broad bean, corn, garlic, onion, sugar beet, and ornamental plants, such as narcissus and tulips, to name a few [77]. This species is well-adapted to temperate conditions, specifically when humidity is adequate. *Ditylenchus dipsaci* is highly tolerant to desiccation, in contrast with other PPNs. While studying the interaction between two garlic pathogens, *D. dipsaci* and *Fusarium oxysporum* f. sp. *cepae*, McDonald et al. [78] unexpectedly reported that their combined effect was less severe in the bulb than when present separately. In fact, the inoculation of *F. oxysporum* after *D. dipsaci* reduced the disease severity index from 61.1 (combined application) to 8.3, suggesting either an antagonistic effect between both pathogens or a defensive response from the plant host [78]. Turatto et al. [11] described the reduced motility (>50%) of *Ditylenchus* spp. in vitro when inoculated with *Bacillus* sp. CBSAL02 and *Pseudomonas* sp. CBSAL05 strains.

Nacobbus aberrans, also known as the false root-knot nematode (FRK), produces galls that are similar in appearance to those caused by RKNs and is therefore often misdiagnosed based on symptoms alone. The FRK was originally described in the American continent and should be regarded as a species complex, due to the high molecular variability among populations and difference in host range. Wong-Villarreal et al. [79] and Méndez-Santiago et al. [80] reported the use of *Serratia ureilytica* and *Serratia* sp. as good candidates for the management of *N. aberrans*. Bernardo et al. [81] reported the efficacy of the arbuscular mycorrhizal fungus *Rhizophagus intraradices* B1 as a promising candidate for biocontrol.

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