

Chapter 10

Efficacy of Microbial Biocontrol Agents in Integration with Other Managing Methods against Phytoparasitic Nematodes



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Abstract Biological control can be a safe alternative to detrimental chemical nematicides if its persistence and performance increase to a satisfactory level. But at present, no biocontrol agent (BCA) can provide adequate nematode control when applied alone. One approach to improve their controlling importance is to use them in integration with one or more compatible practices that enhance BCAs' population, diversity, durability and efficacy. This goal may be achieved by combined use of BCAs with measures aiming at manipulating the soil environment in favour of BCAs, reducing nematode population and enhancing BCAs' activity. Here a brief outline of some measures for controlling phytonematode is illustrated with extra attention to those that can be applied combinedly with biological control. Their advantages and disadvantages as well as their effects on altering biocontrol activity are demonstrated along with selected examples of each tactic. The reviewed strategies in combination with biocontrol are using host plant resistance (tolerance, resistance and induced resistance); agronomic practices (rotation, trap crops, antagonistic crops, cover crops, fallow, flooding, organic amendments and tillage); decrease in phytonematode populations (soil solarisation, biofumigation and chemical nematicides); and application more than one BCA. Finally, the future paths of integrated nematode management are designed.

Keywords Antagonists · Farming practices · IPM · Nematophagous bacteria · Nematophagous fungi

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10.1 Introduction

Food production currently suffers an unprecedented pressure due to increase in the global population and inability to feed the world. It seems that the pressure will be exceedingly increased over the coming years when the population projected to reach 9.3 billion in 2050 (FAO, IFAD and WFP 2013). So, the most important challenge for agricultural industry is to provide more food in spite of diminishing fertile land, water supply and energy resources (Godfray et al. 2010; Gomiero et al. 2011; Ansari and Mahmood 2017a; Ansari and Mahmood 2019a, b). More food can be imagined in three main ways: cultivate more land; intensify the frequency of cropping; and increase the harvested yield in a given area. Several studies have evaluated the contribution of these three ways to the increase in universal food production. In a study, the contribution of more harvested yield, cultivation more land and intensified agriculture to enhancement of world food supply during 1960–1999 was estimated as 78%, 15% and 5%, respectively (Bruinsma 2003). One of the most important components of yield improvement is reducing the damage of the pests to agricultural plants. The estimated amount of losses to global agricultural production implies that plant diseases are a problem of great significance. They cause a serious threat to agricultural productivity and sustainability, and may endanger food security (Strange and Scott 2005). Phytonematodes are a group of plant pathogens whose importance is progressively understood in the last few decades. It is estimated that they now impose about 12% loss to global food production (Nicol et al. 2011). However, it should not be forgotten that indigenous phytonematodes in traditional cropping are not normally an agricultural problem. They usually turn into noxious pests in consequence of alteration in the cropping system, agricultural practices, climate, or being introduced to new regions (Sikora et al. 2005). There is a serious need to control the phytonematodes; however, the task is not easy to achieve. Many approaches can be employed to either increase the plant resistance/tolerance to phytonematodes or reduce nematode populations below its economic injury level. The main controlling method is now based on chemical nematicides which should be apparently substituted with other safer methods (Moosavi and Askary 2015). Biological control offers a safe opportunity for nematode control and many organisms have been identified with hostile activity against phytonematodes (Moosavi and Zare 2015). However, it has been recently shown that phytonematodes can defend themselves by producing antimicrobial peptides whose secretion is regulated by the nematode immunity system (Liang et al. 2019). One strategy to improve the general levels of phytonematode biocontrol is to manipulate the environment in favour of resident microbiota so enhanced their diversity and populations. In spite of its great potential, biological control takes little or no part in present phytonematode management programmes (Stirling 2014). This may be partly due to our insufficient understanding about the traits involved in efficacy of biocontrol agents (BCAs) which in turn leads to inconsistency of their effectiveness. It seems that, at least for now, no BCA can provide sufficient nematode control when implemented by itself. Therefore, a successful nematode-biocontrol programme needs more

approaches than the application of a BCA (Viaene et al. 2013). Using BCAs in an integrated programme can improve their performance against phytonematodes. The main principle of integrated pest management (IPM) is to decrease the pest population under damage threshold by using an integration of measures. These measures are chosen according to our information about pest and plant biology, environmental factors and ecological principles (Stirling 1999). Decrease in phytonematode damage in an IPM programme can be achieved by practices targeting either reducing nematode population or enhancing BCAs' activity (Hidalgo-Diaz and Kerry 2008). This chapter tries to illustrate the measures which can be used in integration with BCAs to enhance nematode control.

10.2 Using Host Plant Tolerance/Resistance

Resistant cultivars present an efficient, environmentally safe, persistent and inexpensive tactic for phytonematode control (Koenning et al. 2001; Castagnone-Sereno 2002; Starr et al. 2013) but with one disadvantage that is effective only when the soil is infested with one (important) species (Hidalgo-Diaz and Kerry 2008). This restriction is because of specificity in resistance which acts against one species of phytonematodes or even more specifically against one race of a species without any effect on other existing parasitic species (Roberts 2002). Therefore, a number of researchers believe that resistance could not be a worldwide solution to phytonematode management. Tolerant cultivars are able to endure severe pathogen infection and produce an acceptable yield (Agrios 2005). The tolerant host plants do not restrict the development of phytonematodes, so their population densities increase during growing season but the yield does not remarkably reduce (Dalmasso et al. 1992). The extent of yield loss corresponds to phytonematode initial population densities (Sikora et al. 2005). Integration of host plant tolerance or resistance with other controlling measures such as biological control could positively increase the efficacy of nematode management.

10.2.1 Host Plant Tolerance

Planting tolerant hosts in combination with BCAs makes the controlling programme of phytonematodes more efficient. The tolerant host could produce acceptable yield while robust BCAs reduce nematode populations. This will decrease the residual nematode population density in soil and consequently the initial nematode population for the next successive crop. On the other hand, decline in females' fecundity on tolerant host might delay the occurrence or selection of virulent nematode species or pathotypes (Hidalgo-Diaz and Kerry 2008; Ansari and Khan 2012a, b). Obligate parasites of phytonematodes have better efficacy on tolerant cultivars than on resistant ones. Contrary to resistant plants, the population density of nematode

which supports the establishment and multiplication of obligate parasites is higher on tolerant plants. For example, densities in soil and parasitising abilities of *Nematophthora gynophila* on cereal and sugar beet cyst nematode increased when the tolerant host of each nematode was cultivated successively (Kerry 1987). Soil suppressiveness to cereal cyst nematodes in monocultures in Western Europe may occur because of concomitant presence of fungal BCAs and partial resistance (Cook and Starr 2006). Suitable integration of tolerant cultivars of sugar beet with facultative parasites of nematode, short crop rotation and nematicide increased the efficacy of the BCAs as well. Concomitant use of mentioned measures could successfully control the first generation of sugar beet nematode (*Heterodera schachtii*) with *Pochonia chlamydosporia* and the second generation with *Cylindrocarpon destructans* (Crump 1989, 1991).

10.2.2 Host Plant Resistance

Resistance can be generated either by selecting plants with natural resistance gene (s) or by inserting new resistance gene into proper crops (Davies and Elling 2015). Several approaches are usually used for engineering resistance including expression of the inserted natural resistance genes in transgenic plants; aiming at and disruption of the initial nematode–plant interaction; aiming directly at the nematode (*Bt* & Cry proteins, plantibodies, lectins, protease inhibitors and RNA interference); and interfere with feeding site formation (Cottage and Urwin 2013). A number of major resistant (*R*) genes with the ability of conferring resistance to sedentary endoparasitic nematodes have been either cloned or mapped from agronomic or wild plants (Davies and Elling 2015). Resistance to phytonematodes may be provided by dominant, recessive, co-dominant *R* genes or by quantitative trait loci (Molinari 2011). Most of the *R* genes that have been already identified are translated to resistant proteins with a similar structure. These proteins consist of a central nucleotide-binding site (NBS) and a C-terminal leucine-rich repeat (LRR) region (Kaloshian et al. 2011). Resistant high-yielding crops offer an idle basis upon which further controlling tactics can be built (Sikora et al. 2005). Since resistance is considered as a major method for nematode management, a few researches have examined the combined effect of host resistance and BCAs. Despite scarce references, it seems that application of BCAs on resistant plants resulted in better nematode management. However, it must be taken into consideration that continuous planting of resistant cultivars often resulted in development and establishment of nematode races which could feed and colonise those resistant plants. Application of *Hirsutella rhossiliensis* on a resistant cultivar of potato to *Pratylenchus penetrans* produced synergistic effect and better nematode control was achieved compared with when each treatment was used alone (Timper and Brodie 1994).

10.2.3 Induction of Host Plant Resistance

Host plants could defend against pathogen infection through a number of different constitutive, induced and systemic defence mechanisms (Walters 2011). Induction of plant immunity system is a fascinating method for controlling phytonematodes (Leadbeater and Staub 2014; Alesadi et al. 2017). The symbiotic fungi-mediated resistance, systemic acquired resistance, induced systemic resistance, and β -aminobutyric acid-induced resistance are the suggested methods for controlling the pathogenic nematodes (Bakker et al. 2006). Plant hormones or their derivatives are considered as defence inducer molecules which could trigger the inducible defence mechanisms. Salicylic acid, jasmonic acid and ethylene are the most famous defence inducers (Conrath 2011; Takur and Sohal 2013). However, it has been illustrated that other hormones like auxins, abscisic acid, cytokinins, gibberellins and brassinosteroids have regulatory role on plant defence (Denancé et al. 2013; Moosavi 2017). Plant defences are induced by nematode attack but can also be started by exogenous application of defence inducers. Application of these molecules may decrease phytonematode invasion, development and reproduction. BCAs may control the pathogens by direct or indirect mechanisms. It has been frequently reported that BCAs can indirectly antagonise the pathogens by improving plant photosynthetic and respiratory activities (Shoresh et al. 2010) or by inducing the host plant resistance (Walters and Bennett 2014). It has been reported that endophytic fungi (non-pathogenic *Fusarium oxysporum*) could stimulate defence mechanisms in tolerant cultivars of bananas against *Radopholus similis* (Paparú et al. 2007). Similarly, *P. chlamydosporia* induced zucchini defence responses to *Meloidogyne javanica* (Lalezar et al. 2016). It has been also reported that induced resistance to nematode by BCAs is inheritable. For example, *Trichoderma atroviride* could stimulate tomato resistance against *M. javanica* which could be inherited to tomato progeny (de Medeiros et al. 2017). The combined application of BCA and defence inducer molecules will satisfactorily control the nematode while defence inducer molecule prevents initial nematode damage and the BCA provides long-term protection (Moosavi and Ghani 2019). Soil application of *P. chlamydosporia* in combination with foliar sprays of benzothiadiazole (BTH) or *cis*-jasmone reduces *Meloidogyne chitwoodi* reproduction on potato. The number of eggs per egg mass was lesser and the proportion of parasitised eggs was greater in plants treated with both the defence activators and the fungus than in the plants treated only with one of the treatments (Vieira Dos Santos et al. 2014). Conversely, integrated use of *P. chlamydosporia* with spraying tomato plants with methyl jasmonate, acibenzolar-S-methyl or ethephon reduced the ability of the fungus to lessen the gall number of *M. javanica* or activate local induced resistance (de Medeiros et al. 2015). Applying salicylic acid as a defence inducer and *Arthrobotrys oligospora* as a BCA against *M. javanica* considerably decreased diameter of nematode galls, number of galls per plant, number of egg masses per plant and number of eggs per egg mass, but their simultaneous application reduced these indices to a greater extent (Mostafanezhad et al. 2014).

10.3 Agronomic Practices

Agronomic practices have been among the most important concepts in managing phytonematodes for a long time. The involved mechanisms for nematode suppression are starvation, entrapping, antagonism, induction of soil antagonistic activity and/or biofumigation (Sikora et al. 2005). Biological control and agronomic measures can synergistically contribute in management of phytonematodes. Here a concised outline of some cultural-based tactics for controlling phytonematode is presented with emphasis on those that can be implemented integratedly with biological control. Their advantages and disadvantages along with selected examples of each tactic are included.

10.3.1 Rotation

The oldest and one of the most operational measures to manage phytonematodes is crop rotation. Succession of the crops can be temporal or spatial. Rotation of susceptible plants with non-host or poor-host provides adequate time after each susceptible host to decrease nematode population under the level which allows the next crop to grow and yield acceptably (Trivedi and Barker 1986). A crop rotation system can be successful only when resistant or tolerant plants are available for cultivation in the target agricultural systems. The host range of parasitic nematodes must also be considered for devising a practical rotational programme. Choosing a proper host plant is so difficult when the host range of the target nematode is an extensive one. Differences in host resistance to various populations of a species are another problem. However, the presence of multiple or polyphagous species of phytonematodes in a given soil restricts the ability of selecting appropriate plants for rotation (Viaene et al. 2013). When multiple species exist in soil, a non-host plant for one species might possibly be a proper host for the non-target species. Despite its deceptive simplicity, devising a specific crop rotation system for controlling phytonematodes needs much knowledge. The nematode population density is to same degree under the influence of both individual crops and their sequence in time and space (Trivedi and Barker 1986). As well, the BCA population is also affected by different plant species. Therefore, more reduction in nematode population will occur if poor or non-host plant for nematode can support the growth of BCAs (Timper 2014). Various plants secrete different root diffusates which are effective on soil and rhizosphere microbial construction. However, our knowledge about the effect of root diffusates on the performance of BCAs is so limited (Viaene et al. 2013). The needed time span between susceptible hosts or the needed number of rotational plants may be varied in relation to many factors. To recommend a rotational scheme we first need information about species, race and the host range of the local nematodes in a particular region. The host status of different crop cultivars and weeds must be determined. An understanding of nematode (species

and/or races) population dynamics on different crops, relationship of nematode populations to crop loss and the environmental effect on the population of nematodes and BCAs is also vital in developing efficient rotation schemes. The attenuation of nematode population densities during rotation differs significantly with the time, place, pathogens, weed hosts, and the nature and length of the rotation (Kratovichil et al. 2004; Viaene et al. 2013). A two- to four-year rotation programme of cultivating non-host plants usually resulted in acceptable management of economically important phytonematodes (Trivedi and Barker 1986). However, rotation is not useful where a large spectrum of nematode species exists and no rotation scheme can adequately control a wide range of nematode species on different plants (Barker 1991). On the other hand, nematode population decline in consequence of cultivating non-host plants for a long time may be detrimental to BCAs especially for obligate ones (Timper 2011; Stirling 2014). Combining rotation with biological control could reciprocally improve efficacy of both tactics when non- or poor-host rotating plants reduce nematode population densities to levels that prevent or lessen initial infection of successive susceptible host. Then application of BCAs in an augmentation or inundation strategy manages the phytonematode during the cultivation of susceptible host. Otherwise the rotation plants must be carefully selected to support the survival of the existent BCAs and therefore to maintain phytonematode suppression. There are contradictory results about the survival and maintenance of BCAs during rotation programme that emphasise on our inadequate knowledge about interactional, ecological and environmental factors which impact on BCAs' potency. It has been demonstrated that parasitism ability of *H. rhossiliensis* on motile phytonematodes depended on nematode population density (Jaffee et al. 1992). Planting susceptible cultivars of soybean to *Heterodera glycines* resulted in more parasitised juveniles (Chen and Reese 1999). But when maize- or soybean-resistant cultivars were cultivated in rotation with susceptible cultivar, the proportion of infected juveniles decreased (Chen and Liu 2007). Planting switchgrass (*Panicum virgatum*) in rotation with peanut for controlling *Meloidogyne arenaria* caused shifting in rhizosphere bacterial diversity. The shifts in bacterial community structure were connected to fluctuations in phytonematode populations (Kokalis-Burelle et al. 2002). In another experiment, *P. chlamydosporia* was applied to a field with high populations of *M. incognita*, and then bean and cabbage (poor-hosts for the nematode) were cultivated prior to tomato (susceptible host). The population densities of *M. incognita* declined considerably during rotation period. But when tomato was again planted in the field, the nematode population density increased only in control treatment and remained low in plots where *P. chlamydosporia* was used several months earlier. This showed that the fungus population maintained at sufficient levels during rotation that could adequately control the nematode on tomato (Atkins et al. 2003). Maize, bean and cabbage are good choice for rotation programme where *M. incognita* is the main pest. These crops are poor hosts for the nematode while *P. chlamydosporia* could grow well in their rhizosphere (Puertas and Hidalgo-Díaz 2007). Contrasting to *P. chlamydosporia*, the efficiency of *Purpureocillium lilacinum* is less affected by the host plant. So, *P. lilacinum* persistence in soil is not related to particular rotation schemes. Among 12 plant species,

the decline of fungus population was seen only when *Phaseolus vulgaris* was planted (Rumbos and Kiewnick 2006). The nematode antagonistic bacteria or fungi with endophytic life style depend on their exclusive hosts on which they can endophytically establish and develop. Therefore, certain crop rotation system could support their survival (Hidalgo-Diaz and Kerry 2008). The host plants can evidently affect the abundance of BCAs through root exudates and other plant characteristics (Timper 2014). Higher populations of BCAs could support host plants against soilborne pathogens (Weller et al. 2012). Therefore, continuous cultivation of a plant species may sometimes resulted in a selective enhancement in population densities of particular BCAs and the formation of suppressive soils (Stirling 1988), but it is not surely evidenced that crop rotation always annihilates suppressiveness in a soil (Timper 2014).

It is too hard to correlate the general suppression of phytonematodes in soil to any specific BCA. However, choosing the appropriate plants for rotation has undeniable effect on preserving nematode suppression by BCAs. Suppressiveness to *Heterodera schachtii* was endangered when wheat was cultivated in a soil but not when an *H. schachtii*-resistant sugar beet was planted. It was assumed that the BCAs could colonise and reproduce in the rhizospheric soil of resistant sugar beet rather than wheat (Westphal and Becker 2001).

The performance of *P. chlamydosporia* in a double-cropping system of lettuce and tomato was examined in soil infested with *M. javanica* for two successive growing seasons. The fungus was detected from *M. javanica* eggs up to 9 months after application to soil and survived at low densities in the rhizospheric soil for the entire growing season (Verdejo-Lucas et al. 2003). The efficacy of *P. chlamydosporia* in reducing *M. javanica* population densities or enhancing yield was different when it was applied in two different cropping systems. Cropping system I included eggplant-okra-tomato-okra-eggplant-tomato-okra while cropping system II composed of eggplant-broad bean-tomato-broad bean-cabbage-tomato-cabbage. Both the nematode population density and yield in cropping system II decreased respectively by 12 and 65% than in cropping system I (Amer-Zareen et al. 2004). The proportion of involvement in nematode decline was different among various cropping systems. During a two-year crop rotation in the absence of potato plants, between 76 and 80% of the *Globodera rostochiensis* decline occurred in relation to spontaneous hatch while only 10% was due to bacterial BCAs (Devine et al. 1999). But when *Purpureocillium* sp. (= *Paecilomyces* sp.) was applied against *G. rostochiensis* in combination with two different leguminous plant, the proportion of *Purpureocillium* involvement in *G. rostochiensis* decline was more than rotation. When the fungus was applied in combination with two different leguminous plants, 89% of nematode population reduced but the decline percent for rotation alone was 31% (López-Lima et al. 2013). There was meaningful difference among various plants (oilseed rape, sugarbeet and wheat in the potato rotation) in supporting the survival or abundance of *P. lilacinum*, *Monographella cucumerina* and *P. chlamydosporia* var. *chlamydosporia* and *P. chlamydosporia* var. *catenulata* (Manzanilla-López et al. 2011).

10.3.2 *Trap Crops*

Usually, sedentary endoparasitic nematodes are the target of trap cropping. The concept of this tactic involves planting a susceptible host with fast and extensive root growth in a nematode-infested soil during a short period of time (Sikora et al. 2005). The motile juveniles of sedentary nematodes invade the roots and soon start their development to sedentary growth stage. Thereafter, the non-motile juveniles are annihilated via destruction of trap crop with herbicide, ploughed in, or physical removal before the juveniles could complete their life cycle and reproduce (Viaene et al. 2013). A crop trap is considered as an idle one if it stimulates the nematode eggs to hatch, be very attractive to juveniles, being heavily infected but not supporting nematode reproduction (Trivedi and Barker 1986). The trap crop should be cultivated quite densely in infested soil so that root system and/or its diffusates can contact as many juveniles as possible. The success of this tactic depends on appropriate cultivation methods, accurate timing and complete destruction of the crop when it is a susceptible one (Viaene et al. 2013). Though proper implementation of trap cropping can be an extremely helpful measure for phytonematode management, it has not been welcomed by the farmers due to the time and cost involved. I found only one literature in which trap cropping was used in combination with BCAs. Dandurand and Knudsen (2016) applied *Solanum sisymbriifolium* as a trap crop against *Globodera pallida* alone or together with *Trichoderma harzianum* or *Plectosphaerella cucumerina*. Soil of three different 'cropping systems' including potato (*Solanum tuberosum*), *S. sisymbriifolium*, or soil only (fallow) was amended with *P. cucumerina*, *T. harzianum* or left unamended. The trap crop *S. sisymbriifolium* significantly decreased nematode reproduction rate by 99% with or without BCAs assistance. Since the outcome of *S. sisymbriifolium* on reproduction rate of the nematode was large, addition of the BCAs made no further reduction.

10.3.3 *Antagonistic Crops*

These plants usually could produce detrimental compounds which have antagonistic effects on phytonematodes. The antagonistic substances may be secreted when the roots are growing or be released after biodegradation in the soil (Hidalgo-Diaz and Kerry 2008). Non-host status of antagonistic crops for some phytonematode species is another mechanism for control (Viaene et al. 2013). Phytonematodes do not usually invade the roots of antagonistic plant, but if penetration occurs, little progress is seen in their life cycle (Trivedi and Barker 1986). The most famous antagonistic plants are marigold, neem, sunn hemp, castorbean, partridge pea, asparagus, rape seed, velvet bean, some grass species (family Poaceae) and sesame (Grubišić et al. 2018). The application of this approach may practically be achieved by pre-plant cover crops, intercropping or green manures (Viaene et al. 2013). The antagonistic crops that could make money have greater potential to be accepted by the growers.

Acceptability and application of *Tagetes* spp. have been greatly increased when food industry began to use them as a food colourant (Hooks et al. 2010). Cultivation of antagonistic plants may offer a substitute for chemical nematicides if integrated with other measures such as BCAs. However, few researches have studied the combined effect of antagonistic plants and biological control on phytonematodes. Forty-nine species of endophytic bacteria were recovered from *Tagetis erecta* and *Tagetis patula*, of those *Microbacterium esteraromaticum* (recovered from *T. patula*) and *Kocuria varians* (recovered from *T. erecta*) significantly reduced the population density of *Pratylenchus penetrans* in the potato rhizosphere without decreasing the tuber fresh weight (Sturz and Kimpinski 2004). There are also reports on the adverse effect of marigolds on useful microorganisms. It was suggested that antifungal molecules were present in fresh marigold tissue (Baker 1981) and Owino (1992) demonstrated that extracts of *T. patula* could prevent *Fusarium solani* and *F. oxysporum* to parasitise *M. javanica* and *M. incognita* eggs on water agar. Therefore, it is feasible to use antagonistic plants in combination with augmented releases of BCAs to enhance phytonematode suppression but this needs more investigation.

10.3.4 Cover Crops

Cover crops refer to plants that are not cultivated for their commercial value but for management of phytonematodes, suppression of weed growth and soil conservation throughout the off season (winter or dry period). Noteworthy, little or no nematode control might be obtained if off season overlaps with nematode low activity or over-seasoning period. The cover crops may finally be incorporated to soil as a green manure or utilised for livestock fodder. Cover crops decrease nematode population densities simply by their non-host status or by their antagonistic, suppressive or damaging properties (Sikora et al. 2005; Viaene et al. 2013). Incorporating the cover crops into the soil usually leads to considerable enhancement in BCAs activity and increase in the host plant growth. Cover crops have the potency to regulate soil microbial structure and ecosystem services (DuPont et al. 2009).

Applying *P. chlamydosporia* simultaneously with planting cover crop had interesting results. The population densities of *P. chlamydosporia* increased in soil where black oat or oil radish was cultivated, but decreased in fallow soil or in soil where tomato was planted. Despite increase in population, the fungus fails to efficiently control *M. javanica* on tomato plant that is being cultivated after either black oats or oil radish. Contradictorily, galling and egg production of the nematode decreased when tomato plants were cultivated after fallow or tomato (Dallemele-Giaretta et al. 2011). In another approach used in warm climate, organic mulch is prepared from intact remainder of the cover plants which provide several advantages than when residues are incorporated into soil. Cover mulch can enhance BCAs activity by supplying a carbon resource, and by preventing excessive changes in soil temperature and moisture. The population densities of nematophagous bacteria were

increased when sunn hemp is used as organic mulch (Wang et al. 2008). Leaving sugarcane residues on soil resulted in greater suppressiveness to *M. javanica* and *Pratylenchus zaei* than adding the residue into soil (Stirling et al. 2011).

10.3.5 Fallow and Flooding

Fallow is a simple tactic in which no crop is planted in a varying period of time, but no measure is employed against weed growth. 'Clean fallow' or 'black fallow' refers to a period of time when no plants (including weeds) are permitted to grow on farm by using herbicide or frequent tillage (Viaene et al. 2013). The phytonematode controlling strategy in fallow is to reduce populations by starvation, while desiccation and exposure to heat emanated from sun may assist (Trivedi and Barker 1986). Fallow has many problems which make it an unpractical method in many countries. The adverse effect on soil conservation via erosion; no contribution to farm income, being less-effective or ineffective in dry weathers, and no or low controlling impact on cyst or some lesion nematodes (like *Pratylenchus brachyurus*) progressively diminish the palatability of this measure. The growth of BCAs may be limited under fallow periods since they need the root diffusates or their phytonematode host to grow. During fallow period, the BCAs usually remain in resting phase without vegetation (Kerry 2000). The abundance of *P. lilacinum*, *Monographella cucumerina* and *P. chlamydosporia* var. *chlamydosporia* (Pc280, potato cyst nematode biotype) and *P. chlamydosporia* var. *catenulata* (Pc392, root-knot nematode biotype) was significantly lower in fallow than their abundance in the presence of different plants (oilseed rape, sugarbeet and wheat) in the potato rotation (Manzanilla-López et al. 2011). The population of *G. rostochiensis* declined by 84% when *Purpureocillium* sp. applied to soil left in fallow while the decline percent in soil left in fallow (without BCA) was as low as 7% (López-Lima et al. 2013). When it is possible, flooding for an extended time may kill phytonematodes because of high moisture level, soil anaerobic conditions and the production of toxic substances (Trivedi and Barker 1986). This measure can be used in non-sloping fields where water is not a limiting factor. In the paddy rice fields where the soil was flooded for 3 months or more, the root-knot nematodes were undetectable on the succeeding tomato crop (Sikora et al. 2005).

When both sterilised and non-sterilised soils were water-saturated, the populations of nematodes significantly reduced in non-sterile soil compared with those reduced in sterile one. This illustrated the potential role of microbial activity in decrease of nematode numbers in flooded soil (Hollis and Rodriguez-Kabana 1966). Though flooding may control phytonematodes, it is not a feasible tactic in many parts of the world due to water deficiency. Another disadvantage is to exclude the inundated farm from cultivation so produce no revenue (Viaene et al. 2013).

10.3.6 Organic Amendments

The growers have been practising this tactic for centuries without noticing its influences on phytonematodes (Renčo 2013). Studying the impact of organic matter amendment on biocontrol and soil microbial populations is a progressively growing research area (Ciancio et al. 2016; Ansari et al. 2019; Ansari and Mahmood 2019a, b). Organic amendments usually cause an enhancement in diversity and populations of soil inhabitant microorganisms and lead to more phytonematode suppression. However, neutral or negative impacts of organic amendment on BCAs have also been reported. It seems that the change in biocontrol activity of antagonists is depended on the kind and amount of organic matter as well as on the types of BCAs (Timper 2014). For example, trapping activity and populations were mutually related for *Dactylellina haptotyla* but not for *Arthrobotrys oligospora* when soil was amended with organic matter (Jaffee et al. 1998; Jaffee 2004). It has been frequently reported that addition of organic matter to soil alone could suppress phytonematode populations (Fatemy and Moosavi 2019) but increase saprophytic ones (Viaene et al. 2013). The added organic matters usually originate from animal dung, chitinous materials, industrial wastes, composts, processing residues and green manure (Sikora et al. 2005; Timper 2014). They may be applied as composted or fresh material or as the exudates from the roots of growing plants (Hildalgo-Diaz and Kerry 2008). Management typically ascribes to any one or more mechanisms as liberation of nematicidal molecules (like glucosinolates) from organic matters; release of allelochemicals (like antibiotics and hydrolytic enzymes) from microorganisms whose populations were enhanced by amendments; augmentation of the BCAs potency; and better plant growth and improved nematode-tolerance (by improving soil structure and water-holding capacity, and by increasing the activity of plant growth-promoting organisms) (Widmer et al. 2002; Thoden et al. 2011). It is rational to expect that organic amendment increases the abundance and performance of facultative parasites of nematode but not of obligate ones. However, the conducted experiments have not supported the hypothesis. Many indirect effects may involve in this rebuttal. For example, incorporations of organic matter into soil may increase the population level of bacteriophagous nematodes which are accessible prey for obligate parasites such as *P. penetrans* (Gomes et al. 2002) or *Drechmeria coniospora* (Van den Boogert et al. 1994). Application of organic matters can enhance the activity of soil resident antagonists. It seems that their application in combination with promising BCAs has potency to manage nematode on a large-field basis. Amending soil with castor oil cakes increased the parasitisation of *Tylenchulus semipenetrans* females by *T. harzianum* (Reddy et al. 1996). The infection rate of *M. javanica* eggs by *Trichoderma longibrachiatum* (Sajadi et al. 2016) and *T. harzianum* (Amir-Ahmadi et al. 2017) was improved by increase in the soil organic matter content. The efficiency of *P. lilacinum* and *Cladosporium oxysporum* increased when applied combinedly with oil cakes. The best eggplant growth and *M. javanica* management was seen in treatments which received *P. lilacinum* and groundnut cake simultaneously (Ashraf and Khan 2010).

Populations of *P. chlamydosporia* and the parasitised percent of *M. incognita* eggs increased when neem (*Azadirachta indica*) leaves were incorporated into soil (Reddy et al. 1999). Similarly, adding dry neem leaves to field soil increased the antagonistic activity of *P. chlamydosporia*, *P. lilacinum* and *T. harzianum* against female and egg masses compared with the antagonistic activity when fungi were applied alone (Khan et al. 2012). The effect of *T. patula* residual on increasing activity of BCAs was reported. However, the enhancement was not adequate to control *Rotylenchulus reniformis* on pineapple (Ko and Schmitt 1996). To examine the rise or fall of biocontrol level of a BCA after specific amendment, we need to design an experiment with a factorial structure. Two winter cover crops (rye and crimson clover) were cultivated for 1 month, then killed and their above ground part was left on soil or removed. Afterward *P. lilacinum* was applied to soil. Suppression of *M. incognita* on cotton in the presence of the fungus and residues was 60% for rye and 49% for crimson clover compared with 35% for soil left in fallow. Greater decrease in the nematode reproduction rate was seen when the above-ground residues were left on the soil surface than when it was eliminated. In the treatments where the above-ground residues were removed, nematode suppression was lower than in the fallow soil (Timper and Parajuli 2012). To separate the effect of nematicidal metabolites from the effect of enhancing BCAs activity, it is better to assess the biocontrol level of phytonematodes several months after adding organic matters into soil. Five months after incorporating sugarcane residue into soil, biological suppression of *P. zaeae* was observed (Stirling et al. 2005). Likewise, after one and 2 years of combined adding of poultry manure and sawdust, biological suppression of *M. javanica* was demonstrated (Stirling et al. 2012).

Amending soil with specific substances such as chitin will enhance the populations of chitinase-producing microorganisms which in turn may increase the degradation of chitinous layer of nematode eggshell, especially those aggregated in gelatinous matrixes or cysts. Amending soil with chitin stimulated the activity of antagonistic fungi in soil and resulted in reduction in population of *M. arenaria* (Godoy et al. 1983). As well, incorporating 1% (w/w) chitin into soil could efficiently suppress *M. incognita* on cotton and enhance the population level of chitinolytic bacteria (Hallmann et al. 1999). The same result was obtained when chitin was applied in *M. arenaria*-infested soil in combination with *P. lilacinum* (Culbreath et al. 1986; Rodriguez-Kabana et al. 1987). Though the abundance of antagonistic BCAs is increased after chitin amendments, the main impact of chitin on nematodes attributed to the liberation of ammonia, at least near to application time (Viaene et al. 2013). As said before, enhancing response may not be always seen by BCAs to organic amendments. The impact of organic amendments on the performance of BCAs may be nematode species-, organic matter type- and organic matter amount-dependent. Compared to bare soil, the vermiform stages of *R. reniformis* were more parasitised by amending soil with sunn hemp (*Crotalaria juncea*) and pineapple (*Ananas comosus*) but not with rapeseed (*Brassica napus*) and marigold (*Tagetes erecta*). More eggs of *R. reniformis* were parasitised only when soil was amended with sunn hemp (Wang et al. 2001). Amending soil with composted leaves of *T. minuta* induced parasitic activity of *P. lilacinum* on

M. javanica eggs but the percent of infected eggs was too low to establish a considerable nematode suppression (Oduor-Owino 2003). Soil amendments may sometimes adversely affect the population densities of feeble saprophytic BCAs which surrender the competition to other strong saprotroph microorganisms whose population is much increased. However, more secreted fungicidal molecules by enhanced populations of soil microbiota should not be neglected (Timper 2014). Controlling ability of *H. rhossiliensis* did not increase subsequent to applying huge amounts of chicken manure, wheat straw or composted cow manure (Jaffee et al. 1994). Organic soil amendments may increase the nutrient level of soil and make the BCAs less aggressive by decreasing their tendency to switch from saprophytic to parasitic phase. In the presence of glucose and quickly absorbable nitrogen sources, the production of serine proteases by *P. chlamydosporia* and *P. lilacinum* was suppressed (Viaene et al. 2013). Supplemented soil with either grape (*Vitis vinifera*) or alfalfa (*Medicago sativa*) leaves resulted in increasing populations of *Arthrobotrys oligospora* and *Dactylellina candidum*, but trap formation was only enhanced with *D. candidum* (Jaffee 2004). It seems that their trophic status involves in this difference. Network-producing nematophagous fungi (such as *A. oligospora*) usually are good saprophytes and by increase in soil nutrient level, their reliance on phytonematodes will decrease. But, reliance of weak saprophytes (such as *D. candidum*) on phytonematodes is more (Moosavi and Zare 2012). Predatory behaviour of nematode-trapper fungi is considered as a tactic of surviving competition when microbial activity increased consequent to organic amendments and is not correlated to nematode population levels (Stirling 1988). Population densities of nematode-trapping fungi were increased 1 month after *T. erecta* residues were incorporated into soil but the effect was not durable and disappeared soon (Wang et al. 2002). Incorporating plant parts which may produce allelopathic molecules into soil can cause adverse effect on BCAs. Amending soil by organic matter with low C/N ratio may also cause negative effect on BCAs due to enhancing ammonia (NH₃) concentrations during decomposition (Rodriguez-Kabana et al. 1987; Oka 2010). Though soil amendment could reduce plant host infection by phytonematode, this task might be achieved only by incorporating a huge quantity of amending matters into soil. The impact of soil amendment on BCAs populations is complicated and cannot be interpreted easily. Critical investigations are needed to reveal the suppression mechanisms of organic amendments; to determine the amounts of organic matter which can practically and efficiently be applied to soil; and to better comprehend the interaction of organic matter with soil biota, host plant and phytonematodes.

10.3.7 Tillage Effect

Routine tillage practice may adversely affect the soil community by mechanical damage (ripping and inverting the soil), being buried deep or by brining to soil surface. Few studies have been found to investigate the effect of combined

application of tillage and BCAs. But investigating the effect of tillage on BCAs has been resulted in inconsistent results. The parasitism of *H. glycines* eggs was more in the soil that was disc ploughed compared with those that were moldboard ploughed or no-tilled (Bernard et al. 1996). No significant differences were detected in parasitism of *H. glycines* juveniles by *H. rhossiliensis* and *H. minnesotensis* in soybean fields with conventional tillage and no-tillage (Chen and Liu 2007), but the parasitised percent of *H. glycines* juveniles by *H. rhossiliensis* was lower in simulated tillage (sieving the soil) than in minimal tillage (Bao et al. 2011). Rotary tilling soil caused 28% decrease in percentage of *P. penetrans*-infected juveniles of *M. incognita* than in no-tilled (Talavera et al. 2002b). However, no significant differences were observed in parasitising *H. glycines* on soybean by *Pasteuria nishizawae* when the plots were subjected to conventional and no tillage (Noel et al. 2010). When conservation tillage was adopted in wheat fields of Australia, the cyst populations of *Heterodera avenae* on roots and its damage to yield were decreased (Roget and Rovira 1987). The population densities of nematodes were a little more in no-tilled regime than in conservation tillage (Fortnum and Karlen 1985). More study is required to understand the effect of tillage on BCAs efficacy.

10.4 Decreasing Phytonematode Populations

Any measure which involves in reducing phytonematode populations may help BCAs to complete their task better. Some of these tactics may be used in combination with BCAs and some may be employed prior to applying BCAs. Soil disinfections by steaming, soil solarisation, biofumigation or broad-spectrum biocides may reduce the populations and activity of soil microbial competitors and applying BCAs after these treatments resulted in easier establishment and survival of the introduced BCAs. On the other hand, biocontrol of lesser populations of nematode is too easier (Viaene et al. 2013). No BCA can suppress phytonematode populations as rapidly as nematicides (Cumagun and Moosavi 2015), so several post-planting nematicides can be used in combination with BCAs where the chemical nematicide impedes initial nematode damage and the BCAs provide long-term protection (Moosavi and Zare 2012; Sokhandani et al. 2016).

10.4.1 Soil Solarisation

Soil solarisation can successfully disinfest soil of weeds, soilborne pests and pathogens where the climate is hot, water is available and the soil depth is shallow. Exposing moistened soil below plastic mulches to solar radiation for at least 4–6 weeks will kill phytonematodes (Hidalgo-Diaz and Kerry 2008); however, the cost of polyethylene sheeting and the needed length of time may be deterrent. The greenhouse effect under polyethylene sheeting causes an increase in soil

temperature up to 35–50 °C in 30 cm upper depth. The efficacy of this tactic to disinfect soil of nematodes depends on soil type, solar intensity, soil moisture content and preceding tillage (Viaene et al. 2013). Successive cultivation of susceptible plants (tomato-melon) to root-knot nematodes became possible by solarising soil for 30 days in summer (Sano 2002). Biological control may integratedly be implemented with soil solarisation if the BCAs possess heat resistance propagules. Spores of *Pasteuria* are moderately resistant to heat and drought (Sikora 1992) so would survive solarisation. The use of soil solarisation and *P. penetrans* had synergistic effect on controlling *M. javanica* on grapevine (Walker and Wachtel 1988) and cucumber (Tzortzakakis and Goewn 1994). However, application of *P. lilacinum* after a 15-day soil solarisation could not adequately reduce root-knot nematode populations (Anastasiadis et al. 2008).

10.4.2 Biofumigation

Producing volatile molecules during hydrolysing of glucosinolate-containing plant residues or organic matters by soil microbiota is called biofumigation. The majority of glucosinolate-containing plants are clustered within the Brassicaceae, Capparaceae and Caricaceae families. These biocidal/nematicidal molecules have high toxicity against soilborne pests and pathogens (Kruger et al. 2013). However, biofumigation usage is now restricted mainly because of the bulky amount of organic materials to be incorporated to soil (Hidalgo-Diaz and Kerry 2008). For better control of *M. incognita*, it has been recommended to replace cover crop (such as small grains) by crops with biofumigation potential (Westphal 2011).

Despite appearing as a fair promising tactic for the control of soilborne diseases, it is improbable that biofumigation could sufficiently suppress the phytonematode by itself. But its application in combination with soil solarisation or resistant hosts could improve its efficacy (Ploeg 2008). The activity of nematode antagonist may increase after biofumigation (Sikora et al. 2005), but little literature has been found to study the combined effect of biofumigation and BCAs.

10.4.3 Chemical Nematicides

The main method to reduce the damage of phytonematodes is now based on chemical nematicides. These compounds could reduce the numbers of nematodes, stop or decrease nematode reproduction, or paralyse them (nematostatic) for a while (Haydock et al. 2013). Present chemical nematicides in the market can be divided to fumigants and non-fumigants and their classification usually is based on their mode of action (Ebone et al. 2019). Chemical nematicides severely endanger human health and environment (Moosavi and Zare 2016). It has been reported that phytonematode populations at the end of the season in the nematicide-treated plots are usually more

than in the untreated plots (Sipes and Schmitt 1998) due to more spread root system which could support more nematode when the effect of nematicide diminishes. However, growth in phytonematode populations may be for lower activity of BCAs in nematicide treated soil (Timper 2014). Notwithstanding these disadvantages, nematicides cannot be eliminated, at least for now, from nematode management programmes. However, it seems that the best approach is to integrate the nematicides with other management methods instead of applying the nematicides as the only control measure (Hillocks 2012). The integrated application of synthetic chemicals and BCAs has drawn much interest for its probable additive or synergistic effects (Spadaro and Gullino 2005). Theoretically, non-fumigant nematicides could increase BCAs' potency if they are applied combinedly. It is highly recommended that nematicides should be applied when more than one phytonematode species exist in soil. The nematicide will suppress the species that might not be susceptible to applied BCA or even the populations that do not encounter with applied BCA. A few investigations have tested the effect of combined application of nematicides and BCAs on phytonematode management, but it has been reported that fungal BCAs from different groups (trapping fungi, *P. lilacinum* and *P. chlamydosporia*) were little affected when they were exposed to standard doses of several different pesticides applied to soil (Kerry 1987). Thus, it is feasible to apply these BCAs with nematicides to extend and enhance nematode management (Sokhandani et al. 2016). The biological suppression of nematodes decreased immediately after nematicide application, but in the next spring biological suppression increased wherever nematicide applied (Timper et al. 2012). Applying *P. lilacinum* and *Trichoderma viride* in combination with mustard cake and furadan (nematicide) resulted in least *M. incognita* reproduction rate as compared to untreated treatments (Goswami et al. 2006). Applying granule formulations containing fosthiazate and *Monacrosporium elliposporum* resulted in better *M. incognita* control and increased the establishment of fungus BCA in soil (Taba et al. 2006). Contradictorily, the populations of nematode-trapping fungi in the fields were greatly enhanced subsequent to sunn hemp incorporation wherever no fumigant nematicide (1, 3-D) had been applied (Wang et al. 2003). This may be due to broader spectrum of organisms (including BCAs) that can be affected by fumigant nematicides. The growth and activity of *P. penetrans* are not affected by many chemical pesticides, except for chloropicrin that is directly toxic to this bacterium (Chen and Dickson 1998). Gall formation was reduced by 50 and 63% when *P. penetrans* was applied in combination with carbofuran on tomato to control *M. javanica* (Brown and Nordmeyer 1985) and *M. incognita* (Somasekhar and Gill 1991), respectively. As well, integrated application of carbofuran and *P. penetrans* reduced J2 penetration of *Heterodera cajani* into pigeonpea roots. A total number of females, eggs per cysts and final population were reduced compared with control treatment (Gogoi and Gill 2001). Aldicarb and ethoprop could not change the percentage of infected *M. arenaria* juveniles by *P. penetrans* (Timper 1999; Timper et al. 2001), but the controlling effect of *P. penetrans* against *M. javanica* on tomato and cucumber crops was additively increased when it was applied in combination with oxamyl (Tzortzakakis and Goewn 1994). *Meloidogyne graminicola* population was decreased by 79% on

rice when *Pseudomonas fluorescens* was combinedly used with carbofuran. The decreased amount of *M. graminicola* population on rice was 69% in simultaneous use of *T. viridae* and carbofuran (Narasimhamurthy et al. 2017). The in vitro response of three different fungal BCAs was examined to frequently used pesticides in potato fields. No prevention was seen in *P. lilacinum* and *Plectosphaerella cucumerina* growth in response to pencycuron or oxamyl, but their growth was slowed down in response to fenpiclonil and tolclofos-methyl. All mentioned chemicals partially inhibited *P. chlamydosporia* growth (Jacobs et al. 2003). Combined application of *T. harzianum* and carbofuran resulted in more prominent suppression of *M. incognita* on french bean (Gogoi and Mahanta 2013), brinjal (Devi et al. 2016), *Mentha arvensis* (Haseeb et al. 2007) and pea (Brahma and Borah 2016).

Integrated application of *P. chlamydosporia* with carbofuran (Gopinatha et al. 2002), with neem cake and carbofuran (Dhawan and Singh 2009) and with dazomat (Nagesh and Jankiram 2004) increased suppression of *M. incognita*. But its integration with fosthiazate did not provide any additional decrease in potato cyst nematodes reproduction rate (Tobin et al. 2008). Optimum levels of *Trichoderma longibrachiatum* concentration and cadusafos dose were determined in their combined application for the control of *M. javania* on zucchini plants. The data were analysed using a custom response surface regression model and the optimum levels of the cadusafos and *Trichoderma* concentration that caused the best plant growth and lowest nematode reproduction were determined as 1.7 mg a.i./kg soil and 10^8 conidia/ml suspension, respectively (Sokhandani et al. 2016).

10.5 Application of Multiple BCA

Little studies directly investigate or compare the effect of combined application of several BCAs against phytonematodes in contrast with application one BCA. It is globally accepted that inconsistency in performance of BCAs is a main barrier to the broad usage of BCAs (Moosavi and Zare 2015); however, integration of two or more robust BCAs may help in overcoming this disadvantage. Arguably, integrated use of BCAs may increase the achieved control especially if the combined BCAs are compatible or have different mode of actions (Moosavi and Zare 2016). Fluctuation in populations of BCAs is hardly happened when several BCAs exist in or introduce into soil. Combined application of BCAs provides several benefits such as more and better colonisation of the rhizosphere; parasitising more than one stage of the life cycle of a nematode as well as parasitising more than one target species; being active in more extensive time span during growing season; possessing various mode of action; and performing more consistent under more broaden range of environmental and soil condition (Crump 1998; Siddiqui and Mahmood 1996; Meyer and Roberts 2002; Ansari and Mahmood 2017b; Ansari et al. 2017a, b). Applying BCAs with diverse mode of action such as *Fusarium oxysporum* (endophyte), *P. lilacinum* (egg parasite) and *Bacillus firmus* (antagonistic bacteria) increased biomanagement of

R. similis on banana (Mendoza and Sikora 2009). The population density of added BCAs is a matter of importance. For example in the conducted experiments, the combined effect of two BCAs with a specific application rate (x) has been usually compared with the effect of each BCA used at the same rate alone (x) and not with one BCA used at twice the rate ($2x$). On the other hand, analysing the data which have presented in conducted investigations usually demonstrated additive effect more than synergistic one (Hidalgo-Diaz and Kerry 2008). Further experiments are required to evidently elucidate the phenomena after combined application of two or more BCAs especially on the ecological basis. BCAs have to survive and act in biologically complex environments where they are subjected to numerous inter- and intera-specific interactions (Knudsen and Dandurand 2014). Consequent to those interactions, the combined application of BCAs may result in competence, independence, additive or synergistic effect. Though analysing the published paper on combined application of BCAs indicated that antagonistic interactions are more probable (Xu et al. 2011), it has been suggested that introducing BCAs to soil as consortium might imitate natural soil condition and could stimulate host plant defence responses and enhance its growth (Sarma et al. 2015). More understanding on host plants' responses to phytonematodes in the presence of several BCAs and the probable interactions is required for sound judgement.

The suppression effect of *A. oligospora* in combination with each of 11 different strains of bacteria on J2 populations of *Meloidogyne mayaguensis* was assessed in tomato rhizosphere. Greater control achieved when *A. oligospora* was integrately applied with three different unidentified bacteria (Duponnois et al. 1998). When *Embellisia chlamydospora*, *P. chlamydosporia* and a sterile fungus were applied alone and in different binary combinations, the lowest number of females and cysts of *H. schachtii* was observed when either *Embellisia* or *Pochonia* was applied in combination with the sterile fungus. No nematode suppression was observed by individual application of the mentioned fungi or by the *Embellisia*–*Pochonia* combination (Hojat Jalali et al. 1998). Applying *T. harzianum* simultaneously with *Monacrosporium lysipagum* (nematode trapper fungus) resulted in better control of *M. javanica* and *H. avenae* (Khan et al. 2006). Together application of *Acremonium strictum* and *T. harzianum* enhanced biocontrol activity against *M. incognita* on tomato significantly (Goswami et al. 2008). When 90 combinations of different *Trichoderma* (18 strains from five species) and nematode-trapping fungi (six strains from four species) were examined against *Caenorhabditis elegans*, integration of *T. harzianum* and *Monacrosporium cionopagum* had the best compatibility (Szabó et al. 2012). Five different fungi (*Pochonia bulbillosa* (Pb), *Pochonia chlamydosporia* var. *catenulata* (Pccat), *Pochonia chlamydosporia* var. *chlamydosporia* (Pcc), *Lecanicillium aphanocladii* (La) and *T. harzianum* (Th)) whose in vitro pathogenicity on the *M. javanica* eggs was similar used alone and in binary or trinary combination for the control of *M. javanica* on eggplant. Combined application of these BCAs had no significant increasing effect on plant growth compared with growth in the pots treated by one BCA. But integrated application of BCAs increased the egg infection rate significantly. None of the treatment could manage *M. javanica* as the same level as cadusafos nematicide (96%); however, the

integrated application of Pccat, La with Pcc (85%) or Th (83%) controlled *M. javanica* acceptably (Moosavi et al. 2015). The bacterium *P. penetrans* was compatibly combined with *P. chlamydosporia* (de Leij et al. 1992), *P. lilacinum* (Gautam et al. 1995) and *Glomus* sp. (Talavera et al. 2002a), and their integrated usage could control *M. incognita* on tomato plants better. Sometimes BCAs may be assisted by soil microbiota to fulfil their tasks. The endospores adherence of *P. penetrans* to *M. graminicola* increased with the help of rhizospheral resident bacteria (Duponnois et al. 1997). The population density of *M. javanica* on a cropping system consisted of eggplant–okra–tomato–okra–eggplant–tomato–okra was further reduced by 24% when *P. chlamydosporia* was applied in combination with *P. penetrans* rather than their solo application (Amer-Zareen et al. 2004). There are several reports that combination usage of BCAs makes no advantages over their individual application. Combined application of *H. rhossiliensis* and *P. chlamydosporia* against *Meloidogyne hapla* on lettuce did not enhance controlling activity compared with their individual usage (Viaene and Abawi 2000). Combined application of *P. penetrans*, *P. lilacinum*, *B. subtilis* and *Talaromyces flavus* caused the same control level of root-knot nematode as their individual application did (Zaki and Maqbool 1991). Mixed usage of *M. lysipagum* with *T. harzianum* made no significant additive control of *R. similis* on banana compared with applying *M. lysipagum* alone (Khan et al. 2006). Combining BCAs sometimes results in lower management potential. The combination of *Bacillus thuringiensis*, *Paecilomyces marquandii* and *Streptomyces costaricanus* was not as effective as individual treatments for decreasing *R. similis* and *Helicotylenchus multicinctus* populations on banana (Esnard et al. 1998). Similarly, integration of *S. costaricanus* and *B. thuringiensis* resulted in lower biocontrol level of *M. hapla* on lettuce compared with biocontrol level achieved with their individual usage (Chen et al. 2000). While solitary application of *Trichoderma virens* and *Burkholderia cepacia* could successfully control *M. incognita* on bell pepper, their combined application was not as successful (Meyer et al. 2001). Integrated application of *Calothrix parietina* with either *P. lilacinum* or *Pichia guilliermondii* reduced their potency against *M. incognita* maybe due to antagonistic activity of *C. parietina* (Hashem and Abo-Elyousr 2011).

10.6 Conclusions and Future Prospects

Though phytonematode control is now based on chemical nematicides, it seems that in the near future it should inevitably be changed to an integrated multi-based management system. It must be also taken into consideration that inundative release of BCAs could not manage the phytonematodes consistently and must be applied in combination with other approaches. But careful consideration is required in choosing the effective measures that should be integrated. The selected ones must have several characteristics such as being compatible, provide synergistic effect, being

economically affordable and impose the least environmental hazard. Maybe multidisciplinary studies could be of help to develop effective combinable measures.

From growers' viewpoint, chemical nematicides have several priorities to biocontrol in characteristics such as cost, transportation, delivery technology, performance and simplicity of storage and application. Therefore, consolidated use of BCAs with other tactics that provide synergistic or additive effect could be of help in accepting biocontrol as a potent substitute. If biological control wants to become an important part of phytonematode management, more improvement is also needed in their producing procedures, formulation, efficacy, consistency and application methods. The improvement must primarily occur in reducing production cost and enhancing potency. Moreover, production of BCA derivatives such as bionematicides is another measure of choice which has both advantages of effectiveness and being eco-friendly. The preparation of natural nematicides whose bioactive ingredients derive from BCAs should be oriented to products with low amount but strongly effective natural molecules which could effectively control the phytonematodes. Another probable approach is host plants transformation with effective genes against phytonematodes supplied by different sources include BCAs. As many people prefer not to consume genetically modified crops, the exploitation of this approach is hesitated. However, transforming BCAs to enhance their detrimental effect against phytonematodes is another option. The efficiency, consistency, virulence, ecological adaptability and easier mass production and formulation of BCAs can be improved by genetic engineering. In fact, numerous nematode-antagonists exist in arable lands and their persistence or activity mainly depends on our chosen cultural practices. However, the possible lack of suitable native BCAs can be compensated by introducing potent antagonists. Integration of biocontrol with compatible measures surely increases nematode suppression to an acceptable level. The farmers should be informed that the increase in populations of beneficial BCAs and adequate nematode suppression may need more than one growing season. It seems that the proper combination of plant-BCA (indigenous or introduced) provides a liable foundation that other locally available measures can be constructed upon it.

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