Chapter 9
Eco-friendly Approaches to the Management of Plant-Parasitic Nematodes

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Abstract Eco-friendly approaches have been increasingly used for the management of plant-parasitic nematodes because of growing worldwide concern regarding health risks and environmental contamination caused by nematicides. Avoiding the introduction and spread of nematodes to non-infested areas is the most efficient method of control. Cleaning machinery and equipment, use of healthy planting materials, and quarantine procedures are good examples of preventive practices. In infested fields, nematode populations can be reduced by combining cultural, physical, and biological methods and genetic resistance of plants. The use of resistant crops is one of the most efficient and eco-friendly methods for reducing losses caused by plant-parasitic nematodes. Based on the information on which nematode species/races are prevalent in the field, the grower should choose a resistant crop, when available. Soil plowing and irrigation – named humid fallow – have been used for the management of root-knot nematodes in common bean (*Phaseolus vulgaris*), lettuce (*Lactuca sativa*), and okra (*Abelmoschus esculentus*) in Brazil. Soil steaming, treatment of planting materials with hot water, and soil solarization are recommended for the control of several plant-parasitic nematode species, based on the lethal action of high temperatures. Biofumigation with residues from some species

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of Brassicaceae and manures releases volatile toxic gases during the degradation process of the organic matter, including isothiocyanates. Non-host or antagonistic plants are also important tools for the integrated management of nematodes. In this context, marigolds (*Tagetes erecta* and *T. patula*), crotalaria (*Crotalaria spectabilis*), sunn hemp (*Crotalaria juncea*), and velvet bean (*Mucuna pruriens*) are widely used as antagonistic plants. Soil amendment with crop residues of neem (*Azadirachta indica*), castor bean (*Ricinus communis*), velvet bean (*Mucuna pruriens*), crotalaria (*Crotalaria spectabilis*), and *Brassica* spp.; oil seed cakes of neem, castor bean, mustard, and sesame; cattle manure; poultry litter; liquid swine manure; and crab shells release nematotoxic substances during decomposition, provide nutrients to the plants, and increase the population of biocontrol agents. More than 200 species of nematode antagonists have been identified, including fungi, bacteria, nematodes, tardigrades, and collemboles. Fungi and bacteria are the most studied and commercially exploited organisms for nematode control. Several commercial bionematicides have been developed from the nematode-trapping fungi *Arthrobotrys*, *Dactylaria*, *Dactylella*, and *Monacrosporium*, the egg-parasitic fungi *Purpureocillium lilacinum* and *Pochonia chlamydosporia*, the antibiotic bacterium *Bacillus* species, and the obligate parasite bacterium *Pasteuria* spp. The anaerobic soil disinfestation is an ecological alternative to soil fumigation for the control of several soilborne pathogens, including nematodes. This technique consists of incorporating organic material that is easily decomposable (C/N ratio from 8 to 20:1) into the soil, irrigating to saturation, and covering the soil with oxygen-impermeable plastic. Accumulation of toxic products from anaerobic decomposition, antagonism by anaerobic organisms, lack of oxygen, and the combination of all of them are the main drivers that explain the efficacy of anaerobic soil disinfestation. Consumers have been demanding higher food security and environmental quality, and this situation will not be different in the future. In this context, scientists' efforts in discovering new nonchemical strategies for nematode control and improvements in the current methods must be continuous.

Keywords Cyst nematode · Lesion nematode · Nematode control · Root-knot nematode · Sustainable agriculture · Sustainable management

9.1 Introduction

Over 4100 species of nematodes parasitize cash and subsistence crops in all continents (Decraemer and Hunt 2006). Losses caused by nematodes in agriculture are estimated to be between US$78 and 125 billion per year (Sasser and Freckman 1987; Nicol et al. 2011). They can cause direct damage to their host and facilitate subsequent infestation by secondary pathogens; besides, some nematodes are vectors of plant viruses (Nicol et al. 2011; Lopes and Ferraz 2016). Most plant-parasitic nematode species spend all their life-span in soil, feeding on host roots (Lopes and Ferraz 2016). Like other soilborne pathogens, nematodes are difficult to control. In general, nematodes are not eradicated from an infested field, and more than one control method is needed to reduce their population to levels that do not cause economic losses (Ferraz et al. 2010). Because of growing worldwide concern regarding health risks and environmental contamination caused by chemical pesticides, eco-friendly approaches have been increasingly used for the management of plant-parasitic nematodes instead of nematicides. Preventive practices; physical, biological, and cultural methods; and genetic resistance of plants are nonchemical strategies that can be used for nematode management, as will be shown in this chapter. All these strategies will be discussed separately here, although they should be applied as part of an integrated management system.

9.2 Preventive Practices

Avoiding the introduction and spread of nematodes to non-infested areas is the most efficient method of control. Cleaning machinery and equipment, use of healthy planting materials, and quarantine procedures are good examples of preventive practices.

Agricultural implements, machinery, vehicles, and tools can carry nematode-infested soil. In Brazil, infested soil adhered to machinery, equipments, and vehicles was the major driver for the dispersal of *Heterodera glycines* throughout soybean-growing areas (Silva 1999). The first reports of this nematode in Brazil date from 1991 to 1992 in six municipalities in the central region of the country. Five years later, the nematode was found in 98 municipalities, covering an area of two million hectares, including states in the South and Southeast (Silva 1999). To avoid nematode dispersal, farmers must use machinery and implements first in non-infested areas before they can be used in infested fields. Besides, soil must be washed off machinery, vehicles, tools, and implements right after the work in the field (Ferraz et al. 2010).

Long-distance dispersal of nematodes also occurs efficiently via planting materials, such as seeds, seedlings, cloves, tubers, cuttings, and rootstocks. *Anguina tritici*, *Aphelenchoides besseyi*, and *Ditylenchus dipsaci* are instances of nematodes that can survive longer than 10 years within seeds or cloves. Cysts of *H. glycines* also can be found mixed with soybean seeds. *Meloidogyne exigua*, *M. incognita*, *M. paranaensis*, and *M. coffeicola* have become widespread in coffee-growing areas in Brazil via infected seedlings. Thus, farmers must use only nematode-free planting materials.

Quarantine procedures are important to limit nematode spread to new areas. The list of major plant-parasitic nematodes of quarantine importance worldwide is led by the potato cyst nematode, *Globodera rostochiensis* and *G. pallida* (Lehman 2004). The exclusion of plants if accompanied by prohibited articles (soil, hay, straw, forest litter, etc.), the prohibition of all known host plants of nematodes that may represent risks for local agriculture, and the requirement of phytosanitary certificates are key actions to avoid the introduction of quarantine nematodes (Lehman 2004). For instance, South Africa excludes 270 hosts to indirectly exclude *Aphelenchoides* *besseyi*, *Ditylenchus dipsaci*, and *Radopholus similis* (Lehman 2004). In Minas Gerais state, which accounts for more than half of the coffee production in Brazil, the production, commercialization, and transit of coffee seedlings within the state are regulated to avoid dispersal of root-knot nematodes (Ferraz et al. 2010).

9.3 Clean Fallow

Plant-parasitic nematodes are biotrophs, and the longer host plants (crops, volunteer plants, or weeds) are absent from the soil, the lower is the survival of these nematodes in the soil. Weeds can be alternative hosts of nematodes (Rich et al. 2009; Godefroid et al. 2017), and they must be mechanically removed or killed by herbicides. This technique is most effective in the hot and dry summer months between crops (Sikora et al. 2005). However, soil erosion and the costs of keeping the soil free of weeds and crops limit the use of clean fallow.

9.4 Soil Plowing and Humid Fallow

High temperatures and low soil moisture cause desiccation of eggs and vermiform stages of nematodes. Most plant-parasitic nematodes are found up to 30 cm beneath the soil surface. For this reason, soil plowing at a depth of 30 cm during dry and warm seasons reduces nematode populations by exposing them to the deleterious effects of desiccation. Dutra and Campos (1998), for instance, reported the reduction of second-stage juveniles of *M. javanica* by more than 50% after soil plowing. The benefit of this operation is more pronounced when the field is left without any crop or weeds. However, the occurrence of erosion and soil disruption are among the main disadvantages of this approach.

Soil plowing and irrigation – called humid fallow – have been used in Brazil for the management of *M. incognita* in common bean (Dutra and Campos 2003a) and of *M. javanica* in okra (Dutra and Campos 2003b) and lettuce (Dutra et al. 2003). The second-stage juvenile (J_2) of root-knot nematode develops, hatches, and moves in the soil until it reaches a root of a host. Under favorable conditions of temperature and soil moisture, these events happen in about 14 days (Campos et al. 2005). Under adverse conditions, juveniles do not hatch, which ensures nematode survival. However, irrigating the soil to field capacity will stimulate J_2 to hatch if soil temperature is in the range of 21–30 °C. If the field is maintained without host plants for 2 weeks or longer, juveniles will consume much of their body reserves and will die of starvation (Van Gundy et al. 1967).

Irrigation and soil plowing must be done on hot and dry days (Campos et al. 2005). Plowing does not need to be deep, and irrigation must be enough to raise soil moisture to field capacity. In a common bean field infested with 60 J_2 of *M. incognita* per 100 cm^3 of soil, grain yield was four times higher in plots where humid fallow was used in comparison to non-plowed and non-irrigated plots (control) (Campos et al. 2005). Plowed and irrigated plots were maintained free of weeds for 14 days, when common bean was sown. The costs of this tactic were only 4% of those spent by applying the nematicide aldicarb (Campos et al. 2005).

9.5 Heat-Based Methods to Control Plant-Parasitic Nematodes

Most plant-parasitic nematodes die when exposed to soil temperatures exceeding 45–50 °C for 1 h or less (Tsang et al. 2003; Wang and McSorley 2008). Sublethal temperatures (38–45 °C) may also cause nematode death, but a longer exposure time is required (Wang and McSorley 2008). The lethal action of high temperatures is the core principle behind the efficiency of the use of steam, treatment of planting materials with hot water, and soil solarization in the control of plant-parasitic nematodes.

9.5.1 Steam

Soil steaming is used in several countries as an alternative for soil treatment in glasshouses, seed beds, and small areas (Ferraz et al. 2010; Marbán-Mendoza and Manzanilla-López 2012). Temperatures over 70 °C can be reached with this technique and can inactivate propagules of various pathogens, weeds, and insects, as well as part of the beneficial soil microbiota. One of the disadvantages of the method is the formation of phytotoxic substances in the heated soil, such as soluble salts, ammonia, and manganese (Ferraz et al. 2010). Ideally, a waiting period of 20–40 days is required before planting to eliminate phytotoxic compounds (Tihohod 1993). The costs of this method can also be a limitation on its use, including equipment, pipes, water, and fuel or electricity (Marbán-Mendoza and Manzanilla-López 2012).

9.5.2 Treatment of Planting Materials with Hot Water

The immersion of plant material (seeds, bulbs, cloves, seedlings, tubers, rootstocks) in hot water for a certain period may inactivate nematodes. The success of the treatment depends on the adjustment of the binomial water temperature-treatment time. High temperatures may kill nematodes but also damage plants. Thus, sublethal temperatures can be used for a longer period, without any damage to the plants. Immersion of plant materials into cold water prior to hot water treatment can reactivate quiescent juveniles and enhance the effect of the heat on nematodes. For instance, pre-soaking

Table 9.1 Examples of hot water treatments for the control of nematodes in planting materials

Crop	Planting material	Nematode	Temperature/time
Solanum tuberosum	Tuber	*Meloidogyne* spp.	46–47.5 °C/120 min
		Pratylenchus coffeae	52 °C/15–20 min or 53 °C/10–15 min
Vitis vinifera	Rootstock	*Meloidogyne* spp.	54.4 °C/3 min; 50 °C/10 min or 47.8 °C/30 min
		Xiphinema index	52 °C/5–10 min
Triticum aestivum	Seed	*Ditylenchus* sp.	54 °C/15 min
Musa spp.	Rhizome	*M. incognita; Helicotylenchus multicinctus; Pratylenchulus brachyurus; Radopholus similis*	55 °C/20 min
Citrus spp.	Rootstock	*Tylenchulus semipenetrans*	49 °C/10 min 45 °C/25 min
Dioscorea spp.	Tuber	*Meloidogyne* spp.	51 °C/30 min
		Scutellonema bradys	50–55 °C/40 min
Allium sativum	Clove	*D. dipsaci*	45 °C/20 min
Allium cepa	Bulb	*D. dipsaci*	44–45 °C/180 min

Adapted from Ferraz et al. (2010)

rice seeds in cold water for 18–24 h before immersing them in water at 51–53 °C for 15 min controls *Aphelenchoides besseyi* (Bridge and Starr 2007).

Results using this approach can vary, depending on the plant species and cultivar, nematode inoculum density, and the conditions of the treatment. Examples of recommended treatments for nematode management in planting materials are described in Table 9.1.

9.5.3 Soil Solarization

This technique consists of mulching a wet soil with transparent plastic film (50–200 μm thick) during periods of higher solar incidence. Lethal and sublethal temperatures can be reached in the first weeks of the treatment, inactivating nematodes (Table 9.2) and other soilborne pathogens, as well as insects and weeds (Katan and Gamliel 2011). Soil warming also can weaken plant pathogens and increase the population of biological control agents (Katan and Gamliel 2009).

The soil usually remains covered for 4–8 weeks (Katan and Gamliel 2011). The soil must be prepared by harrowing, plowing, and removing sharp objects. Then, the soil is irrigated to field capacity and covered with plastic. The water in the soil activates pathogen propagules and enhances heat conduction. The borders of the plastic should be buried to avoid heat loss.

Table 9.2 Control of plant-parasitic nematodes by soil solarization

Nematode	Crop	Time (days)
Meloidogyne javanica, *M. incognita*	Cucumber	35–60
M. incognita	Olive	21
Meloidogyne spp.	Tomato	21–60
M. javanica	Okra	139
M. javanica, R. reniformis, *Paratrichodorus minor*, *Mesocriconema* spp.	Tomato	32–42
Globodera rostochiensis	Potato	62–63
Meloidogyne spp.	Eggplant	30–60
Pratylenchus thornei	Chickpea	28–56
M. incognita, *M. javanica*	Pepper	45
R. reniformis	Lettuce, cowpea	28–56
P. thornei	Potato	31

Adapted from Ferraz et al. (2010)

In this method, the solar radiation is trapped under the plastic film and raises the temperature of superficial layers of the damp topsoil (up to 20 cm deep) (Katan and Gamliel 2011). During the warmest periods of the year, temperatures in solarizated soil usually range from 35 to 60 °C (DeVay 1991). However, the temperature and the efficiency of the control decrease with depth in soil profile (Katan and Gamliel 2011), which means that soil has to be kept covered for longer periods of time. The efficiency of solarization depends on the occurrence of high temperatures and high luminous intensity. In temperate regions or during cooler times of the year, this technique may not be efficient. The costs of plastic tarp can also limit its use in larger areas.

The thickness of the plastic tarp has no direct influence on the solarization efficiency (Katan and Gamliel 2009). The most used plastic films range from 50 to 150 μm. Thin films (25–30 μm) tend to tear easily. The thicker ones are more expensive; however, they can be reused (150–200 μm). Double layers of plastic can increase control efficiency, increasing soil temperature by more than 10 °C (Katan and Gamliel 2009), although the costs of treatment are also increased.

9.6 Biofumigation

The incorporation of certain organic amendments into the soil, especially residues from some species of Brassicaceae and manures, releases volatile toxic gases during the degradation process of the organic matter. The suppression of pests and pathogens by the release of biocide compounds into the soil is called “biofumigation,” because of the microbial decomposition of organic amendments (Kirkegaard et al.

1998). The soil must have sufficient moisture for intense microbial activity and decomposition of organic amendments.

For better results from biofumigation, it is essential to prevent the escape of volatile toxic compounds from the soil. Therefore, the soil can be covered with transparent plastic immediately after crushing and incorporating the organic materials. Alternatively, superficial layers of soil may be compacted with rollers. Transparent plastic cover increases soil temperature and accelerates the degradation of the residues (Kirkegaard et al. 1998; Gamliel et al. 2000). Therefore, the association of biofumigation with solarization may have a synergistic effect on the control of nematodes, and the time that the soil remains covered may be reduced. Thicker plastics (100–150 μm) are recommended for use in biofumigation to avoid the occurrence of holes and the loss of volatile toxic substances. Increasing the population of biological control agents of nematodes is an additional benefit of biofumigation. For example, biofumigation with chicken manure controlled *M. incognita* in lettuce, and the rhizosphere of lettuce plants was rapidly colonized by species of *Bacillus* and *Pseudomonas* after removing soil cover (Gamliel and Stapleton 1993).

The residue of Brassicaceae (*Brassica* spp.) has been the most studied organic material for biofumigation, due to a range of toxic substances released during its decomposition. Brassica plants are rich in glucosinolates, which are hydrolyzed by myrosinase into degradation products, such as isothiocyanates and nitriles (Brown and Morra 1997). Glucosinolates are nontoxic compounds, but isothiocyanates are toxic to nematodes and other soilborne pathogens, such as *Fusarium oxysporum* f. sp. *lycopersici*, *Macrophomina phaseolina*, *Sclerotium rolfsii*, *Pythium ultimum*, and *Ralstonia solanacearum* (Stapleton et al. 1998; Njoroge et al. 2009; Bensen et al. 2009). Papaya seeds are also rich in glucosinolates, and amending soil with this material controls root-knot nematode (Neves et al. 2012). Other organic amendments can also be used in biofumigation for the management of nematodes, such as residues of neem (*Azadirachta indica*), castor bean (*Ricinus communis*), velvet bean (*Mucuna pruriens*), crotalaria (*Crotalaria* spp.), marigold (*Tagetes* spp.) (Gamliel et al. 2000), chicken litter (Leon et al. 2000), and cattle manure (Leon et al. 2001).

9.7 Crop Rotation and Antagonistic Plants

Non-host or antagonistic plants have been used to control nematodes for decades. Nematodes are unable to penetrate the roots of non-host plants. Antagonistic plants can limit nematode penetration by releasing repellent substances into the rhizosphere. Some plants allow nematodes to penetrate the roots, but they do not develop to adult stages. Examples of crops recommended for the control of soybean cyst nematode (*Heterodera glycines*), root-knot nematode (*Meloidogyne incognita* and *M. javanica*), reniform nematode (*Rotylenchulus reniformis*), and lesion nematode (*Pratylenchus brachyurus*) are presented in Table 9.3.

Table 9.3 Antagonistic and non-host plants of *Heterodera glycines* (Hg), *Meloidogyne javanica* (Mj), *Meloidogyne incognita* (Mi), *Rotylenchus reniformis* (Rr), and *Pratylenchus brachyurus* (Pb)

	Nematode				
Crop	Hg	Mj	Mi	Rr	Pb
Black oat	–	+	+	–	±
Pearl millet	–	±	+	–	±
Soybean	+	+	+	+	+
Brachiaria	–	–	–	–	+
Forage sorghum	–	±	±	–	+
Sunflower	–	+	+	–	±
Corn	–	±	+	–	+
Sorghum	–	±	+	–	+
Cotton	–	–	+	+	+
Sugarcane	–	+	+	–	+
Peanut	–	±	–	–	+
Common bean	+	+	+	+	+
Cowpea	+	+	±	±	+
Cassava	–	+	+	+	+
Rice	–	+	+	–	+
Crotalaria spectabilis	–	–	–	–	–
Crotalaria breviflora	–	–	–	–	–
Crotalaria juncea	–	±	±	–	+
Mucuna pruriens	–	±	±	–	+

Adapted from Inomoto and Asmus (2009). (+) Crop increases nematode population. (±) Variation in the response to nematode population. (–) Crop reduces nematode population

Crotalaria (*Crotalaria spectabilis*), sunn hemp (*Crotalaria juncea*), velvet bean (*Mucuna pruriens*), and marigolds (*Tagetes erecta* and *T. patula*) are widely recommended to reduce nematode populations in the soil. *Crotalaria* species and *M. pruriens* have the advantage of producing large amounts of N-rich biomass, acting as green manure, and increasing the soil population of biocontrol agents (Inomoto and Asmus 2014).

Care must to be taken in choosing cover crops or non-host plants to manage nematodes. Certain crops can suppress a prevalent nematode in the field, but they can allow the reproduction of other nematodes. For instance, cotton following soybean in a rotation system will reduce the *M. arenaria* population, but will favor the reproduction of *Pratylenchus brachyurus*, *Rotylenchus reniformis*, and *M. incognita* races 3 and 4 (Ferraz et al. 2010). Thus, local nematode species and their population levels in the field must be known before recommending crops for the management system.

The nematode population can be reduced by half after one cycle of a non-host plant. The population of *R. reniformis* declined from 1102 to 581 nematodes per 200 cm^3 of soil when rye was cultivated following cotton (Asmus and Ishimi 2009). Reproduction factors (RF) of the reniform nematode were about 0.4 and 0.18 in the first and second years of rotation with corn, respectively (Asmus and Richetti 2010). In the case of highly susceptible crops, the nematode population must be at low densities in the field to prevent significant losses. Then, longer periods of rotation may be needed. In the Alto Paranaiba region, a major vegetable production area in Brazil, forage grasses (*Brachiaria decumbens* and *B. ruziziensis*) are cultivated for 2 or 3 years in *Meloidogyne*-infested fields before growing carrots, potato, and red beet.

Host status for nematodes may vary across species within the same genus of plants or among cultivars from the same species. Borges et al. (2010) reported that black oat (*Avena strigosa*) was highly resistant to *P. brachyurus* (RF < 1.0), while Algerian oat (*A. byzantina*) and white oat (*A. sativa*) were susceptible to the nematode (RF from 1.93 to 2.63). However, none of these three types of oats were resistant to *M. incognita* (Borges et al. 2009). Thus, they are not recommended as cover crops in fields with mixed populations of *P. brachyurus* and *M. incognita*. In another study, silage sorghum cultivar BRS 601 was resistant to *M. javanica*, while the cultivars IPA 7301011, BRS 700, and BRS 701 were good hosts (Inomoto et al. 2008).

9.8 Organic Amendments

The nematicidal effect of various materials has been widely reported. Soil amendment with crop residues, animal manure, composts, cakes from oil pressing, chitinous wastes, and other organic materials can release nematotoxic substances during decomposition, increase the population of biocontrol agents, and provide nutrients to the plants. Examples of nematicidal organic amendments are crop residues of neem (*Azadirachta indica*), castor bean (*Ricinus communis*), velvet bean (*Mucuna pruriens*), crotalaria (*Crotalaria spectabilis*), and *Brassica* spp.; oil seed cakes of neem, castor bean, mustard, and sesame; cattle manure; poultry litter; liquid swine manure; and crab shells (Ferraz et al. 2010; Stirling 2014). The organic material added into the soil can act as a soil conditioner, improving biological, chemical, and physical properties of soil. As a result, plants tend to be more tolerant to nematodes (Hoitink and Fahy 1986; McSorley and Gallaher 1995; Ritzinger and McSorley 1998; Bridge 2000). The combination of soil amendment with crucifer residues or animal manures and solarization enhances nematode suppression (Gamliel et al. 2000; Ferraz et al. 2010).

In general, organic amendments with C/N ratio from 14 to 20/1 have nematicidal properties and do not limit plant development (Rodríguez-Kábana et al. 1987). Materials with C/N ratio below 12 can be phytotoxic, and above 23 they are nontoxic to nematodes (Rodríguez-Kábana et al. 1987).

The use of organic amendments can be limited by the amount required for nematode control, usually from 4 to 10 ton ha^{-1} (Rodríguez-Kábana et al. 1987). As pointed out by Marbán-Mendoza and Manzanilla-López (2012), high transport costs, the lack of large-scale manufacturing, and inconsistency in production parameters are other limitations of using organic amendments to manage plant-parasitic nematodes. Application of organics either individually or in consortium of different living organisms may act as soil conditioner leading to ameliorated plant health (Ansari and Mahmood 2017).

9.9 Biological Control

Natural enemies can suppress plant-parasitic nematodes in the soil. More than 200 species of nematode antagonists have been identified, including fungi, bacteria, nematodes, tardigrades, and collemboles (Stirling 2014). Fungi and bacteria are the most studied and commercially exploited organisms for nematode control (Table 9.4).

Experimental and commercial bioproducts based on the nematode-trapping fungi *Arthrobotrys*, *Dactylaria*, *Dactylella*, and *Monacrosporium* and the egg-parasitic fungi *Purpureocillium lilacinum* and *Pochonia chlamydosporia* have been produced for the control of nematodes in several countries (Stirling 2014). These fungi can survive saprophytically in soil, and they can be mass-produced using cheap materials (Stirling 2014).

In Brazil, a commercial bionematicide based on chlamydospores of *Pochonia chlamydosporia* has been used for the management of nematodes in banana (Freitas et al. 2009), carrot (Bontempo et al. 2014, 2017), and lettuce (Dallemole et al. 2013). An experimental formulation based on a mixture of *Arthrobotrys robusta*, *Arthrobotrys oligospora*, *Arthrobotrys musiformis*, *Dactylella leptospora*, and *Monacrosporium eudermatum* controlled *Pratylenchus jaehni* in orange orchard (Martinelli et al. 2012).

Bacillus and *Pasteuria* have been widely studied for biological control of nematodes (Chen and Dickson 2012; Zhou et al. 2016; Rao et al. 2017). Several commercial bionematicides have been developed from *Bacillus* species (Table 9.4). *Bacillus* species are easily mass-produced in vitro; they form resistant endospores and have a broad range of activity against nematodes, such as producing toxins, inducing host resistance, and altering root exudates (Chen and Dickson 2012). In recent research, liquid formulations based on *Bacillus* species controlled *M. incognita* in tomato (Zhou et al. 2016) and carrot (Rao et al. 2017) in field conditions.

Pasteuria parasitizes juveniles and adults of plant-parasitic nematodes, including *Meloidogyne* spp. (parasitized by *Pasteuria penetrans*), *Pratylenchus* spp. (parasitized by *P. thornei*), *Heterodera* spp. and *Globodera* spp. (parasitized by *Pasteuria nishizawae*), and *Belonolaimus longicaudatus* (parasitized by *Candidatus Pasteuria* usage). *Candidatus* P. hartismerei and *Candidatus* P. goettingianae are species with provisional names described as parasites of the plant-parasitic nematodes *Meloidogyne ardenensis* (Bishop et al. 2007) and *Heterodera goettingiana* (Sturhan et al. 1994), respectively. *Pasteuria penetrans* is by far the most studied species of this bacterium (Chen and Dickson 2012). It has been used as a biological control agent of different species of *Meloidogyne* (Freitas et al. 2009; Chen and Dickson 2012). In a 102.4-hectare plantation of jaborandi (*Pilocarpus microphyllus*) in Brazil, a single application on the soil surface (treated area of 170 m^2) of tomato root powder suspension with endospores of *P. penetrans* (10^3 endospores/g of soil at 20 cm depth) controlled *M. incognita* (Freitas et al. 2009). Two years after the application, the soil was suppressive to the nematode (Freitas et al. 2009). For research purposes, large-scale production of *Pasteuria* endospores has been achieved by

Table 9.4 Bionematicides on the worldwide market

Biocontrol agent	Mechanism of action	Product	Company	Country
Arthrobotrys oligospora	Nematode-trapping fungus	Nematofagin	Mycopro	Russia
Arthrobotrys oligospora, *Arthrobotrys botryospora*	Nematode-trapping fungus	Nemout 0.65 WP	Agri - Mart Inc.	USA, Costa Rica
Arthrobotrys sp., *Glomus* sp., *Pochonia* sp.	Multi-spectrum activity	Pochar	Microspore Green Biotechnology	Italy
Bacillus spp.	Antibiotic bacterium	Nemato-Cure	Biotech International Ltd.	India
Bacillus amyloliquefaciens	Antibiotic bacterium	Nemacontrol	Simbiose	Brazil
Bacillus chitinosporus	Antibiotic bacterium	Biostart	Microbial Solutions	South Africa
Bacillus chitinosporus, *B. laterosporus*, *B. licheniformis*	Antibiotic bacterium	Biostart Rhizoboost	Rincon-Vitova	USA
Bacillus firmus	Antibiotic bacterium	BioNemaGon	Agri Life	India
Bacillus firmus	Antibiotic bacterium	BioNem WP, BioSafe	Agrogreen	Israel
Bacillus firmus	Antibiotic bacterium	Andril, Nortica, Oleaje, Poncho, Vortivo	Bayer	USA, Brazil
Bacillus licheniformis, *B. subtilis*	Antibiotic bacterium	Presence, Quartzo	FMC Química do Brasil Ltda	Brazil
Burkholderia cepacia	Antibiotic bacterium	Deny	Stine Microbial Products	USA
Mycorrizhal fungi	Endophytes	Prosper-Nema	Circle One, Inc.	USA
Myrothecium verrucaria	Antibiotics produced by the fungus	DiTera	Valent	USA
Pasteuria nishizawae	Obligate parasite of J_2 to adult	Clariva	Syngenta	USA
Pochonia chlamydosporia	Egg-parasitic fungus	Rizotec	Rizoflora Biotecnologia S.A.	Brazil
Pochonia chlamydosporia	Egg-parasitic fungus	Xianchongbike	Tianjin Blue Ocean Chemical Co. Ltd.	China
Pochonia chlamydosporia	Egg-parasitic fungus	KlamiC	CENSA	Cuba

(continued)

Table 9.4 (continued)

Biocontrol agent	Mechanism of action	Product	Company	Country
Pochonia chlamydosporia	Egg-parasitic fungus	PcMR-1	Clamitec-Myco-Solutions Ltd.	Portugal
Purpureocillium lilacinum	Egg-parasitic fungus	Biomyces	Bio Tropical S.A.	Colombia
Purpureocillium lilacinum	Egg-parasitic fungus	Bionemat, Nemator	Biotech International Ltd.	India
Purpureocillium lilacinum	Egg-parasitic fungus	Bio-Nematon	T. Stanes & Company Ltd.	India
Purpureocillium lilacinum	Egg-parasitic fungus	Bioniconema	Nico Orgo Manures	India
Purpureocillium lilacinum	Egg-parasitic fungus	BiostatWP	Bayer	Chile
Purpureocillium lilacinum	Egg-parasitic fungus	Mytech	Lachlan Kenya	Kenya
Purpureocillium lilacinum	Egg-parasitic fungus	Nemakontrol	Solagro	Peru
Purpureocillium lilacinum	Egg-parasitic fungus	Nemata	Live Systems Technology	Colombia
Purpureocillium lilacinum	Egg-parasitic fungus	Nematofree	International Panaacea Ltd.	India
Purpureocillium lilacinum	Egg-parasitic fungus	BioAct	BioAct Corp.	The Philippines
Purpureocillium lilacinum	Egg-parasitic fungus	BioAct	Biotech Resources for Agriculture and Industry, Inc.	The Philippines
Purpureocillium lilacinum	Egg-parasitic fungus	BioAct WG, Nemacheck	Australian Technology Innovation Corp.	Australia
Purpureocillium lilacinum	Egg-parasitic fungus	BioAct	Intrachem Bio Itala	USA
Purpureocillium lilacinum	Egg-parasitic fungus	Xianchongquaike	Beijing Zhengnong Agri-Tech Co. Ltd.	China
Purpureocillium lilacinum	Egg-parasitic fungus	BioAct WG, MeloCon, Paecil, Nemout WP	Prophyta	Germany
Purpureocillium lilacinum	Egg-parasitic fungus	Yorker	Agriland Biotech Ltd.	India
Purpureocillium lilacinum	Egg-parasitic fungus	FB Nemakill	Parama Agri Clinic	India
Purpureocillium lilacinum	Egg-parasitic fungus	Paecil	Shakti Biotech	India
Purpureocillium lilacinum	Egg-parasitic fungus	Bio-nematicide	ANC Enzyme Solutions Pte Ltd.	Singapore

(continued)

Table 9.4 (continued)

Biocontrol agent	Mechanism of action	Product	Company	Country
Purpureocillium lilacinum	Egg-parasitic fungus	PIPlus	Biological Control Products	South Africa
Purpureocillium lilacinum	Egg-parasitic fungus	PL Gold	Becker Unerwood Co.	South Africa
Purpureocillium lilacinum	Egg-parasitic fungus	MeloCon	Certis	USA
Pseudomonas fluorescens	Antibiotic bacterium	Sudozone	Agriland Biotech Ltd.	India
Streptomyces avermitillis	Toxic metabolites produced by bacterium	Abamectin	Many products	Worldwide
Trichoderma harzianum	Toxins produced by the fungus	Ecosom-TH	Agri Life	India

Adapted from Chen and Dickson (2012) and Dallemole-Giaretta et al. (2014)

growing a host plant (tomato, for instance) infected by *Meloidogyne* parasitized by *Pasteuria*. The high degree of specificity to nematode hosts and the limitation of artificial production of endospores are difficulties involved in using *Pasteuria* as a biocontrol agent (Stirling 2014). Recently, the company Pasteuria Bioscience (Florida, USA) developed a method for mass production of this bacterium. In 2012, Syngenta acquired this company. One year later, they launched a product to manage the soybean cyst nematode, based on *P. nishizawae* (Table 9.4).

9.10 Anaerobic Soil Disinfestation (ASD) or Biological Soil Disinfestation (BSD)

This ecological alternative to soil fumigation was developed in Japan (Shinmura 2000; Shinmura 2004) and The Netherlands (Blok et al. 2000) and has been used since then for the control of several soilborne pathogens, such as *Fusarium*, *Verticillium*, *Rhizoctonia*, *Sclerotium*, *Sclerotinia*, *Pythium*, *Phytophthora*, *Macrophomina*, *Ralstonia*, and nematodes (Rosskopf et al. 2014; Shennan et al. 2014; Shrestha et al. 2016). This technique consists of incorporating organic material that is easily decomposable (C/N ratio from 8 to 20:1) into the soil, irrigating to saturation, and covering the soil with oxygen-impermeable plastic (Rosskopf et al. 2014; Shennan et al. 2014). Carbon source will stimulate rapid growth and respiration of soil microbiota, reducing available oxygen. As soil pore spaces are filled with water, and the plastic cover limits inflow from the atmosphere, anaerobic conditions are created in the soil, stimulating the activity of facultative anaerobic microorganisms (Rosskopf et al. 2014; Shennan et al. 2014; Shrestha et al. 2016).

Accumulation of toxic products from anaerobic decomposition (acetic, butyric, and propionic acids, CO_2, NH_3, H_2S, CH_4, and N_2O), antagonism by anaerobic organisms, lack of oxygen, and the combination of all of them are the main drivers that explain the efficacy of ASD (Runia et al. 2014; Shennan et al. 2014).

Rice or wheat bran, soybean flour, ethanol, molasses, manure, and fresh crop residues have been assessed as carbon sources at rates ranging from 0.3 to 9 kg/m^2 (Shrestha et al. 2016). The incubation period has varied from 3 to 10 weeks (Shrestha et al. 2016). A meta-analysis published recently revealed that ASD suppresses bacterial, oomycete, and fungal pathogens by 59 to 64%, while the effect of the technique on plant-parasitic nematodes ranged from 15 to 56% (Shrestha et al. 2016). The number of studies aiming to assess the effect on nematodes was approximately seven times fewer than for other pathogens, and the authors recognized that this low number of studies influenced the evaluation of nematode suppression, with large confidence intervals due to error (Shrestha et al. 2016). They also encouraged more studies on the effect of ASD for the control of nematodes. Regarding the overall effects on pathogens, an incubation period of 3 weeks was the most effective, and amendments in liquid form (such as ethanol or liquid molasses) were more effective than solid forms.

9.11 Resistant Crops

The use of resistant crops is one of the most efficient and eco-friendly methods for reducing losses caused by plant-parasitic nematodes. Based on the information on which nematode species/races are prevalent in the field, the grower should choose a resistant crop, when available. Ideally, resistant genotypes should control nematodes, be adapted to a wide range of environmental conditions, and have high yield potential.

Resistant crops are developed through conventional breeding approaches or through molecular techniques (Fuller et al. 2008). Introgression of resistance genes from wild relatives into crop cultivars has been widely used to generate nematode-resistant crops. Many resistant crops based on this conventional approach are recommended for use in several countries. In Brazil, conventional resistant genotypes of soybean, coffee, corn, tomato, cucumber, melon, and lettuce are available for the management of nematodes (Ferraz et al. 2010; Matsuo et al. 2012). Recently, genetic engineering has emerged as a powerful approach that may provide novel and durable nematode-resistant crops. Expression of natural resistance genes in heterologous species, cloning of proteinase inhibitor coding genes, anti-nematodal proteins, and use of RNA interference to suppress nematode effectors are transgenic strategies used for nematode resistance in plants (Fuller et al. 2008; Ali et al. 2017). More details on transgenic approaches for nematode control are found in Ali et al. (2017).

Globally, most of the resistant crops available for commercial use target the control of sedentary endoparasites, such as *Meloidogyne*, *Heterodera*, and *Globodera*, or sedentary semiendoparasites, including *Rotylenchulus* and *Tylenchulus* (Roberts

2002). Few resistant genotypes have been released for the management of migratory endoparasites and ectoparasites (Peng and Moens 2003), despite the importance of species such as *Pratylenchus brachyurus*, *Radopholus similis*, *Xiphinema index*, *Ditylenchus dipsaci*, and *Aphelenchoides besseyi* (Jones et al. 2013).

Repeated use of resistant genotypes may select for virulent biotypes or cause a shift in the balance of nematode populations. Soybean cultivars resistant to *H. glycines* races 3 and 1 are widely used in Brazil. Eleven races of this nematode are found in the country (Dias et al. 2009), which increases the chance of the emergence of virulent populations when cultivars resistant to the same races are constantly used (Dias et al. 2009). In the USA, repeated cultivation of soybean cultivars resistant to *M. incognita* created a selective pressure for *M. arenaria* (Fassuolitis 1987). The use, over decades, of potato cultivars that are resistant to *G. rostochiensis* in the UK has exerted selective pressure for *G. pallida* (Thomas and Cottage 2006). Crop rotation with non-host plants should be integrated with the use of resistant crops to avoid the appearance of virulent biotypes and the population growth of other species.

9.12 Concluding Remarks

The demand for eco-friendly methods for nematode control has been increasing. Consumers have been demanding higher food security and environmental quality, and this situation will not be different in the future. In this context, scientists' efforts in discovering new nonchemical strategies for nematode control and improvements in the current methods must be continuous. Advances in biotechnology may contribute to the development of resistant crops, accurate and rapid methods for the diagnosis of quarantine-listed nematodes, and efficient protocols for the screening of biocontrol agents. Multinational companies have been increasingly interested in the production of bioproducts, and this fact may expand the availability of commercial bionematicides. Biofuel production is a potential source of organic amendments for use in agriculture. Even with several different prospects for the control of nematodes, the use of preventive practices and the combination of strategies will have a relevant place in the management of plant-parasitic nematodes.

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